CHAPTER 7

NEST MICROCLIMATE

INTRODUCTION

Innate selection of beneficial nest-site microclimate by birds can moderate extreme environmental conditions and has the potential to improve reproductive success and increase fitness (Webb and King 1983, Walsberg 1985). Although nest microclimate may influence avian reproductive success, other factors such as habitat and food availability also are important (Cody 1985, Gloutney and Clark 1997). Potential covariance with other evolutionary forces such as predation further complicates any investigation of microclimatic nest-site selection (Martin 1995).

Most studies of microclimatic nest-site selection have concentrated on non-passerines. Waterfowl (Gloutney and Clark 1997), hummingbirds (Calder 1973), and woodpeckers (Connor 1975, Inouye 1976, Inouye et al. 1981) in particular have been evaluated with respect to various aspects of microclimatic regulation. Selected species from each of these groups have demonstrated a preference for specific physical attributes within their nesting habitat as strategies to maximize heat gain, minimize heat loss, or manipulate wind exposure depending on the situation. Several species of woodpeckers excavate cavities whose entrance holes are oriented toward or away from the sun, again depending on the situation and the need to regulate nest microclimate.

Microclimatic selection by passerines has received less attention than that of non-passerines, with most investigations of passerines directed at either ground-nesters or those building covered nests. Horned Lark (*Eremophila alpestris*) is probably the most thoroughly studied ground-nesting passerine, and numerous studies indicate that it selects nest locations based on compass orientation as a way to manipulate wind exposure, solar insolation, and resulting nest microclimate (Cannings and Threlfall 1981, With and Webb 1993, Hartman and Oring 2003). Cactus Wren (*Campylorhynchus brunneicapillus*) and Verdin (*Auriparus flaviceps*) orient the entrances to their covered nests either away from or toward prevailing winds in different parts of the nesting season to moderate nest microclimate (Austin 1974, 1976).

Microclimatic nest-site selection has been investigated in only a few open-cup, shrub- or tree-nesting passerines. The Warbling Vireo (*Vireo gilvus*) is very sensitive to fluctuations in nest microclimate (Walsberg 1981), and the San Miguel Island Song Sparrow (*Melospiza melodia micronyx*) may benefit from microhabitats that maintain higher nest relative humidity (Kern et al. 1990).

Gloutney and Clark (1997) pointed out that nonrandom distribution of nests strongly supports the microhabitat (i.e., microclimate) selection hypothesis. For example, nest-site selection for thermal advantages has been offered as an explanation as to why nonrandom nest-site placement occurs in many species (Kern and van Riper 1984, Bekoff et al. 1987, van Riper et al. 1993).

Nests placed in dense vegetation have been suggested to be less susceptible to predation (Cody 1985), and may also benefit from protection from wind, nocturnal heat loss, and diurnal heat gain (Walsberg 1981, 1985). Because the microhabitat of an individual can influence energy expenditure (Warkentin and West 1990), calories conserved through beneficial nest-site selection can aid reproductive efforts and improve fitness (Gloutney and Clark 1997).

Air temperature alone cannot portray the microclimate of an incubating bird (Gloutney and Clark 1997). Solar insolation, vapor pressure (i.e., relative humidity), and wind speed interact in a complex manner with temperature to define microclimate (McArthur 1990), so that many physiological investigators instead calculate 'operative temperature,' the complex formula that integrates all of the above factors (Gloutney and Clark 1997).

The purpose of this microclimate investigation was to document temperature, relative humidity, and soil moisture at nests of Southwestern Willow Flycatchers, an open-cup nesting passerine. We tested the null hypothesis that no difference existed between (1) a flycatcher nest site, (2) a randomly located adjacent site within that flycatcher territory, and (3) unoccupied riparian habitat outside of that territory. Air temperature, relative humidity, and soil moisture were used as indices to microclimate, although it was recognized that substantial interaction likely occurred between those three variables.

METHODS

OVERVIEW

We located active flycatcher nests at four life history study areas (Pahranagat, Mesquite, Mormon Mesa, and Topock) between May and July 2003. Temperature, relative humidity, and soil moisture were measured at three locations relative to each nest for the purpose of examining microclimate at three levels of potentially increasing differences in flycatcher nesting habitat use, as follows:

1. Within 1 m of a nest (i.e., the nest site).
2. Within the territory associated with that nest (but 5–10 m from the nest; i.e., within-territory site).
3. Within unoccupied riparian habitat 50–200 m from the nearest known nest or territory (i.e., non-use site).

We began collecting microclimate data simultaneously at nest, within-territory, and non-use sites within 48–72 hours of the time an active nest was vacated. A nest was defined as vacated if it met one of the following criteria: (1) it had been abandoned for any reason (including brood parasitism) at any stage of the nesting cycle after the first flycatcher egg was laid, (2) it had fledged young and was no longer active, or (3) it had been depredated after the first egg was laid. This technique minimized disturbance due to equipment placement or increased human activity near the nest as recommended by Hartman and Oring (2003), while still allowing for quantitative post-use comparisons of microclimate.

Temperature, relative humidity, and soil moisture data were collected over a period of at least 14 full days (midnight to midnight), after which time we transferred the equipment and effort used to collect microclimate data to the nest, within-territory, and non-use sites for another recently-vacated nest (i.e., including a second brood or second nesting attempt). The 14-day study period for each nest became the focus of all final analyses. Renests, or second nests of a known pair, were treated as independent data points because nests were the unit of analysis of this study and not individuals or pairs. All equipment used to collect microclimate data was removed after 14 full days from the time the last active nest had been vacated.

TEMPERATURE AND RELATIVE HUMIDITY (T/RH) MEASUREMENTS

Measurements of T/RH were recorded automatically every 15 minutes using a HOBO H8 Pro (Onset Computer Corporation, Pocasset, MA) that combines a thermometer (degrees Celsius), relative humidity monitor, and digital data logger (hereafter referred to as a sensor array). We camouflaged all HOBO sensor arrays by placing them in an inverted small, plastic bowl coated with spray adhesive and local vegetation. The opening at the bottom was covered with shadecloth, allowing free air circulation around the sensor array. The HOBO sensor arrays were placed in four different location types in a manner consistent with an overall randomization design, as follows:

(1) Seasonal-variation (SV) sensor arrays: When field personnel arrived at the four life history study areas in early May, they placed SV sensor arrays at representative locations within the riparian and adjacent desertscrub habitat. The riparian SV sensor arrays were designed to monitor T/RH fluctuations throughout the nesting season within the riparian zone to document ambient environmental conditions throughout the study period. Riparian SV sensor arrays were placed in the nearest tree or woody shrub at their representative sites using a prearranged random number selection sequence (see 3C–3E below). The desertscrub SV sensor arrays at each study area were placed in desert habitat outside of the riparian zone to document local extremes in T/RH.

(2) Nest-site (NS) sensor arrays: Once a known nest was vacated, an NS sensor array was placed less than 1 meter from the nest, preferably hanging directly below it. Sensor arrays were camouflaged so as not to disturb birds that may have returned to the nest to recycle nesting material. Canopy closure was visually estimated as < 25%, 25–75%, or >75% at all nest, within-territory, and non-use sites, and habitat type was identified as native (cottonwood/willow), exotic (tamarisk), or mixed native and exotic (see data forms in Appendix A).

(3) Within-territory (WT) sensor arrays: A WT sensor array was placed at a location within the territory of the pair that attended the corresponding nest. The WT sensor array sites were determined by means of the following instructions and the use of random number sequences:

A. The compass direction to walk from the nest, given in degrees from North, was determined from a random number sequence.
B. The distance (between 5 and 10 m) to walk in the designated direction was determined from a random number sequence. Once that distance was traveled, the closest woody tree or shrub was selected for sensor array placement. If several trees were tied for closest,

one of the field crew tossed a rock over his or her shoulder and the woody tree or shrub closest to its resting place was the one in which the sensor array was placed.

C. The sensor array was placed within the documented range of flycatcher nest heights (Sogge et al. 1997), and maximum height depended upon local tree or shrub maximum height at each of the four life history study areas. Sensor arrays were placed at a height between 1.5 and 5.0 m, as determined from a random number sequence, at Mesquite, Mormon Mesa, and Topock, and between 1.5 and 10.0 m (or as high as reasonably possible) at Pahranagat. If the random number at Pahranagat was greater than approximately 7 m, the sensor array was placed as close to the random height as reasonably possible. If the tree or shrub chosen for a sensor array location was of insufficient height to accept the height from the random number sequence, then field personnel placed the sensor array at the first height in the sequence that was less than the height of the tree or shrub.
D. The distance (0–3 m) at which the sensor array was placed from the bole of the tree or center of the shrub was determined from a random number sequence. If the tree or shrub was of insufficient radius to accept the distance from the random number sequence, then field personnel placed the sensor array at the first number in the sequence that was less than the radius of the tree or shrub.
E. The compass direction, given in degrees from north, at which the sensor array was placed from the bole of the tree or center of the shrub was determined from a random number sequence. If there was no branch in this compass direction that would support the sensor array at the height and distance specified in (C) and (D), field personnel proceeded clockwise around the tree or shrub until a suitable branch was located.

If, as presented in C and D, a number from a subsequent random number sequence (sequence meaning a row in the random number table) was used because the number in the initial sequence was too high, then both sequences were considered used and no longer available for future use. If these directions took field personnel outside of the riparian zone or to a site without trees or shrubs, they returned to the nest site and used the next sequence of random numbers.

(4) Non-use habitat (NU) sensor arrays: At all life history study areas, we identified NU habitat after the first territories and nests were located. Two computer-generated circles were centered on each nest site or territory center, one 50 m in radius and one 200 m in radius. The area between the two circles that was within the study area boundaries and was at least 50 m from all other nests or territory centers was classified as NU and divided into equal numbered grids on digitized, geo-referenced, and numbered aerial photographs. The grids to be used for NU purposes were selected using computer-generated random numbers, and the centroid of each selected grid became the random point near which the sensor arrays were placed. The NU site was located in the field using the UTM coordinates and a Rino 110 GPS unit. The exact location of the sensor array was determined by selecting the closest woody tree or shrub and using the procedures in 3C–3E above. If the NU site was inaccessible (e.g., impenetrable vegetation or deep water) or was in clearly unsuitable habitat (e.g., open marsh), the next UTM coordinate for a random NU site was used.

Soil Moisture (SM) Measurements

We took SM measurements using two methods: (1) SV SM sensor arrays were placed at representative locations throughout the four study areas at the same sites as the SV T/RH arrays in riparian habitat to document daily range and rate of change, and (2) hand-held probes were used to document SM at NS, WT, and NU sites during the 14-day period after nests were vacated. No SV SM sensor arrays were placed in desertscrub habitat.

(1) In mid-May, field personnel placed SV sensor arrays at representative sites within the riparian zone at each of the four life history study areas. If the locations for any of the SV SM sensor arrays were inundated or exhibited 100% saturated soils, field personnel placed the sensor array 5 m beyond the edge of the inundated or saturated area in a compass direction determined by a random number sequence. The decision rule for 100% saturated soil was as follows: a 1-cm-deep trench created with a stick filled with water or unstable mud in less than one minute.

SM data was collected at 1-hour intervals using a Smart Soil Moisture Sensor SM monitor connected to a 4-channel HOBO Micro Station data logger (both by Onset Computer Corp., Pocasset, MA). All SM sensor arrays were buried horizontally with the flat side perpendicular to the ground surface and the top edge of the sensor 1 cm beneath the soil surface.

(2) We used hand-held probes (20-cm Ech2o probes connected to Ech2o check readouts, by Decagon Devices Inc., Pullman, WA) to gather SM data during the 14-day period after nests were vacated at NS, WT, and NU sites. SM data were collected directly underneath the T/RH sensor arrays on 3–7 days during the 14-day sample period. Measurements were taken between 0700 and 1000 hours to eliminate the potential bias of time-of-day changes in the soil capillary fringe. A trench slightly narrower than the probe was excavated with a putty knife to ensure good soil-to-probe contact. Probes were inserted horizontally into the trench with the top of the sensor 1 cm beneath the soil surface. SM was assumed to be 100% at sites that were flooded, inundated, or met the 100% saturated decision rule, and no SM measurements were collected at these sites.

If a willow flycatcher pair initiated a second nest within 10 m of its initial nest at which T/RH and SM were being documented, field personnel used hand-held probes to gather SM data at the same time that the second nest was being checked for contents/status (approximately every three days) to minimize disturbance. Therefore, it was likely that the number of SM measurements would be seven at vacated nests where no second nest was located nearby, while the number of SM measurements was likely to be closer to three at vacated nests where a second nest was located nearby. Although a minimum of three to seven SM measurements were essential for statistical purposes, SM measurements were taken on as many days as possible during the 14-day sample period.

Soil samples were collected at each SM site (SV, NS, WT, NU) when sensor arrays were initially set up. Samples were approximately the size of a medium apple, collected from the surface down to and including a depth of 5 cm, and placed in a heavy zip-lock plastic bag labeled with the site designation. Because soil texture strongly influences capillary action and therefore overall SM (Sumner 2000), analysis of soil composition may be conducted in future years as time and funding allow.

STATISTICAL ANALYSES

We downloaded data from the T/RH and SM sensor arrays at SV, NS, WT, and NU sites into databases at the end of the field season. We merged all data to create one dataset for further analysis, with the exception of the SV dataset, which was summarized separately for descriptive purposes and was not included in any of the analyses. Data from SM sensor arrays occasionally exhibited negative values, an anomaly that may have been the result of poor calibration with saline and/or sandy soil. All negative SM data were omitted from all summaries and analyses. We calculated the following variables for each sensor array, by day and by overall study period:

- Mean soil moisture
- Mean diurnal temperature
- Mean maximum diurnal temperature
- Mean diurnal relative humidity
- Mean nocturnal temperature
- Mean minimum nocturnal temperature
- Mean nocturnal relative humidity
- Mean daily temperature range (mean diurnal maximum minus nocturnal minimum)

The overall study period constituted the entire season for SV sensor arrays and the 14 days of monitoring for sites associated with nests (NS, WT, and NU). We determined diurnal and nocturnal periods by using the actual daily sunrise and sunset times reported for the region by the National Weather Service (2003).

We used Tukey's multiple comparison test with a one-way Analysis-of-Variance (ANOVA) to determine whether placing the sensor arrays *after* the nest had been vacated was appropriate, by testing the mean weekly diurnal temperatures of the SV sensor arrays at each study area. Any consecutive weeks at a study area that were significantly different would be an indication that placing the sensor arrays after nests had been vacated was inappropriate.

We used probability plots and other distribution tests to test the response variables for normality. Chi-square (X^2) and one-way ANOVA tests were used to test the single effects of the three location types (NS, WT, NU) and other predictor variables for all response variables. If significant differences were found ($P<0.05$), we used Tukey's multiple comparison test to determine pairwise differences.

We used multiple factor ANOVA (multiple ANOVA) analyses with and without interaction terms to determine significant differences in means between location types for all temperature, humidity, and soil moisture variables. Multiple ANOVA tests for a difference in means, while controlling for the variance by study area, habitat, and canopy closure. The full initial analysis was:

Response variable = Location Type + Study Area + Habitat + Canopy + (Location Type * Study Area) + (Location Type * Habitat) + (Location Type * Canopy) + (Study Area * Habitat) + (Study Area * Canopy) + (Habitat * Canopy) + (Location Type * Study Area * Habitat) + (Location Type * Study Area * Canopy) + (Location Type * Habitat *

Canopy) + (Study Area * Habitat * Canopy) + (Location Type * Study Area * Habitat * Canopy).

The R^2 value for the multiple ANOVA analyses identified the extent of the variation in the response variable that was explained by the predictor variables in each analysis. Tukey's multiple comparison test was used to determine pairwise differences for significant variables. The *P* values presented in the multiple ANOVA analyses were for type III sum of squares. All analyses were conducted using SAS® Version 8 (SAS Institute 1999).

RESULTS

SEASONAL VARIATION

Twenty SV T/RH sensor arrays and 16 SV SM sensor arrays were placed at the four life history study areas from 14 to 22 May and remained in place until late August. Because of mechanical malfunction, some SV sensor arrays did not initiate data collection or stopped collecting data during mid-season. This was true of all five SV T/RH sensor arrays at Topock. All but one of the SV SM sensor arrays functioned throughout the season. The results from all SV sensor arrays indicated desertscrub sites were substantially hotter and drier than riparian sites (Tables 7.1 and 7.2).

Table 7.1. Seasonal variation in riparian habitat by study area for Southwestern Willow Flycatcher microclimate data from along the Virgin and lower Colorado Rivers, May–August 2003. All values are ± 1 standard deviation (in parenthesis); N/A=data not available.

Descriptive statistics	Pahranagat	Mesquite	Mormon Mesa	Topock
N (Temp./Humidity)	1	3	3	0
N (Soil Moisture)	3	4	4	4
Mean soil moisture (%)	24.9 (±13.0)	20.6 (±14.2)	25.1 (±9.8)	25.3 (±6.5)
Mean diurnal temperature (°C)	26.4 (±2.3)	30.7 (±2.5)	32.3 (±4.1)	N/A
Mean maximum diurnal temperature (°C)	35.4 (±3.8)	39.7 (±4.2)	43.3 (±5.2)	N/A
Mean diurnal relative humidity (%)	39.0 (±15.6)	42.4 (±12.1)	39.3 (±13.3)	N/A
Mean nocturnal temperature (°C)	21.9 (±2.6)	24.2 (±3.0)	21.5 (±4.2)	N/A
Mean minimum nocturnal temperature (°C)	17.0 (±3.3)	19.0 (±3.6)	16.6 (±4.6)	N/A
Mean nocturnal relative humidity (%)	40.3 (±15.9)	52.8 (±14.9)	58.5 (±14.3)	N/A
Mean daily temperature range (°C)	18.4 (±5.1)	20.7 (±5.7)	26.7 (±5.1)	N/A

Table 7.2. Seasonal variation in desertscrub habitat by study area for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, May–August 2003. All values are ± 1 standard deviation (in parenthesis); N/A=data not available.

Descriptive statistics	Pahranagat	Mesquite	Mormon Mesa	Topock
N (Temp./Humidity)	2	2	1	0
Mean diurnal temperature (°C)	32.5 (±3.7)	37.1 (±3.1)	36.7 (±3.4)	N/A
Mean maximum diurnal temperature (°C)	41.0 (±4.6)	45.1 (±4.4)	45.0 (±4.6)	N/A
Mean diurnal relative humidity (%)	20.4 (±12.2)	17.3 (±9.9)	18.0 (±9.4)	N/A
Mean nocturnal temperature (°C)	25.0 (±3.2)	30.1 (±2.5)	29.8 (±3.1)	N/A
Mean minimum nocturnal temperature (°C)	19.0 (±3.6)	23.9 (±3.1)	24.3 (±3.5)	N/A
Mean nocturnal relative humidity (%)	26.7 (±16.3)	22.1 (±12.9)	23.2 (±11.1)	N/A
Mean daily temperature range (°C)	21.9 (±4.4)	21.2 (±4.9)	20.8 (±4.8)	N/A

DATA COLLECTION AFTER NESTS WERE VACATED

Only two sets of consecutive weeks were found to be significantly different in mean diurnal temperature: the first and second week in August at Mormon Mesa ($P<0.05$) and the third and fourth week in May at Mesquite ($P<0.05$). These two anomalous sets of weeks were not during the peak of the nesting season (June-July), which exhibited fairly consistent mean diurnal temperatures from week to week.

LOCATION TYPES: DESCRIPTIVE STATISTICS AND SINGLE EFFECTS ANALYSIS

We placed sensor arrays at all nests within each of the four life history study areas. Data on T/RH were successfully collected for 48 NS, 46 WT, and 38 NU sites (Tables 7.3 through 7.6). The location type data were normally distributed for all response variables, so that no transformations or elimination of outliers were needed.

All study areas except Pahranagat showed a significant difference in percent canopy closure between pairwise location types (NS, WT, NU; Tables 7.3 through 7.6). The NU sites were primarily responsible for this difference, since they had a significantly greater proportion of sites with less than 25% canopy as compared to NS sites at Mesquite or WT sites at Mesquite, Mormon Mesa, and Topock.

Single effects analyses (Tables 7.3 through 7.6) indicate that during daytime, NS sites were cooler and more humid than NU sites at Mesquite and Pahranagat, although they were similar at Mormon Mesa and Topock (Figures 7.1 and 7.2). The NU sites were hotter and drier than either NS or WT sites at Mesquite and Pahranagat, but were similar to NS and WT sites at Mormon Mesa and Topock.

Mean nocturnal temperatures and humidity were generally similar between location types, although the average minimum nocturnal temperatures were lower for NU sites. In general, NU sites had the greatest mean daily temperature range, and NS sites had the lowest mean daily temperature range.

SM was similar among location types; however, the descriptive statistics (Tables 7.3 through 7.6) showed wide variance in percent SM readings. Despite the SM difference among location types at Pahranagat (*P* = 0.048), we decided to exclude SM from all subsequent analyses.

Table 7.3. Descriptive statistics (Chi-square) and single effects (ANOVA) for Southwestern Willow Flycatcher microclimate data by location type at Pahranagat, June–August 2003. Values for soil moisture and subsequently listed response variables are ± 1 standard deviation (in parenthesis); N/A=data not available.

Response variables	**Nest Site**	**Within Territory**	**Non-use**	**X^2 or F-value**	***P***	**Significant pairwise differences**
N (Temp./Humidity Sensor Arrays)	11	9	8	--	--	--
N (Soil Moisture Probes)	11	10	9	--	--	--
Habitat						
Native (cottonwood or willow)	11 (100.0)*	9 (100.0)	8 (100.0)	N/A	N/A	N/A
Exotic (tamarisk)	0 (0.0)	0 (0.0)	0 (0.0)			
Mixed (native and exotic)	0 (0.0)	0 (0.0)	0 (0.0)			
Canopy closure						
Less than 25%	0 (0.0)	1 (11.1)	0 (0.0)	4.5	0.345	--
25%-75%	1 (9.1)	2 (22.2)	3 (37.5)			
More than 75%	10 (90.9)	6 (66.7)	5 (62.5)			
Mean soil moisture (%)	24.9 (±8.5)	25.3 (±9.8)	15.4 (±9.9)	3.4	0.048	--
Mean diurnal temperature (°C)	27.7 (±1.5)	28.8 (±1.5)	30.6 (±2.4)	6.0	0.007	NU>NS
Mean maximum diurnal temperature (°C)	38.6 (±3.3)	40.9 (±3.6)	42.4 (±5.8)	2.0	0.163	--
Mean diurnal relative humidity (%)	43.4 (±7.6)	41.0 (±7.7)	31.1 (±7.5)	6.4	0.006	NS>WT>NU
Mean nocturnal temperature (°C)	24.3 (±1.2)	24.6 (±1.2)	25.7 (±2.5)	1.7	0.210	--
Mean minimum nocturnal temperature (°C)	15.0 (±2.3)	14.4 (±2.2)	16.2 (±3.3)	1.1	0.361	--
Mean nocturnal relative humidity (%)	43.8 (±7.8)	42.9 (±8.7)	37.2 (±9.7)	1.5	0.249	--
Mean daily temperature range (°C)	16.1 (±3.0)	18.8 (±4.2)	18.3 (±3.4)	1.7	0.206	--

*N followed by % of column totals

Table 7.4. Descriptive statistics (Chi-square) and single effects (ANOVA) for Southwestern Willow Flycatcher microclimate data by location type at Mesquite, June–August 2003. Values for soil moisture and subsequently listed response variables are ± 1 standard deviation (in parenthesis).

Response variables	Nest Site	Within Territory	Non-use	X^2 or F-value	*P*	Significant pairwise differences
N (Temp./Humidity Sensor Arrays)	18	17	17	--	--	--
N (Soil Moisture Probes)	14	13	17	--	--	--
Habitat						
Native (cottonwood or willow)	9 (50.0)*	11 (64.7)	8 (47.1)			
Exotic (tamarisk)	2 (11.1)	0 (0.0)	2 (11.8)	X^2=2.6	0.628	--
Mixed (native and exotic)	7 (38.9)	6 (35.3)	7 (41.2)			
Canopy closure						
Less than 25%	0 (0.0)	1 (5.9)	9 (52.9)			
25%-75%	13 (72.2)	13 (76.5)	7 (41.2)	X^2=19.5	<0.001	NS>NU, WT>NU
More than 75%	5 (27.8)	3 (17.7)	1 (5.9)			
Mean soil moisture (%)	16.8 (±10.4)	18.5 (±9.7)	11.1 (±12.3)	F=2.0	0.155	--
Mean diurnal temperature (°C)	30.8 (±2.3)	32.2 (±2.7)	36.1 (±3.8)	F=15.1	<0.001	NU>NS, NU>WT
Mean maximum diurnal temperature (°C)	41.8 (±4.3)	45.8 (±5.7)	51.9 (±6.9)	F=13.9	<0.001	NU>NS, NU>WT
Mean diurnal relative humidity (%)	51.2 (±12.6)	46.3 (±10.2)	35.6 (±7.1)	F=10.4	<0.001	NS>NU, WT>NU
Mean nocturnal temperature (°C)	24.2 (±1.9)	24.1 (±2.0)	24.0 (±2.3)	F=0.0	0.957	--
Mean minimum nocturnal temperature (°C)	16.6 (±2.3)	15.9 (±2.4)	14.7 (±2.5)	F=2.6	0.081	--
Mean nocturnal relative humidity (%)	62.8 (±10.4)	61.0 (±9.4)	59.0 (±8.5)	F=0.7	0.484	--
Mean daily temperature range (°C)	19.3 (±4.6)	22.4 (±5.2)	29.0 (±5.6)	F=16.3	<0.001	NU>NS, NU>WT

*N followed by % of column totals

Table 7.5. Descriptive statistics (Chi-square) and single effects (ANOVA) for Southwestern Willow Flycatcher microclimate data by location type at Mormon Mesa, June–August 2003. Values for soil moisture and subsequently listed response variables are ± 1 standard deviation (in parenthesis).

Response variables	**Nest Site**	**Within Territory**	**Non-use**	**X^2 or F-value**	***P***	**Significant pairwise differences**
N (Temp./Humidity Sensor Arrays)	12	11	6	--	--	--
N (Soil Moisture Probes)	6	7	8	--	--	--
Habitat						
Native (cottonwood or willow)	4 (33.3)*	4 (36.4)	0 (0.0)			
Exotic (tamarisk)	1 (8.3)	1 (9.0)	3 (50.0)	6.9	0.143	--
Mixed (native and exotic)	7 (58.3)	6 (54.5)	3 (50.0)			
Canopy closure						
Less than 25%	0 (0.0)	0 (0.0)	1 (16.7)			
25%-75%	10 (83.3)	11 (100.0)	3 (50.0)	8.3	0.083	WT>NU
More than 75%	2 (16.7)	0 (0.0)	2 (33.3)			
Mean soil moisture (%)	5.4 (±6.2)	9.2 (±7.7)	7.0 (±10.4)	0.3	0.715	--
Mean diurnal temperature (°C)	33.1 (±3.4)	33.6 (±3.0)	33.4 (±3.1)	0.1	0.933	--
Mean maximum diurnal temperature (°C)	46.6 (±4.7)	47.7 (±5.3)	47.8 (±4.3)	0.2	0.8261	--
Mean diurnal relative humidity (%)	39.1 (±9.6)	37.4 (±7.6)	37.7 (±8.7)	0.1	0.8878	--
Mean nocturnal temperature (°C)	23.9 (±3.2)	23.5 (±3.2)	21.2 (±3.2)	1.5	0.251	--
Mean minimum nocturnal temperature (°C)	16.6 (±2.6)	15.9 (±2.6)	13.5 (±2.2)	3.0	0.070	--
Mean nocturnal relative humidity (%)	56.5 (±6.0)	56.8 (±7.3)	62.5 (±10.1)	1.5	0.245	--
Mean daily temperature range (°C)	23.7 (±5.1)	24.7 (±3.8)	27.4 (±2.9)	1.5	0.241	--

*N followed by % of column totals

Table 7.6. Descriptive statistics (Chi-square) and single effects (ANOVA) for Southwestern Willow Flycatcher microclimate data by location type at Topock, June–August 2003. Values for soil moisture and subsequently listed response variables are ± 1 standard deviation (in parenthesis); N/A=data not available.

Response variables	Nest Site	Within Territory	Non-use	X^2 or F-value	*P*	Significant pairwise differences
N (Temp./Humidity Sensor Arrays)	7	9	7	--	--	--
N (Soil Moisture Probes)	8	8	8	--	--	--
Habitat						
Native (cottonwood or willow)	0 (0.0)*	0 (0.0)	0 (0.0)			
Exotic (tamarisk)	7 (100.0)	9 (100.0)	7 (100.0)	N/A	N/A	N/A
Mixed (native and exotic)	0 (0.0)	0 (0.0)	0 (0.0)			
Canopy closure						
Less than 25%	0 (0.0)	0 (0.0)	2 (28.6)			
25%-75%	5 (71.4)	4 (44.4)	5 (71.4)	9.2	0.056	WT>NU
More than 75%	2 (28.6)	5 (55.6)	0 (0.0)			
Mean soil moisture (%)	28.7 (±4.7)	21.4 (±8.9)	27.1 (±5.8)	2.6	0.098	--
Mean diurnal temperature (°C)	33.0 (±2.1)	32.2 (±2.5)	34.2 (±4.6)	0.8	0.476	--
Mean maximum diurnal temperature (°C)	43.9 (±4.8)	42.6 (±4.8)	48.0 (±9.8)	1.4	0.283	--
Mean diurnal relative humidity (%)	53.2 (±5.7)	56.5 (±9.1)	55.7 (±12.5)	0.3	0.783	--
Mean nocturnal temperature (°C)	27.0 (±1.2)	26.7 (±1.4)	25.7 (±1.4)	2.0	0.161	--
Mean minimum nocturnal temperature (°C)	19.3 (±1.3)	19.2 (±1.2)	17.9 (±2.0)	1.9	0.171	--
Mean nocturnal relative humidity (%)	65.1 (±3.4)	66.5 (±4.7)	68.7 (±5.2)	1.2	0.325	--
Mean daily temperature range (°C)	17.4 (±3.9)	16.3 (±4.5)	21.7 (±8.3)	1.9	0.182	--

*N followed by % of column totals

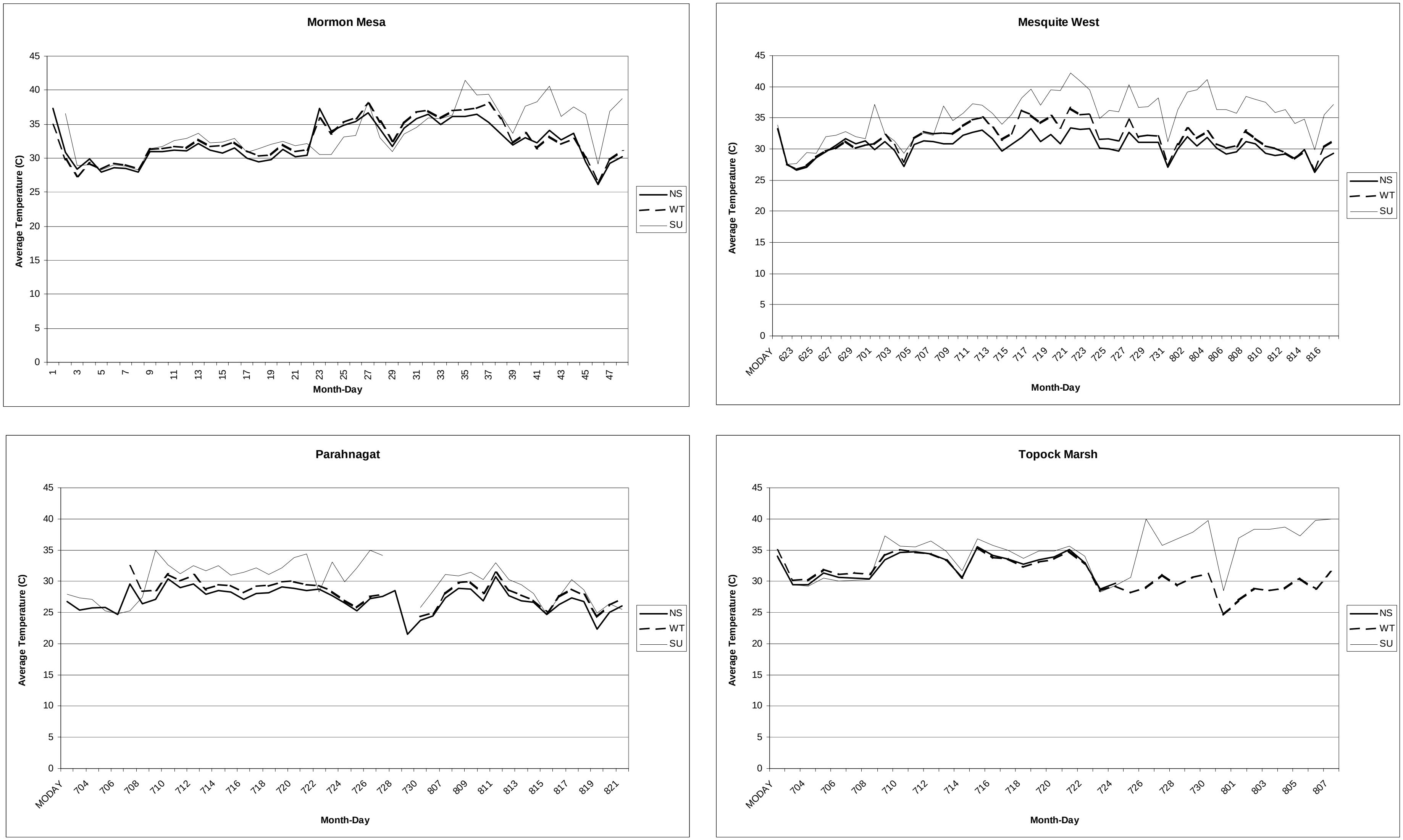

Figure 7.1. Mean diurnal temperature by study area and location type for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, June–August 2003.

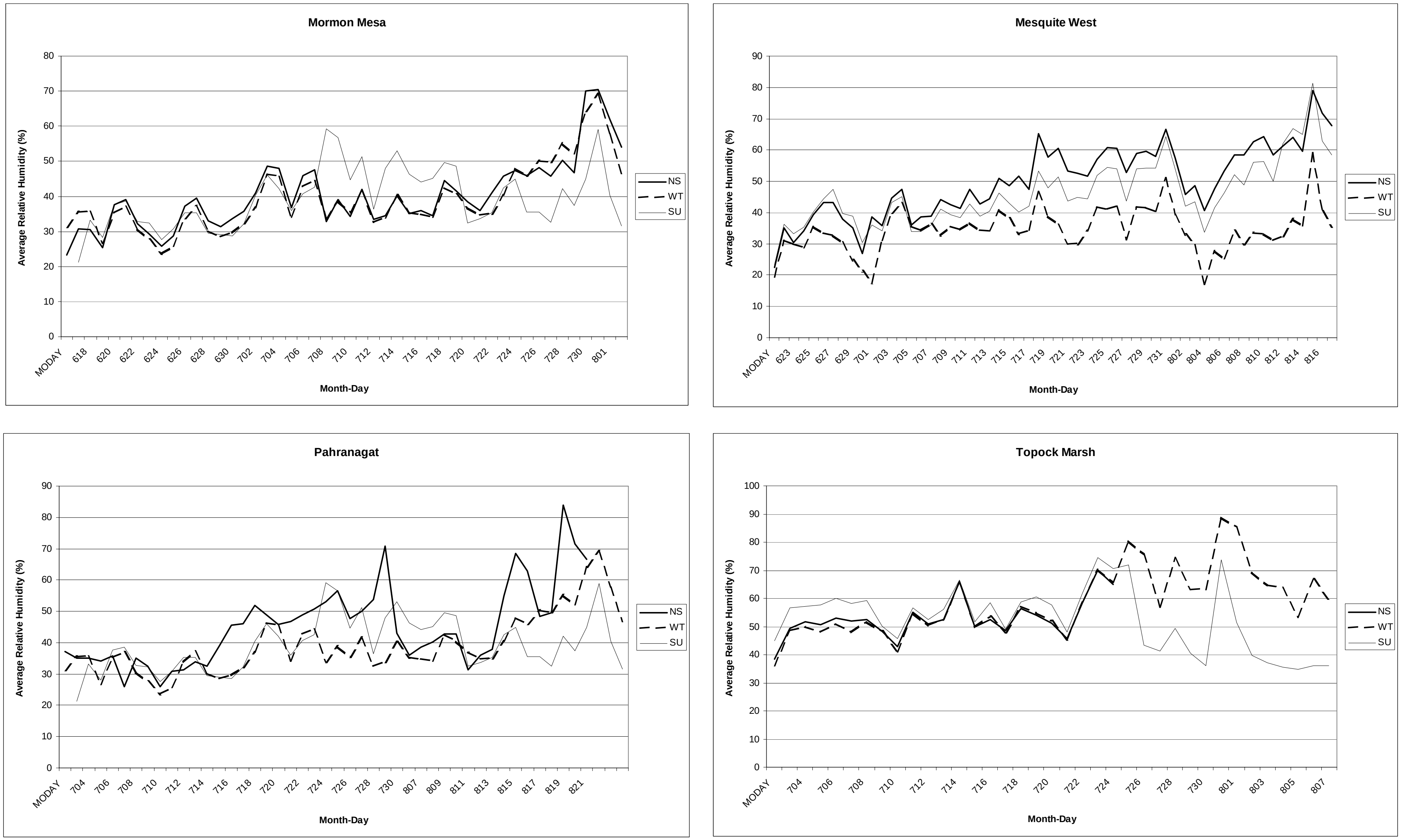

Figure 7.2. Mean diurnal relative humidity by study area and location type for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, June–August 2003.

INDIVIDUAL EFFECT OF PREDICTOR VALUES

Single effects analyses (Tables 7.7 through 7.10) illustrate the individual effect that each predictor had on response variables. Location type (Table 7.7) was significantly related to mean diurnal temperature, mean maximum diurnal temperature, mean diurnal relative humidity, and mean daily temperature range.

Study areas differed significantly for all response variables (Table 7.8). Topock exhibited the highest overall (i.e., diurnal and nocturnal) humidity and highest nocturnal temperatures of all study areas. Diurnal temperatures at Topock were statistically similar to the two other hottest study areas (Mormon Mesa and Mesquite). However, Topock was similar to Pahranagat in that those two study areas exhibited the lowest mean daily temperature range. Pahranagat exhibited the lowest nocturnal humidity, lowest diurnal temperature, and lowest mean minimum nocturnal temperature. Pahranagat and Mormon Mesa exhibited the lowest diurnal humidity.

Habitat types were also significantly different for all response variables (Table 7.9). Native habitats, which were almost synonymous with Pahranagat, exhibited the lowest diurnal and nocturnal temperatures and the lowest mean daily temperature range as compared to exotic or mixed habitats. Exotic habitat, typified by the tamarisk monoculture at Topock, had the highest overall humidity, the highest nocturnal temperatures, and was tied with mixed habitat for the highest diurnal temperatures. Mixed habitats had the highest mean daily temperature range.

Categories of canopy closure differed significantly for mean diurnal temperature, mean maximum diurnal temperature, mean nocturnal relative humidity, and mean daily temperature range (Table 7.10).

Table 7.7. Single effects ANOVA testing location type by response variable for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, June–August 2003. Location type values are ± 1 standard deviation (in parenthesis).

Response variables	Location type			F-value	*P*	Significant pairwise differences
	Nest Site	Within Territory	Non-use			
Mean diurnal temperature (°C)	31.0 (±3.4)	31.9 (±2.9)	34.2 (±4.1)	9.8	<0.001	NU>WT>NS
Mean maximum diurnal temperature (°C)	42.6 (±5.0)	44.7 (±5.5)	48.6 (±7.6)	10.4	<0.001	NU>WT>NS
Mean diurnal relative humidity (%)	46.7 (±11.3)	45.1 (±10.9)	38.7 (±11.8)	5.8	0.004	NS>WT>NU
Mean nocturnal temperature (°C)	24.6 (±2.3)	24.6 (±2.3)	24.2 (±2.8)	0.3	0.768	--
Mean minimum nocturnal temperature (°C)	16.6 (±2.6)	16.2 (±2.7)	15.4 (±2.9)	2.1	0.130	--
Mean nocturnal relative humidity (%)	57.2 (±11.2)	57.5 (±11.1)	56.8 (±13.6)	0.1	0.956	--
Mean daily temperature range (°C)	19.4 (±5.0)	21.0 (±5.4)	25.2 (±6.9)	11.1	<0.001	NU>WT>NS

Table 7.8. Single effects ANOVA testing study area by response variable for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, June–August 2003. Study area values are ± 1 standard deviation (in parenthesis).

Response variables	Study area				F-value	*P*	Significant pairwise differences
	Pahranagat (PA)	Mesquite (MW)	Mormon Mesa (MM)	Topock (TM)			
Mean diurnal temperature (°C)	28.9 (±2.1)	33.0 (±3.7)	33.3 (±3.1)	33.1 (±3.2)	13.0	<0.001	MM>PA, MW>PA, TM>PA
Mean maximum diurnal temperature (°C)	40.4 (±4.4)	46.4 (±7.0)	47.3 (±4.7)	44.6 (±6.8)	7.7	<0.001	MM>PA, MW>PA
Mean diurnal relative humidity (%)	39.1 (±9.0)	44.5 (±12.0)	38.2 (±8.4)	55.3 (±9.1)	14.6	<0.001	TM>MW, TM>PA, TM>MM, MW>MM
Mean nocturnal temperature (°C)	24.8 (±1.7)	24.1 (±2.0)	23.2 (±3.3)	26.5 (±1.4)	10.2	<0.001	TM>MW, TM>PA, TM>MM, PA>MM
Mean minimum noc-turnal temperature (°C)	15.2 (±2.6)	15.7 (±2.5)	15.7 (±2.7)	18.8 (±1.6)	11.8	<0.001	TM>MW, TM>PA, TM>MM
Mean nocturnal relative humidity (%)	41.6 (±8.8)	61.0 (±9.5)	57.9 (±7.6)	66.7 (±4.5)	47.2	<0.001	TM>MW, TM>PA, TM>MM, MW>PA, MM>PA
Mean daily tempera-ture range (°C)	17.6 (±3.6)	23.5 (±6.5)	24.8 (±4.4)	18.3 (±6.0)	13.3	<0.001	MM>TM, MM>PA, MW>PA, MW>TM

Table 7.9. Single effects ANOVA testing habitat type by response variable for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, June-August 2003. Habitat type values are ± 1 standard deviation (in parenthesis).

Response variables	Habitat type			F-value	*P*	Significant pairwise differences
	Native (cottonwood or willow)	Exotic (tamarisk)	Mixed (native and exotic)			
Mean diurnal temperature (°C)	30.6 (±3.1)	33.5 (±3.3)	34.0 (±3.3)	16.1	<0.001	Mix>Nat, Tam>Nat
Mean maximum diurnal temperature (°C)	42.9 (±5.8)	45.9 (±6.7)	48.1 (±6.2)	8.8	<0.001	Mix>Nat
Mean diurnal relative humidity (%)	43.3 (±11.3)	51.9 (±11.1)	37.8 (±8.9)	15.0	<0.001	Tam>Nat> Mix
Mean nocturnal temperature (°C)	24.0 (±2.4)	25.7 (±2.0)	24.2 (±2.6)	6.3	0.002	Tam>Mix, Tam>Nat
Mean minimum nocturnal temperature (°C)	15.5 (±2.7)	17.8 (±2.6)	15.9 (±2.3)	8.9	<0.001	Tam>Mix, Tam>Nat
Mean nocturnal relative humidity (%)	53.1 (±13.4)	66.1 (±6.5)	56.6 (±7.7)	15.8	<0.001	Tam>Mix, Tam>Nat
Mean daily temperature range (°C)	20.3 (±5.7)	20.7 (±7.0)	24.8 (±5.2)	7.2	0.001	Mix>Tam, Mix>Nat

Table 7.10. Single effects ANOVA testing canopy closure by response variable for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, June–August 2003. Canopy closure values are ± 1 standard deviation (in parenthesis).

Response variables	Canopy closure categories			F-value	*P*	Significant pairwise differences
	< 25%	25-75%	> 75%			
Mean diurnal temperature (°C)	36.5 (±4.4)	32.7 (±3.1)	29.8 (±2.4)	27.7	<0.001	(<25)>(25–75)>(>75)
Mean maximum diurnal temperature (°C)	52.8 (±7.6)	45.8 (±5.9)	41.0 (±3.8)	24.9	<0.001	(<25)>(25–75)>(>75)
Mean diurnal relative humidity (%)	37.9 (±8.4)	44.1 (±12.0)	45.4 (±11.8)	2.3	0.109	--
Mean nocturnal temperature (°C)	24.6 (±2.0)	24.3 (±2.6)	24.7 (±2.2)	0.5	0.638	--
Mean minimum nocturnal temperature (°C)	15.1 (±2.7)	16.3 (±2.7)	16.2 (±2.8)	1.2	0.293	--
Mean nocturnal relative humidity (%)	61.1 (±7.1)	59.2 (±10.3)	52.2 (±14.2)	6.0	0.003	(<25)>(>75), (25–75)>(>75)
Mean daily temperature range (°C)	28.5 (±5.9)	22.5 (±5.6)	17.6 (±4.4)	24.5	<0.001	(<25)>(25–75)>(>75)

MULTIPLE ANOVA MODEL

Location type remained a significant predictor for mean diurnal temperature, mean maximum diurnal temperature, mean diurnal relative humidity, and mean daily temperature range even after adjusting for study area, habitat, and canopy closure (Table 7.11). When significant interaction terms were added to the analysis, location type remained significant for mean diurnal temperature and mean maximum diurnal temperature, but not for mean diurnal relative humidity or mean daily temperature range (Table 7.12).

Because location type as a significant predictor of the above response variables was most likely due to the disproportionately large sample size from Mesquite, the multiple ANOVA analysis was rerun without including any data from that study area. The new analysis remained significant for all response variables, but location type was not a significant predictor (Table 7.13).

The next analysis removed NU sites to make a discrete comparison between only NS and WT sites at all study areas because all the significant differences for the single effects of location type came from NU sites. This multiple ANOVA showed that NS sites remained significant predictors of mean maximum diurnal temperature and mean daily temperature range. However, only mean maximum diurnal temperature remained significant (Table 7.14) when significant interaction terms were added. Across all study areas, mean maximum diurnal temperature at NS sites was 4.0^{o}C cooler than at NU sites and 2.1^{o}C cooler than at WT sites (Table 7.7), although temperature differences by location type differed by study area (Tables 7.3 through 7.6).

Table 7.11. Single effects (without interaction terms) multiple ANOVA for location type testing of predictor variables by response variable for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, June–August 2003. Canopy closure categories=percentages.

Response variables	F-value for overall model	*P* for overall model	R^2 (%)	F-value for location type	*P* for location type (Type III SS)	Other significant predictors	Significant pairwise differences
Mean diurnal temperature (°C)	12.2	<0.001	47.3	5.1	0.008	Habitat, Canopy closure	NU>NS, Mix>Nat, (<25)>(25–75)>(>75)
Mean maximum diurnal temperature (°C)	9.0	<0.001	40.0	5.1	0.008	Canopy closure	NU>NS, (<25)>(25–75)>(>75)
Mean diurnal relative humidity (%)	10.2	<0.001	43.0	6.7	0.002	Study area, Habitat	NS>NU, WT>NU, MW>MM, TM>MM, MW>PA, TM>PA, Nat>Mix
Mean nocturnal temperature (°C)	4.1	<0.001	23.3	1.1	0.354	Study area	PA>MM, TM>MM
Mean minimum nocturnal temperature (°C)	4.9	<0.001	26.3	1.7	0.188	Study area	TM>MM, TM>MW, TM>PA
Mean nocturnal relative humidity (%)	17.9	<0.001	57.0	0.7	0.484	Study area, Habitat	MM>PA, MW>PA, TM>PA, Mix>Nat, Tam>Mix
Mean daily temperature range (°C)	12.2	<0.001	47.4	7.5	<0.001	Study area, Canopy closure	NU>NS, NU>WT, MM>PA, MM>TM, MW>TM, (<25)>(25–75), (<25)>(>75)

Table 7.12. Single effects (with significant interaction terms) multiple ANOVA for location type testing of predictor variables by response variable for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, June–August 2003. Canopy closure categories=percentages.

Response variables	F-value for overall model	*P* for overall model	R^2 (%)	F-value for location type	*P* for location type (Type III SS)	Other significant predictors in reduced model	Significant pairwise differences
Mean diurnal temperature (°C)	10.6	<0.001	51.6	3.7	0.028	Study area, Canopy closure, Habitat * Study area	MM>PA, MW>PA
Mean maximum diurnal temperature (°C)	9.0	<0.001	40.0	5.1	0.008	Canopy closure	NU>NS, (<25)>(25–75), (<25)>(>75)
Mean diurnal relative humidity (%)	8.9	<0.001	47.2	2.7	0.070	Study area, Habitat, Habitat * Canopy closure	MW>MM, TM>MM, MW>PA, TM>PA, Nat>Mix, Tam>Mix
Mean nocturnal temperature (°C)	4.1	<0.001	23.3	1.1	0.354	Study area	TM>MM, PA>MM
Mean minimum nocturnal temperature (°C)	4.9	<0.001	26.3	1.7	0.188	Study area	TM>MM, TM>MW, TM>PA
Mean nocturnal relative humidity (%)	8.0	<0.001	71.1	1.6	0.210	Study area, Habitat, Type * Study area * Canopy closure	--
Mean daily temperature range (°C)	5.9	<0.001	59.2	0.0	0.972	Canopy closure, Study area * Canopy closure	--

Table 7.13. Single effects (with significant interaction terms) multiple ANOVA for location type testing of predictor variables by response variable for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, June–August 2003. Canopy closure categories=percentages. The Mesquite study area was not included in this analysis.

Response variables	F-value for overall model	*P* for overall model	R^2 (%)	F-value for location type	*P* for location type (Type III SS)	Other significant predictors in reduced model	Significant pairwise differences
Mean diurnal temperature (°C)	10.7	<0.001	60.8	0.5	0.624	Habitat, Canopy closure, Habitat * Study area	MM>PA
Mean maximum diurnal temperature (°C)	7.9	<0.001	47.1	0.2	0.847	Study area, Canopy closure	MM>TM, (<25)>(25–75),(>25)>(>75)
Mean diurnal relative humidity (%)	12.1	<0.001	66.3	0.9	0.408	Study area, Habitat, Canopy closure, Habitat * Canopy closure	TM>MW>PA>MM, Nat>Mix, Tam>Mix, (>75)>(25–75)
Mean nocturnal temperature (°C)	4.1	<0.001	23.3	1.1	0.354	Study area	TM>MM, PA>MM
Mean minimum nocturnal temperature (°C)	4.9	<0.001	35.6	0.4	0.689	Study area	TM>MM, TM>PA
Mean nocturnal relative humidity (%)	12.9	<0.001	83.3	2.7	0.078	Study area, Habitat, Habitat * Canopy closure	--
Mean daily temperature range (°C)	6.5	<0.001	68.8	1.0	0.391	Habitat, Canopy closure, Study area * Canopy closure	--

Table 7.14. Single effects (with significant interaction terms) multiple ANOVA for location type testing of predictor variables by response variable for Southwestern Willow Flycatcher microclimate data along the Virgin and lower Colorado Rivers, June–August 2003. Canopy closure categories=percentages. This analysis did not include NU location type, but did include all study areas.

Response variables	F-value for overall model	*P* for overall model	R^2 (%)	F-value for location type	*P* for location type (Type III SS)	Other significant predictors in full analysis	Significant predictors in reduced analysis
Mean diurnal temperature (°C)	11.5	<0.001	57.3	3.7	0.060	Habitat, Study area * Habitat	--
Mean maximum diurnal temperature (°C)	6.8	<0.001	39.1	5.9	0.017	Study area, Habitat	MM>TM, Mix>Nat, Tam>Nat
Mean diurnal relative humidity (%)	7.3	<0.001	46.7	2.4	0.127	Study area, Habitat, Habitat * Canopy closure	MW>MM, TM>MM, MW>PA, TM>PA, Nat>Mix
Mean nocturnal temperature (°C)	3.6	0.001	25.1	0.0	0.951	--	--
Mean minimum nocturnal temperature (°C)	5.5	<0.001	34.1	0.9	0.335	Study area	TM>MM, TM>MW, TM>PA
Mean nocturnal relative humidity (%)	8.0	<0.001	68.8	1.4	0.236	Study area, Habitat, Habitat * Canopy closure	--
Mean daily temperature range (°C)	4.7	<0.001	52.9	0.1	0.771	Habitat, Canopy closure	--

DISCUSSION

SEASONAL VARIATION

The finding that desertscrub habitat was substantially hotter and drier than riparian habitat was consistent with what would be expected, although it was useful to document the difference for comparative purposes.

DATA COLLECTION AFTER NESTS WERE VACATED

Results from the SV sensor arrays validated our method of initiating data collection immediately after nests were vacated to minimize human disturbance. Only two sets of consecutive weeks outside of the peak of flycatcher nesting season were found to be significantly different in mean diurnal temperature. However, future studies should revisit this approach to data collection for additional validation.

LOCATION TYPES: DESCRIPTIVE STATISTICS AND SINGLE EFFECTS ANALYSIS

Three of the four study areas showed a significant difference in percent canopy closure between location types, with the NU sites primarily responsible for the difference. This was because NU sites had a significantly greater proportion of sites with less than 25% canopy closure as compared to NS sites. This suggests habitat with greater canopy closure was much less available in the 50–200 m ring (potential NU sites) around nests. This finding is consistent with the vegetation analyses presented in the previous chapter and concurs with results reported by other investigators (Sogge and Marshall 2000, Allison et al. 2003) showing that flycatchers may prefer habitat with dense vegetation that provides a more favorable microclimate.

Diurnal conditions at NS sites were generally cooler and more humid than NU sites, while NU sites tended to be hotter and drier and exhibited lower minimum nocturnal temperatures than NS and WT sites. This difference between NU sites versus NS and WT sites was because many NU sites had canopy closure <25% but no NS or WT sites did. Greater canopy closure tends to moderate microclimate by shading the habitat from short-wave solar radiation during midday, conserving long-wave radiation that would otherwise dissipate into the atmosphere at night, and helping to conserve humidity.

Consultation with the engineers at Onset Computers indicated that incomplete contact between the SM probe and the dense, riparian clay soils may have caused the wide variance in mean SM values, which caused us to drop SM from the multiple ANOVA analyses. In subsequent years other methods will be evaluated to better quantify percent SM in order to include SM as a variable in the final microclimate analyses.

INDIVIDUAL EFFECT OF PREDICTOR VALUES

The four life history study areas differed significantly for all response variables. The differences between Topock (hotter and most humid) and Pahranagat (coolest and least humid) were likely due to their contrasting geographic settings. The Topock study area lies farthest south, is lowest in elevation, and is surrounded by an extensive complex of inundated wetlands. Pahranagat is located farthest north, is highest in elevation, and is surrounded by comparatively small wetlands and a relatively deep lake. Extreme differences in habitat type between the two areas may also affect local microclimate. Topock comprises of very dense, monotypic tamarisk of relatively low stature, while Pahranagat consists of native riparian forest exhibiting the highest mean canopy height of all the study areas (see previous chapter).

Percent canopy closure differed significantly for mean diurnal temperature, maximum diurnal temperature, nocturnal relative humidity, and daily temperature range. Sites with greater than 75% canopy closure were responsible for most of the difference because they exhibited the lowest diurnal temperatures, the highest nocturnal relative humidity, and the lowest mean daily temperature range. As discussed above, greater canopy closure moderates overall temperature fluctuations.

MULTIPLE ANOVA

In summary, our findings indicate that Southwestern Willow Flycatchers prefer habitats exhibiting the lowest mean maximum diurnal temperatures for nest placement (i.e., the coolest locales). To a lesser extent, flycatchers also selected microclimates within their territories exhibiting the lowest mean diurnal temperature for nest placement (i.e., locales with the most thermally moderate microclimate). NU sites tended to exhibit less canopy closure, were hotter and drier during daytime, and had a greater mean daily temperature range (i.e., were less thermally stable) than either nest (NS) or territory (WT) locales. These characteristics may have been partially responsible for the absence of nesting flycatchers in adjacent NU habitat because pairs attempting to nest there may have to expend more energy on thermoregulation for themselves and for their nest contents, an expenditure that would theoretically reduce fitness.

COMPARISON WITH OTHER FINDINGS

Allison et al. (2003) reported that habitat within Southwestern Willow Flycatcher nesting territories exhibited greater canopy closure than non-nesting plots in Arizona, a relationship they suggested might provide a more favorable (i.e., more moderate) microclimate at nests. Our finding that NS and WT sites had greater canopy closure than NU sites was consistent with Allison et al. (2003). Our vegetation findings (see previous chapter) parallel this, in that canopy closure was greater at NS than NU sites.

At the four life history study areas, McKernan and Braden (2001a, 2001b) reported that mean daily temperature range (they used the term "variation in temperature") was significantly greater at NU sites than either NS or WT sites, but that NS and WT sites were similar. However, their difference between NU and NS sites was small, which was apparently the reason they discounted the difference as biologically insignificant and reported the following: "Selection of nest sites or territories by the…flycatcher was not found to be affected by specific requirements in temperature, relative humidity, or stability in these microclimate variables. Therefore, the microclimate variables are unlikely to limit habitat suitability for the species" (McKernan and Braden 2001b:78). They also reported that "…microclimate variables between native and non-native habitat types, under the same hydrological conditions, do not limit habitat suitability for the …flycatcher" (McKernan and Braden 1999:58, McKernan and Braden 2001b:81).

Our single effects analysis indicated a significantly greater mean daily temperature range at NU compared to NS sites (similar to that of McKernan and Braden 2001b), although we also detected greater mean daily temperature range at WT than at NS sites. However, after adjusting for study area, habitat, and canopy closure, and after significant interaction terms were included in our final multiple ANOVA analysis, mean maximum diurnal temperature was the only response variable that significantly predicted location type.

In addition, we suggest the differences among our mean maximum diurnal temperatures at the three location types, although small, appear to be biologically meaningful since they paralleled significant vegetative differences identified in the previous chapter and reported by Allison et al. (2003). Therefore, we propose that microclimate (in a complex interaction with habitat type, vegetative structure, and perhaps other factors) appears likely to limit nesting habitat suitability.

This key difference between our findings and those of McKernan and Braden (2001b) should be interpreted with caution as we were unable to replicate their field methods, and we used a different approach to statistical analysis. Additional microclimate data collected in subsequent years will show whether the patterns observed in 2003 are consistent across years and will help clarify whether suitable nesting habitat for willow flycatchers is limited by microclimate.