Water Requirements for Southwestern Willow Flycatcher Habitat and Nesting at the Pueblo of Isleta

2008 FINAL REPORT

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Introduction

SWFL Habitat: Vegetation and Surface Water

The southwestern willow flycatcher (SWFL, *Empidonax traillii extimus*) breeds in riparian habitats of the southwestern United States. In 1995, the southwestern subspecies of the willow flycatcher was listed by the U.S. Fish and Wildlife Service (USFWS) as federally endangered (USFWS 1995). A primary cause of the species' decline is habitat loss due to water diversion, impoundment, and channelization (USFWS 2002).

Throughout the southwest, SWFLs nest in dense riparian vegetation near lentic water; e.g., slow-moving streams, river backwaters, oxbows, or marshy areas (Sogge and Marshall 2000). These riparian habitats are created by hydrological events such as periodic flooding, sediment deposition, inundation, and groundwater recharge. SWFLs often place their nests in trees or shrubs that are rooted in or hanging over standing water (Whitfield and Enos 1996, Sferra et al. 1997). Surface water may be present early in the breeding season, but drying may leave soils damp or even dry later in the season. If traditional nesting areas become consistently dry due to drought or reservoirs receding, flycatchers may use the site for a breeding season or two, but over longer dry periods suitable riparian vegetation cannot be maintained, and dry sites are ultimately abandoned (Sogge and Marshall 2000).

Plant species composition and structure vary widely across the SWFL breeding range. Regardless of plant species composition or height, occupied breeding sites usually consist of dense vegetation in the patch interior or several dense patches interspersed with open water or sparser vegetation. The densest vegetation typically occurs in the first three to four meters above ground. Thickets of trees and shrubs used for nesting range in height from 2-30 m (6 to 98 ft, USFWS 2002).

Water could impact SWFL nesting in several ways. The native plants that provide SWFL nest sites are riparian obligates – water is essential for development of required vegetation. If suitable SWFL habitat goes without water for several years, substrate plants may die and habitat quality can decline (USFWS 2002). It is therefore clear that water affects SWFLs through its effects on vegetation. Second, food availability for SWFLs may be "largely influenced by the density and species of vegetation, proximity to and presence of water, saturated soil levels, and microclimate features such as temperature and humidity" (USFWS 2004). Absence of water may therefore mean a reduced food supply for adults and nestlings.

Finally, flycatchers may choose nesting territories based on the presence of water. Occupied sites were much more often adjacent to water than unoccupied patches (Copeland et al. 2009 and references therein). In particularly dry years, SWFLs at traditional nesting sites on the Middle Rio Grande nested in reduced numbers relative to wetter years (Smith and Johnson 2004, 2005) or failed to nest altogether (Johnson et al. 1999).

At the territory scale, results are more variable, depending in part on how plots were established. Nest plots have been found to be closer to water than non-nest plots (Allison et al. 2003 [non-significant], Stoleson and Finch 2003, Smith and Johnson 2004 [non-significant]). In four studies, nest plots were not different in distance to water from non-nest plots, although for these studies nest and control plots were on the same territories, which is expected to bias results (Copeland 2004; Smith and Johnson 2005, 2006; McLeod et al. 2007; the first and last cited in Copeland et al. 2009). In a study from Camp Pendleton, CA, 12 of 13 transient male territories were detected within 50 m of water, but only about half (9/17) of breeders were within 50 m. The rest were more than 150 m away (Kus 2000), which suggests that SWFLs preferred breeding territories close to, but not directly adjacent to, flowing water.

. At the nest scale, one New Mexico study found that distance of nests from the main river channel was correlated with flow volumes (Brodhead and Finch 2005). In New Mexico, stream flows (which indicate current and longer-term climatic conditions) have been reported to correlate with nest success during two narrow time windows, late June-early July, and late July (Brodhead and Finch 2005). Thus, the presence of adequate water appears to affect not only vegetation, but nesting decisions and even nesting success.

More researchers are beginning to investigate the importance of water to SWFL territory establishment and nesting success, but additional information is needed before the effects of timing, distribution, and abundance of water on SWFL reproduction are well understood. Areas of particular interest include: 1. relationship of water to vegetation type and structure, 2. effects of the duration and timing of water on territory selection and nest success, 3. the mechanisms by which water availability influences SWFL reproductive success; for example, relationships between water and food availability and between food availability and nesting success.

SWFLs at the Pueblo of Isleta

SWFLs have been known to nest at the Pueblo of Isleta since 1994, when the first systematic studies of the area were performed (Mund et al. 1994). SWFLs were also present in 1995 (Mehlman et al. 1995) and 1996 (B. Howe and J. Richardson 1996 data sheets). With assistance from Natural Heritage New Mexico (NHNM) and funding from the U.S. Army Corps of Engineers, the Middle Rio Grande Endangered Species Collaborative Program, the Pueblo of Isleta, and NHNM, the Pueblo conducted surveys in 2000 and surveys, nest monitoring, and habitat research in 2003-2008 (Johnson and Smith 2000; Smith and Johnson 2004, 2005, 2006, 2007, 2008).

In an effort to enhance SWFL breeding habitat, the Pueblo of Isleta began a project to introduce surface water to traditional SWFL nesting areas on the Pueblo. In 2004, the Pueblo installed a turnout gate to allow water movement from the Isleta Interior Drain into SWFL habitat at the Isleta Return Channel site, where SWFLs nested in 2000 and 2003-2008 (Johnson and Smith 2000; Smith and Johnson 2004, 2005, 2006, 2007, 2008). In 2004, the newly-installed turnout delivered water to the northern part of the study area, but no water reached the center of the study site where SWFLs have traditionally nested. In 2005, river flows were extremely high due to winter-spring precipitation and runoff, and the entire study area was inundated (Figure 1). In 2006, the Pueblo installed a trench to move water further into the habitat, but water stalled before it reached any territories. In 2007 and 2008, territories were flooded due to groundwater levels and no progress was made on the trench.

We know from previous studies (Johnson and Smith 2000; Smith and Johnson 2004, 2005, 2006, 2007, 2008) that in average years water tends to collect in some parts of the habitat and not others, such that some areas are consistently wet and some parts consistently dry. We observed exceptionally wet years in 2005 and 2008, when the entire habitat was inundated for most of the breeding season. Even in such unusual years, higher areas dried before lower-lying spots. Thus, we can infer past water distribution in the habitat from present moisture distribution. Mapping wet versus dry areas of the study site and comparing vegetation between them provides information on the effects of varying saturation histories on current vegetation.

Finally, monitoring the effects of water management on SWFL territory establishment and nesting success provides insight into the effects of water on SWFL reproduction. Parasitism by brown-headed cowbirds (BHCO, *Molothrus ater*) and predation are important components of nesting success. Both could potentially be affected by water availability via its effects on vegetation. Water could also affect number of young fledged by influencing insect populations.

Figure 1 Isleta Return Channel 2004 (left) and 2005 (right), showing extreme fluctuations in water levels between average and excessively wet years. SWFL nesting area is left of road/investigators. In 2005 water flowed across the road and into the nesting area.

Relationship of Surface Water to Nesting Success at the Pueblo of Isleta

From 2000-2008, water levels in the traditional nesting area at the Pueblo (Isleta Return Channel) have varied widely (Table 1). In 2000, the southern two-thirds of the study site were inundated or moist in the early part of the season. In 2003, all territories were completely dry. In 2004, the southern part of the site had saturated soil, and several territories were at least partially inundated at the beginning of the nesting season. After the extremely wet winter of 2005, the entire site was flooded at the beginning of the season, to a depth of over a meter in some places, and soil in all territories remained saturated throughout the nesting period. In 2006, the entire site was very dry early then became wet after the breeding season was already underway. In 2007, the south and parts of the north were inundated early in the season, and in 2008, the entire site was completely inundated for most of the nesting season.

Predation, nest parasitism by brown-headed cowbirds, and nesting success at the Pueblo appeared to vary with water levels among years (Table 1). Predation was highest and nesting success low in the two years that were dry early in the season (2003, 2006). Parasitism was highest in the driest year (2003). The highest nesting success occurred in the year that the site was flooded early in the season and later dried out (2007) and the year that the site was partially dry early and dried later (2004).

The data in Table 1 suggest that a relationship may exist between the amount and timing of surface water at the Pueblo of Isleta and SWFL nesting success, mediated in part by parasitism and predation rates. This relationship is apparently not a simple matter of more water being better. Our data to date suggest that SWFLs do better in years of intermediate soil moisture but particularly when that moisture comes early in the season, as in 2004 and 2007.

Table 1. SWFL nesting success, parasitism, and predation in dry, wet, and average years at Pueblo of Isleta.

Year	Soil Saturation	Number of Nests	Number of Successful Nests	% Nests Parasitized	% Nests Depredated	% Nests Failed (Other)	% Nest Success
2008	site flooded most of the season	7	2	0	29	43*	29
2007	wet early, dry late	5	4	0	0	20	80
2006	dry early, wet late	9	3	11	33	22	33
2005	site flooded	7	3	14	14	43**	43
2004	partial early	10	5	0	0	50	50
2003	dry	6	2	33	50***	0	33

* Only two nests this year showed evidence of depredation. The other failures were from unknown causes.

** One nest was both parasitized and abandoned

***One nest was both parasitized and depredated.

The goal of this project is to understand surface water requirements for territory establishment, nesting, and habitat development and maintenance at the Pueblo of Isleta. Objectives of the three-year study were to:

1. conduct breeding-season SWFL surveys at the study area,
2. conduct SWFL nest monitoring at the study area,
3. conduct vegetation measurements on nesting territories,

4. compare vegetation type and structure at nests and away from nests to determine desired vegetation parameters,
5. document and map saturated soils on the study area,
6. investigate the relationship of soil saturation on the study site to territory selection and nesting success, and
7. investigate relationships of water availability to vegetation type and structure.

Due to the complete inundation of the study site, we were unable to sample insects at dry versus wet areas, so this additional objective for 2008 was not met. We added one additional objective in 2008, to determine if temperatures at nests differed from those at similar, non-nest sites within territories.

Methods

SWFL Surveys

In 2000 and 2003-2008, we conducted protocol surveys at the Isleta Return Channel and the South of Isleta Marsh Expanded site. All maps showing locations of territorial males and nests were created in ESRI ArcGIS, version 9.2 (ESRI 2006).

We followed survey protocols and habitat evaluation as outlined in the USFWS SWFL survey protocol (Sogge et al. 1997). No imminent project was planned within the survey areas; therefore, we followed a three-visit schedule, per the 2000 addendum to the protocol (USFWS 2000). Starting 19 May in 2008, we visited the Isleta Return Channel and South of Isleta Marsh sites within the recommended dates: survey 1 - 15-31 May; survey 2 – 1-21 June; survey 3 – 22 June-10 July. We conducted surveys between sunrise and 9:00 a.m. Both sites were completely inundated but this did not change our survey method.

We determined status as migrant, territorial male, unpaired male, or pair (breeding/non-breeding) based on behavior. Any bird detected at a site in May or early June that was not present in the third survey was considered to be a migrant. SWFLs were differentiated from other flycatcher species by vocalizations, and we considered any birds detected between 15 June and 25 July to be of the southwestern subspecies (*E. t. extimus*, Rourke et al. 1999).

We determined breeding status based on activity of territorial birds. The observer sat or stood quietly in the habitat and watched for the presence of a female, listened for *whitt* and interaction calls between the pair mates, and looked for territorial defense, copulation, carrying of nesting material, carrying of food, incubation, or feeding of young.

All survey results were reported on standard SWFL survey and detection forms (Appendix 1, Sogge et al. 1997). In addition, as required by our USFWS permit, during the course of the study, we informed biologists at the USFWS New Mexico Ecological Service Office and New Mexico Game and Fish Department of detections of SWFLs and their nests.

Nest Monitoring

We monitored SWFL nests to determine success, brood parasitism, and number of fledglings. Nest monitoring followed standard SWFL nest monitoring protocol (see details in Rourke et al. 1999). We kept nest calendars to estimate transition times and allow accurate assessment of nest fate with minimum disturbance. To avoid triggering premature fledging, we did not visit nests during the last few days of the nestling period. Nests were checked every two or three days near hatching, or if the approximate hatch date was unknown. Otherwise, nests were checked every four to seven days. During nest checks, we entered the territory and determined adult activity, approached the nest from a different direction each time, quickly checked the contents with a mirror pole, and left by a different path to avoid leaving a dead end scent path for predators. To determine whether a nest fledged young, we checked for fledglings being fed in the territory. All nest site coordinates were recorded with GPS units, taken in North American Datum (NAD) 83, and plotted on digital USGS 7.5 minute quad maps. Territories in which nests failed were visited at least twice to check for re-nesting.

Vegetation Characteristics

In 2004-2008, we collected vegetation measurements at nests using methods developed by Dr. Peter Stacey of the University of New Mexico (P. Stacey pers. comm. 2004, based on Kus 1998). This method differs from the method used before 2004 on the Pueblo but is the same as that used in other SWFL habitats in New Mexico in 2004 and earlier.

We recorded two types of vegetation measurements. First, we recorded nest-centered data similar to Rourke et al. (1999, p. 24), including data on nest height, substrate tree species and height, and distance to water. When distances could not be estimated on site they were measured using GIS on a digital aerial photo.

Second, we estimated vegetation cover in four, 5 m diameter plots by noting the volume occupied by vegetation between the ground and 3 m, 3-6 m above the ground, and 6 m to the top of highest canopy over the plot (Kus 1998). One plot was centered at the nest tree, and three more plots were located 15 m from the nest tree at due north, 120º, and 240º compass headings. We recorded estimates as percent volume occupied by all plants and percent of the total plant cover volume contributed by the three most common species. Volume estimates were recorded in categories of 0, 1-10, 11-25, 26-50, 51-75, 76-90, and 90-100%.

We compared microclimate at nests to sites within territories at the same height as the nest. After nests had failed or fledged, we placed temperature loggers at three nests and 15 m to the north of the nest, at the north subplot for vegetation. After 35 days we collected the loggers and compared the resulting temperature logs for each pair of loggers.

Soil Moisture

In late April 2006, Pueblo of Isleta Water Resources Department personnel, under the direction of John Sorrel and Cody Walker, dug a shallow (about 20 cm) trench from the area near the new turnout (installed in 2004) from the Isleta Interior Drain to deliver water to the northern part of the site.

To track soil moisture changes throughout the site, we installed Tidbit temperature loggers (Onset Computer Corporation) at 50 m intervals on a predetermined grid covering the study area. The rationale behind using temperature loggers as indicators of soil moisture is that temperature fluctuations over a 24-hour period are lower for wet loggers than for dry loggers. We programmed the temperature loggers to record soil temperatures every half hour throughout the time they were deployed.

We installed 40 loggers in 2006, 42 in 2007, and 41 in 2008, avoiding areas where the habitat was unsuitable, in a large section of gallery forest where we have never detected SWFLs. We installed the data loggers (Figure 2) in early to mid-May in areas covered by less than 1 m of water and in areas of deeper water after the flooding subsided. To install loggers, we dug a hole approximately 25 cm deep, filled it ¾ full with coarse silica sand, and buried the loggers in the sand. A piece of wire was threaded through a hole in the logger and attached to 1m rebar driven into the ground. The rebar and nearby vegetation were flagged and a GPS location was taken at each logger. After the breeding season was over, we collected the loggers from the field and uploaded the data.

We compared daily temperature fluctuations at each logger with direct observations of soil moisture during the season. When the soil was muddy or flooded, the temperature difference between the daily maximum and minimum was 3° C or less. This difference was the same for 2006 and 2007. We classified days at individual logger sites as dry if the 24-hour temperature fluctuation was 3° or more and wet if the difference was less than 3°. Based on the wet and dry logger classifications and direct observations of soil moisture, we drew polygons around wet areas using ArcGIS. We incorporated these polygons into soil moisture maps of the habitat for the first and fifteenth of each month throughout the breeding season.

Results

SWFL Surveys

At the main site in 2008, we spent about 36 hours in the habitat mapping SWFL territories, including the surveys. Males established nine territories but only four males paired; the unpaired males dispersed after a few weeks. Two males present for only a few days were classified as migrants. We found seven nests on the four pair territories (Table 2, Figure 3). At the south site, we spent about 20 hours mapping territories and surveying for birds. Three males established territories, and two paired with females. Only one pair went on to nest; the other three birds may have been migrating willow flycatchers not of the southwestern subspecies (Table 2, Figure 3).

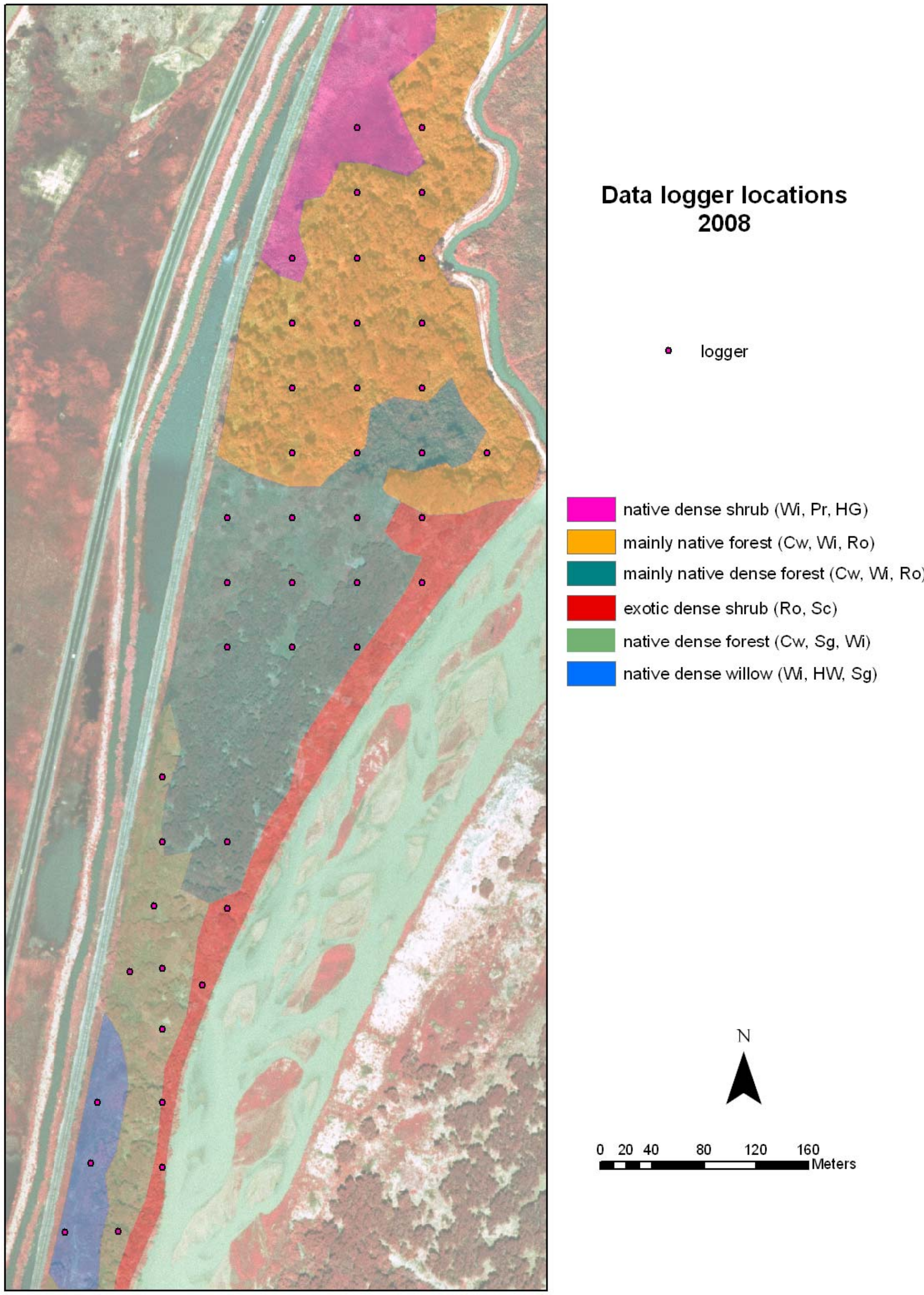


Figure 2. Data logger locations, 2008.

Table 2. Summary of survey dates and results.

Site	Year	Dates Visited	Adults	Pairs	Territories	Nests	Fledglings
Isleta Return Channel	2008	5/19, 6/2, 6/24, 7/7	13	4	9	7	6
Isleta Return Channel	2007	5/15, 5/22, 6/4, 6/19, 6/26	13	5	8	5	13
Isleta Return Channel	2006	5/16, 6/7, 6/29, 7/7	12	5	9	9	10
Isleta Return Channel	2005	5/16, 6/7, 6/30, 7/5	12	6	9	7	8
Isleta Return Channel	2004	5/18, 5/19, 6/18, 7/6, 7/19	14	7	7	10	13
Isleta Return Channel	2003	5/23, 6/13, 6/18, 6/19, 6/30	12	5	5	6	7
South of Isleta Marsh (expanded)	2008	5/23, 6/13, 6/30	5	2	3	1	3
South of Isleta Marsh (expanded)	2007	5/29, 6/5, 7/6	1	0	1	0	0
South of Isleta Marsh (expanded)	2006	5/18, 6/1	0	0	0	0	0
South of Isleta Marsh (expanded)	2005	6/1, 6/14, 7/25	0	0	0	0	0
South of Isleta Marsh (expanded)	2004	5/25, 7/12	0	0	0	0	0
South of Isleta Marsh (expanded)	2003	5/23, 6/19, 6/27	0	0	0	0	0

Nest Monitoring

None of the seven 2008 nests at the main site or the one nest at the south site was parasitized by BHCOs. Two of seven nests (29%) at the main site fledged one or more SWFL young, with a total of six young fledged. The nest at the south site fledged three young. Over the six years, pair success at the main site was correlated with nest success (Spearman's r=0.83, P=0.04). Thus, associations between reproductive success and water levels apply generally to both nest success and pair success (Tables 1, 3).

In 2008 at the main site, five of seven nests failed, two due to predation and three due to unknown causes (Table 4). Over the six years we monitored nests, nests failed due to predation, abandonment, parasitism, starvation, and weather (Table 4). Five nests disappeared due to unknown causes. The most common causes of failure were predation (nine nests) and abandonment (six nests). We suspect that at least some of the nests that disappeared for unknown reasons (five) were depredated. Some could also have been

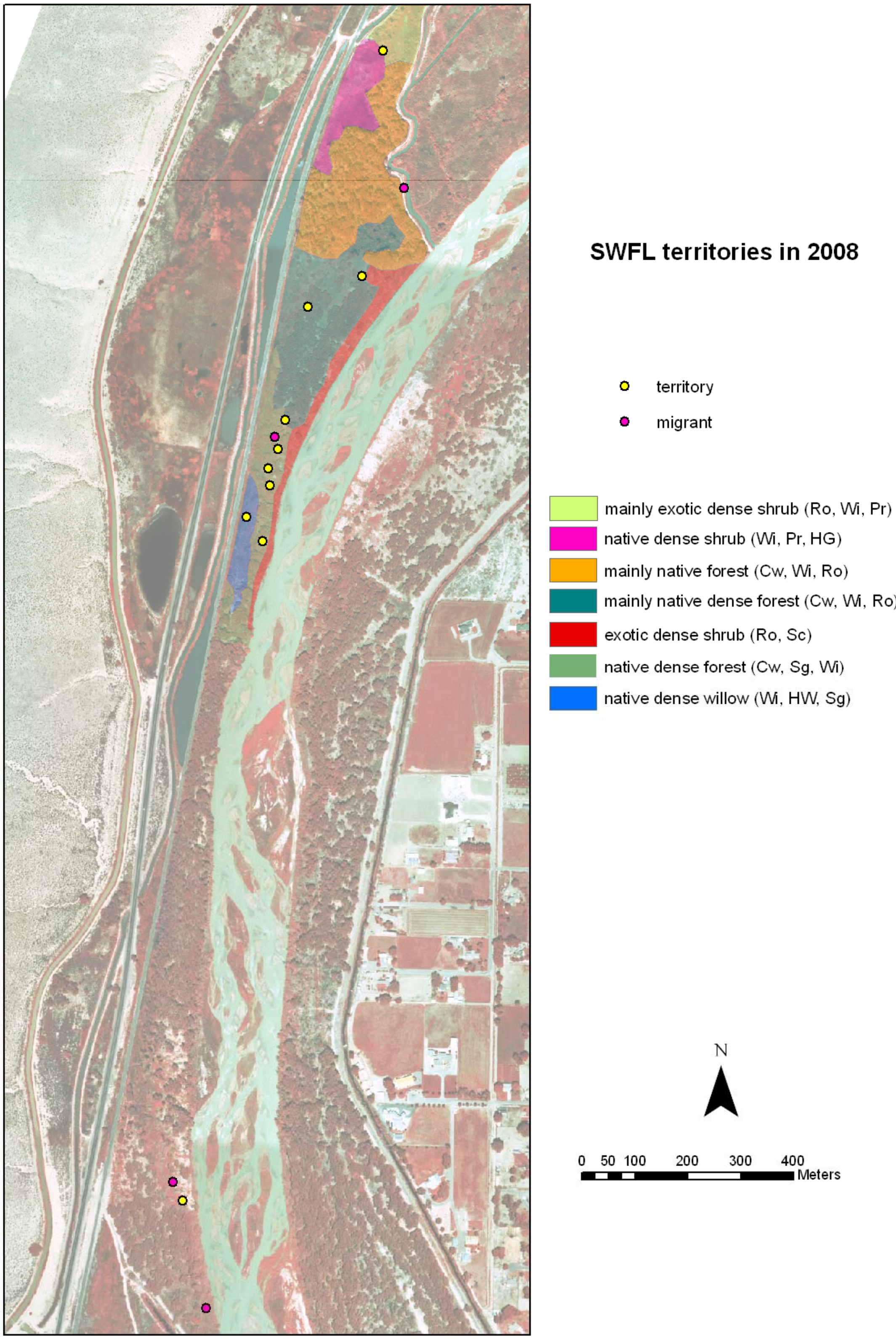


Figure 3. SWFL territories 2008, showing the main and south sites.

Table 3. Nest and pair success rates and number of pairs breeding for five years at the Isleta Return Channel Site. Pair success exceeds nest success because some pairs successfully re-nested.

Year	Nest Success	Pair Success*	N Pairs Breeding
2008	29%	50%	4**
2007	80%	80%	5
2006	33%	60%	5
2005	43%	50%	6
2004	50%	71%	7
2003	33%	40%	4

* Pair success counts only those pairs that actually started nests.

** Includes only birds at the main site- not the south site.

Table 4. Causes of nest failure, 2003-2007. Percent success for each year is shown in parentheses.

	Year						
Reason for Failure	2003	2004	2005	2006	2007	2008	Total
Depredated	3		1	3		2	9
Abandoned		2	2	2			6
Parasitized	2		1	1		0	4
Starved/Died in Nest		1			1		2
Blew Down		1					1
Disappeared		1	1	0		3	5
Succeeded	2 (0.33)	5 (0.50)	3 (0.43)	3 (0.33)	4 (0.8)	2 (0.29)	19 (0.43)
TOTAL	6*	10	7**	9	5	7	44

* one nest was both parasitized and depredated

** one nest was both parasitized and abandoned

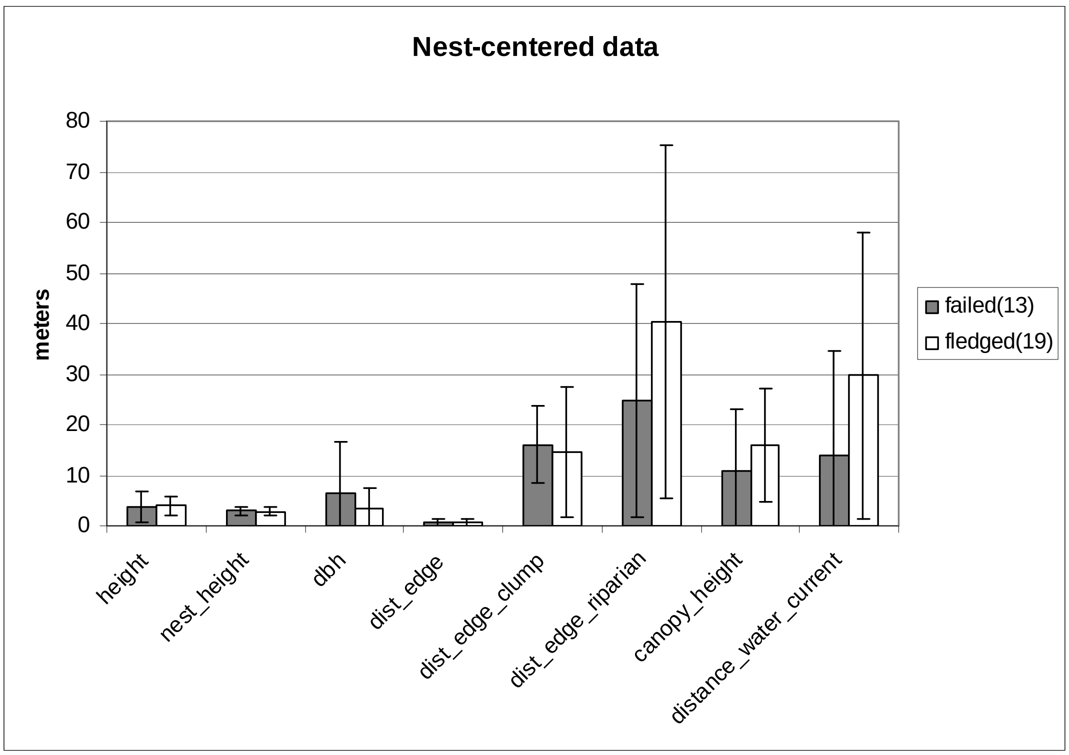
destroyed by wind or rain storms. Annual nest success rates varied from 29% to 80%, with an overall success rate of 43% over the six years (Table 4).

Vegetation Measures at Nest Plots

SWFL nests were placed in Russian olive (*Eleagnus angustifolia*), coyote willow (*Salix exigua*), and saltcedar (*Tamarix ramosissima*) in 2004, 2005, 2007; only Russian olive and coyote willow in 2003 and 2006; and coyote willow and saltcedar in 2008 (Table 5). Nest centered measures for combined 2004-2008 fledged and failed nests are shown in Figure 4. None of the measures was significantly different between successful and unsuccessful nests (means and standard deviations shown in Figure 4).

Table 5. Species of substrate tree by nest.

Tree species	Nest 2003	Nest 2004	Nest 2005	Nest 2006	Nest 2007	Nest 2008
Russian olive	1, 1b, 2, 3, 5	1, 1b, 1c (all the same tree), 4, 4b	6	5, 7, 8b, 8c*	1	--
coyote willow	4	2,5,8	1, 10, 4	4, 10	5, 6	2, 10a-c, 11a, Y(south site)
saltcedar		3, 7	4b, 7, 11		4, 7	7, 11b



*nest 8a disappeared before the species of the nest tree was recorded.

Figure 4. Nest-centered data at Isleta Return Channel site for 2003-2008 failed (N=13) and fledged (N=19) nests.

At the 0-3m and 3-6m height intervals for 2004-2008, total vegetation cover was significantly denser at the nest (center) than at the three nearby subplots (Figure 5; subplots averaged, 0-3m: Wilcoxon statistic=50.5, P=0.001; 3-6m: Wilcoxon statistic=51.5, P=0.003; >6m: Wilcoxon statistic=96.5, P=0.13; N=29 for all tests).

Exotic vegetation cover was also denser at the nest for the two lower height intervals (Figure 5; 0-3m: Wilcoxon statistic=91.5, P=0.02; 3-6m: Wilcoxon statistic=71.0, P=0.008; >6m: Wilcoxon statistic=82.0, P=0.4; N=29 for all tests).

Temperature logs showed that loggers placed away from nests had higher average daytime temperatures over the sampling period than the corresponding loggers placed at nests (Figure 6). This outcome is consistent with our finding that vegetation is denser at nests than in near-nest plots.

Vegetation density per unit volume on nest and near-nest plots did not differ significantly between successful and unsuccessful nests, at any of the three height intervals (means and standard deviations shown in Figure 7).

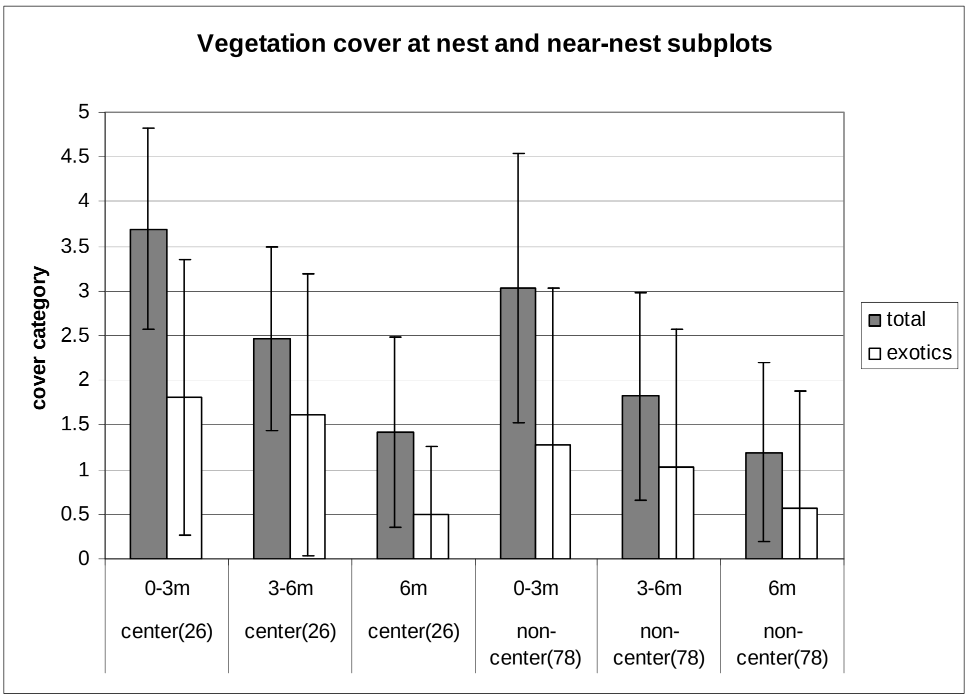


Figure 5. Exotic and overall vegetation cover averages for 2004-2008 at nest and near-nest subplots. Means with standard deviation bars; sample sizes in parentheses.

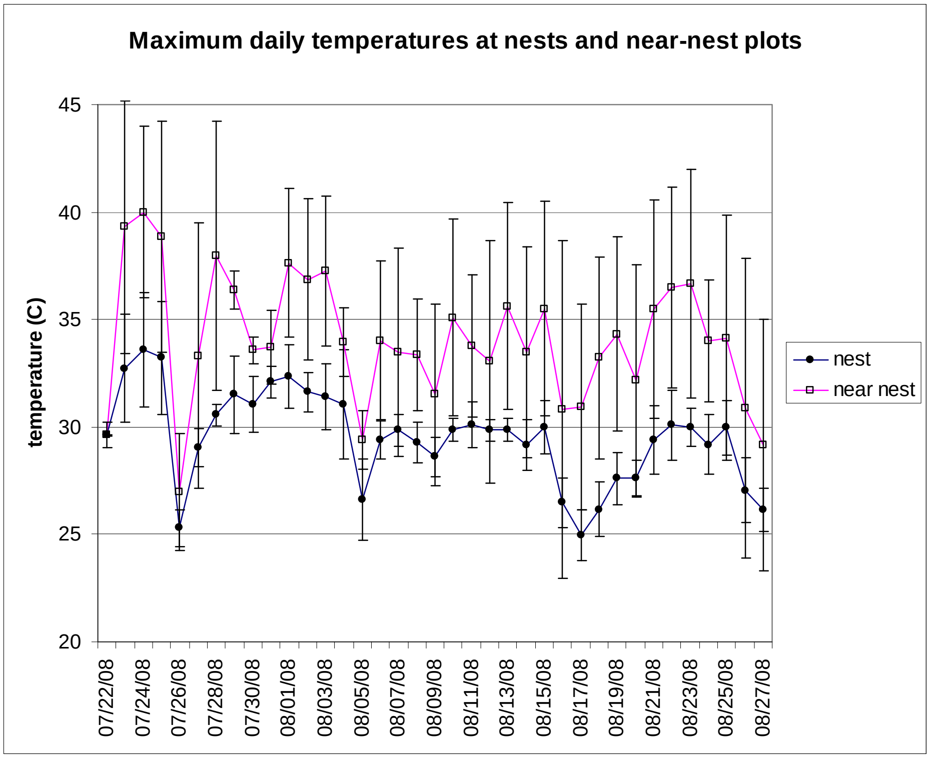


Figure 6. Average maximum temperatures logged at three nests and three near-nest subplots over 35 days in 2008.

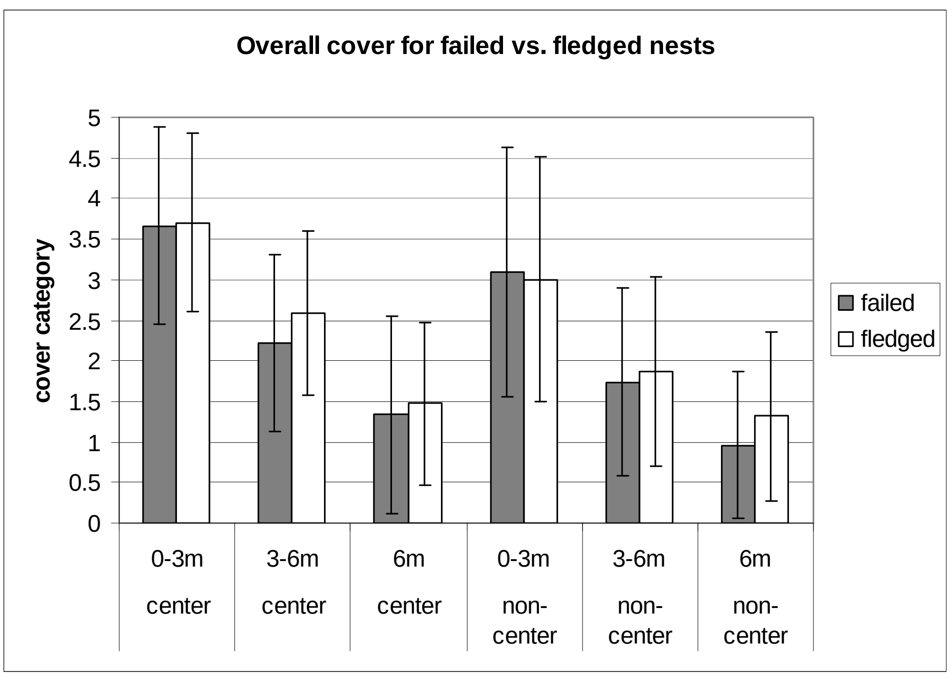


Figure 7. Overall vegetation cover (per unit volume) at failed and fledged nests, averaged over 2004-2008. Means with standard deviation bars.

Soil Moisture and Vegetation

The revised vegetation map shows six main map units (MUs) covering the study site (Figures 8-14). The northernmost unit, Native Dense Shrub (pink on the map) contains coyote willow with common reed (*Phragmites australis*) and herbaceous grassy mesic vegetation. Also in the north is Mainly Native Forest (brown), containing cottonwood (*Populus deltoides*), coyote willow, and Russian olive in a gallery forest structure. Mainly Native Dense Forest (teal) contains mature cottonwood, with a dense coyote willow and Russian olive understory. Exotic Dense Shrub (red) is characterized by Russian olive and saltcedar. Native Dense Forest (green) contains cottonwood, Gooding's willow (*Salix goodingii*), and coyote willow. Native Dense Willow (blue) contains coyote willow, herbaceous wetland, and Gooding's willow with no large overstory trees. Table 6 shows the percentage of the study site covered by each vegetation type. All except two of the types, Exotic Dense Shrub and Native Dense Shrub, meet the definition of suitable SWFL habitat. Thus, roughly 110,000 m^2 (82%) of the study area is covered in suitable SWFL habitat (Table 6).

The MUs most often covered in water over the last three years were Exotic Dense Shrub and Native Dense Forest, followed by Mainly Native Dense Forest and Mainly Native Forest, which averaged similar, but lower, proportions of wet soils (Table 7). These general classifications are supported by our vegetation density estimates at nests. Mean vegetation density from 0-6m at both center and non-center plots was highest (sample sizes did not permit statistical comparisons) in Native Dense Forest, followed by Native Dense Willow and then Mainly Native Dense Forest.

Table 6. Area and percent of study site covered in each vegetation type.

Vegetation Type	**Area (m^2)**	**% of area**
Mainly Native Forest (Cw, Wi, Ro) brown	44041	33%
Native Dense Forest (Cw, Sg, Wi) green	15811	12%
Mainly Native Dense Forest (Cw, Wi, Ro) teal	43342	32%
Exotic Dense Shrub (Ro, Sc) red	14698	11%
Native Dense Willow (Wi, HW, Sg) blue	6419	5%
Native Dense Shrub (Wi, Pr, HG) pink	9126	7%
Total	133438	100%

Table 7. Percent wet soil in each vegetation type at three sampling times, 2006-2008.

Vegetation type	Date	6/15	7/1	7/15
Exotic Dense Shrub	'06		19.9	15.4
	'07	48.9	45.6	44.8
	'08	42.8	57.3	52.4
Mainly Native Dense Forest	'06		5.1	1.6
	'07	27.7	9.9	23.9
	'08	11.2	37.1	41.6
Mainly Native Forest	'06		10.5	
	'07	11.1	15.1	27.1
	'08	7.4	41.9	51.2
Native Dense Forest	'06		74.5	6.4
	'07	34.0	4.7	11.9
	'08	69.5	59.0	49.7
Native Dense Shrub	'06		14.1	
	'07	2.5	2.1	21.5
	'08	24.1	32.7	56.8
Native Dense Willow	'06		58.9	
	'07			
	'08	90.3	96.0	92.5

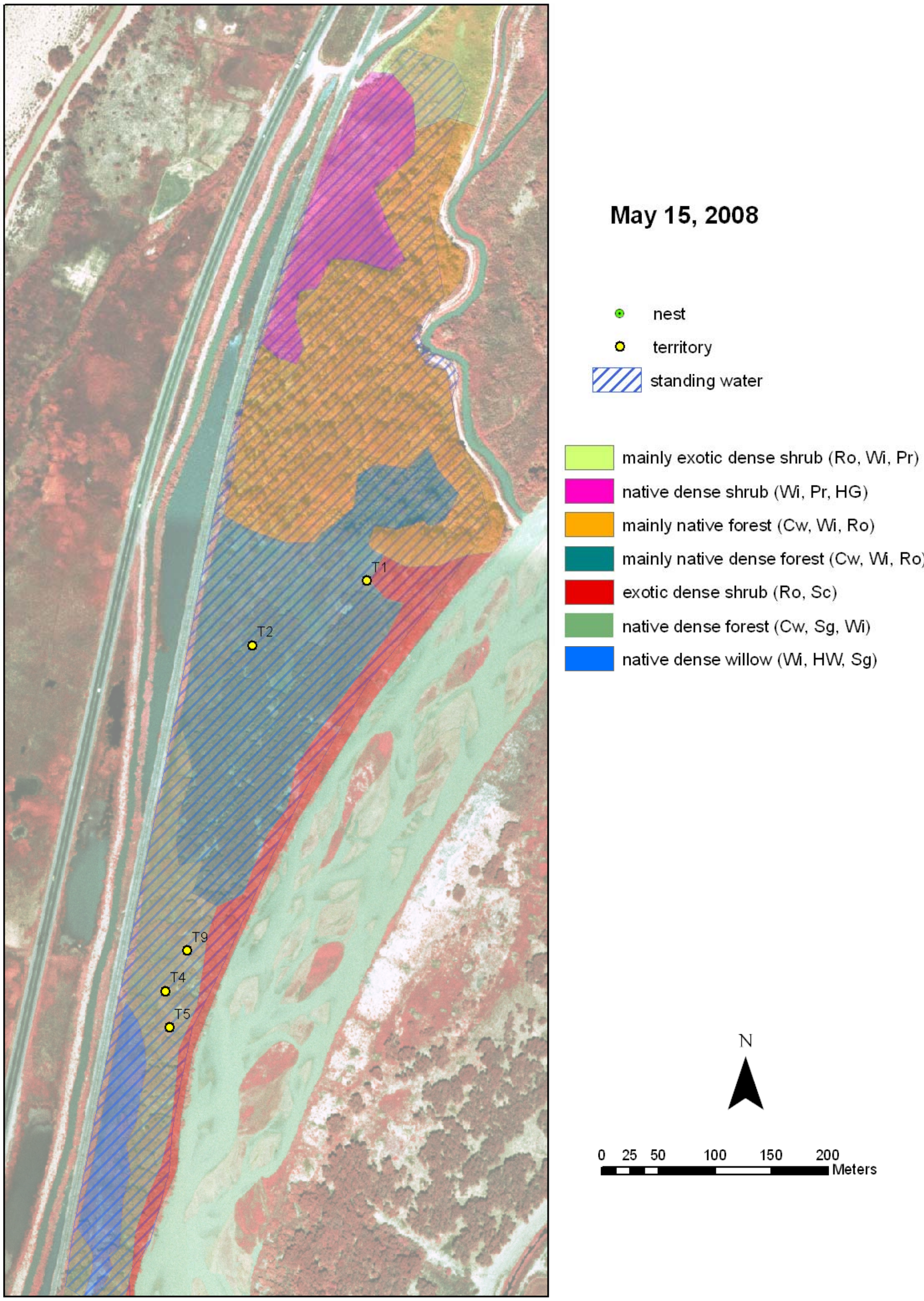


Figure 8. Water, SWFL territories and nests on 5/15/2008.

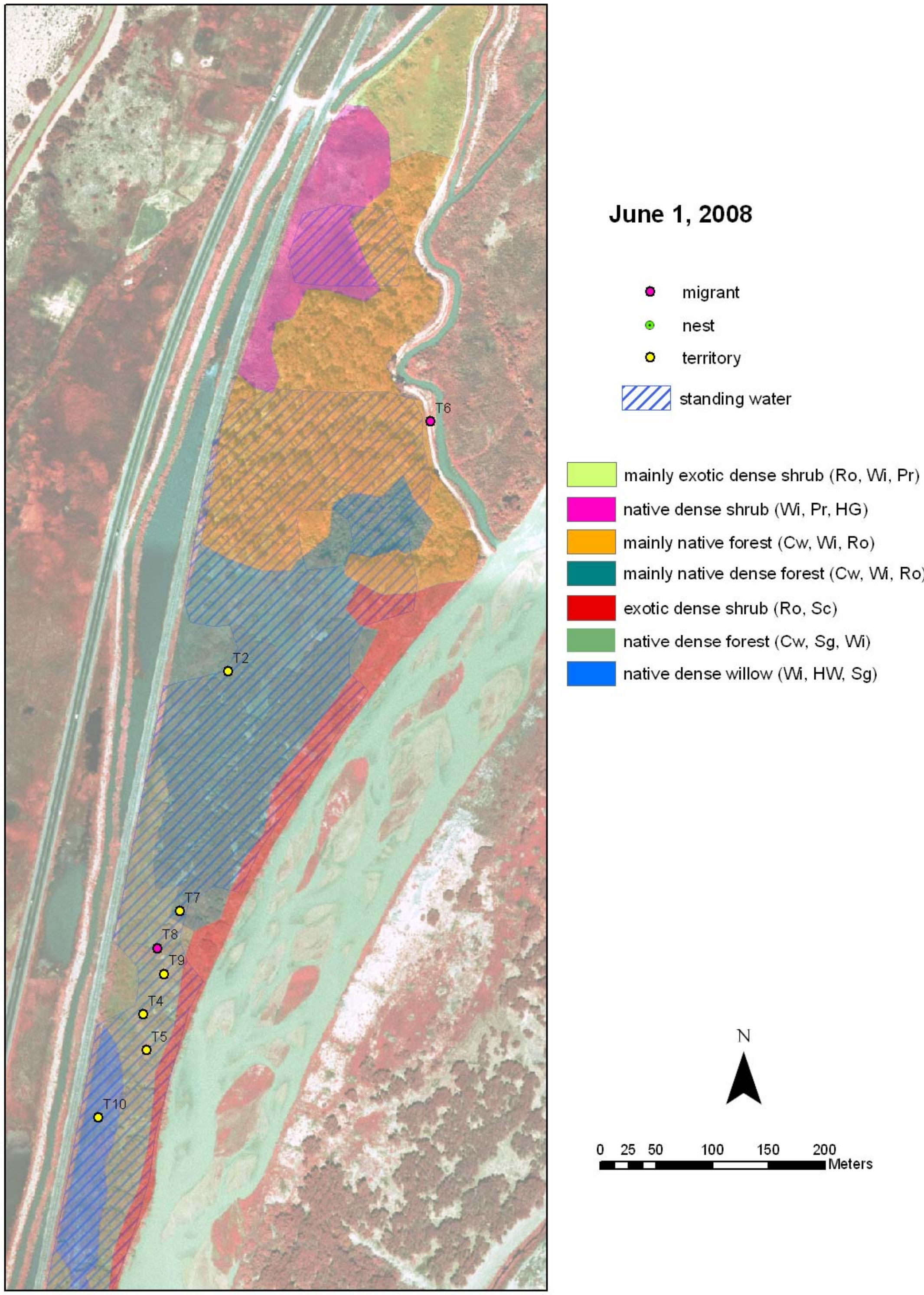


Figure 9. Water, SWFL territories and nests on 6/1/200

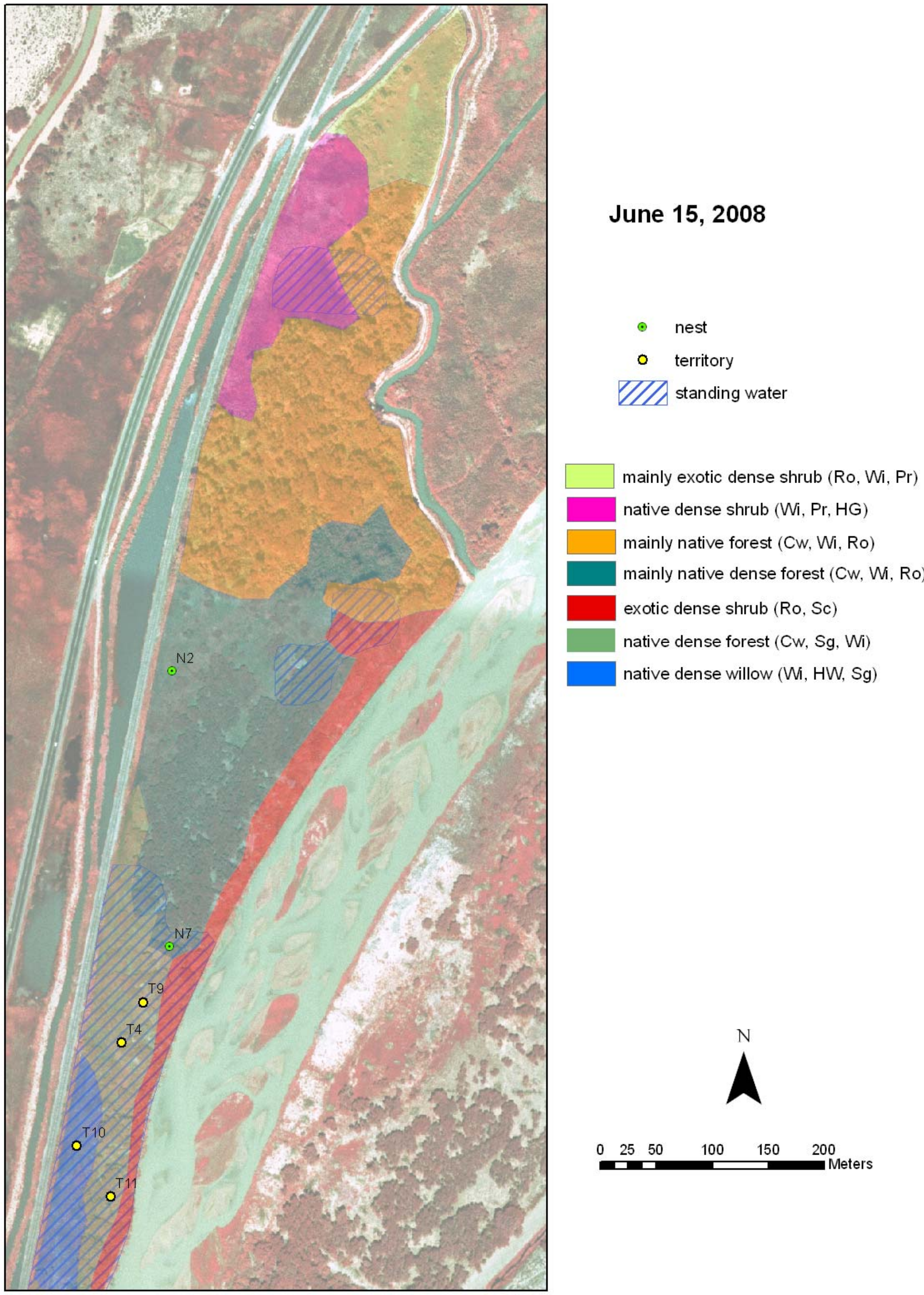


Figure 10. Water, SWFL territories and nests on 6/15/2008.

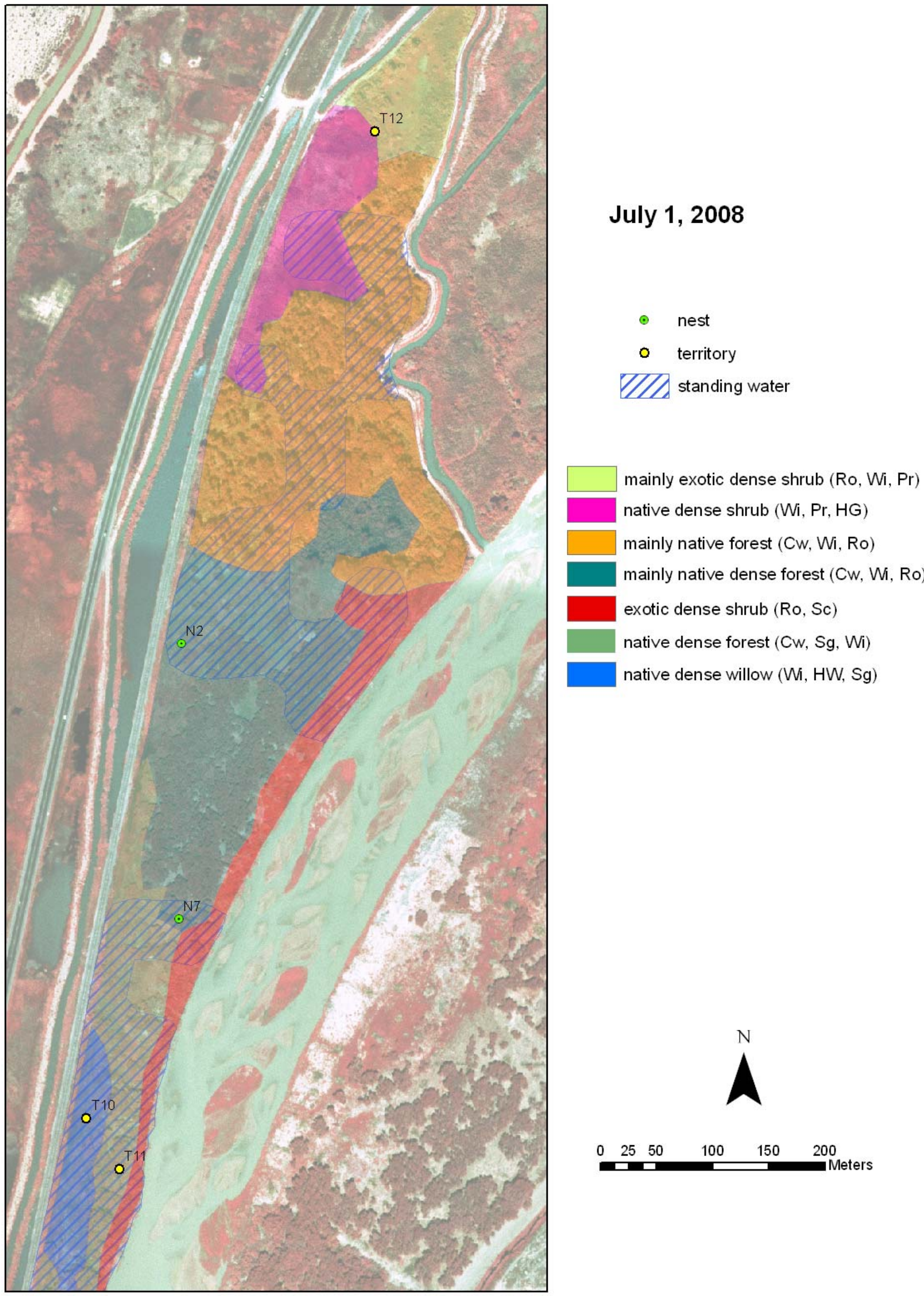


Figure 11. Water, SWFL territories, and nests on 7/1/2008.

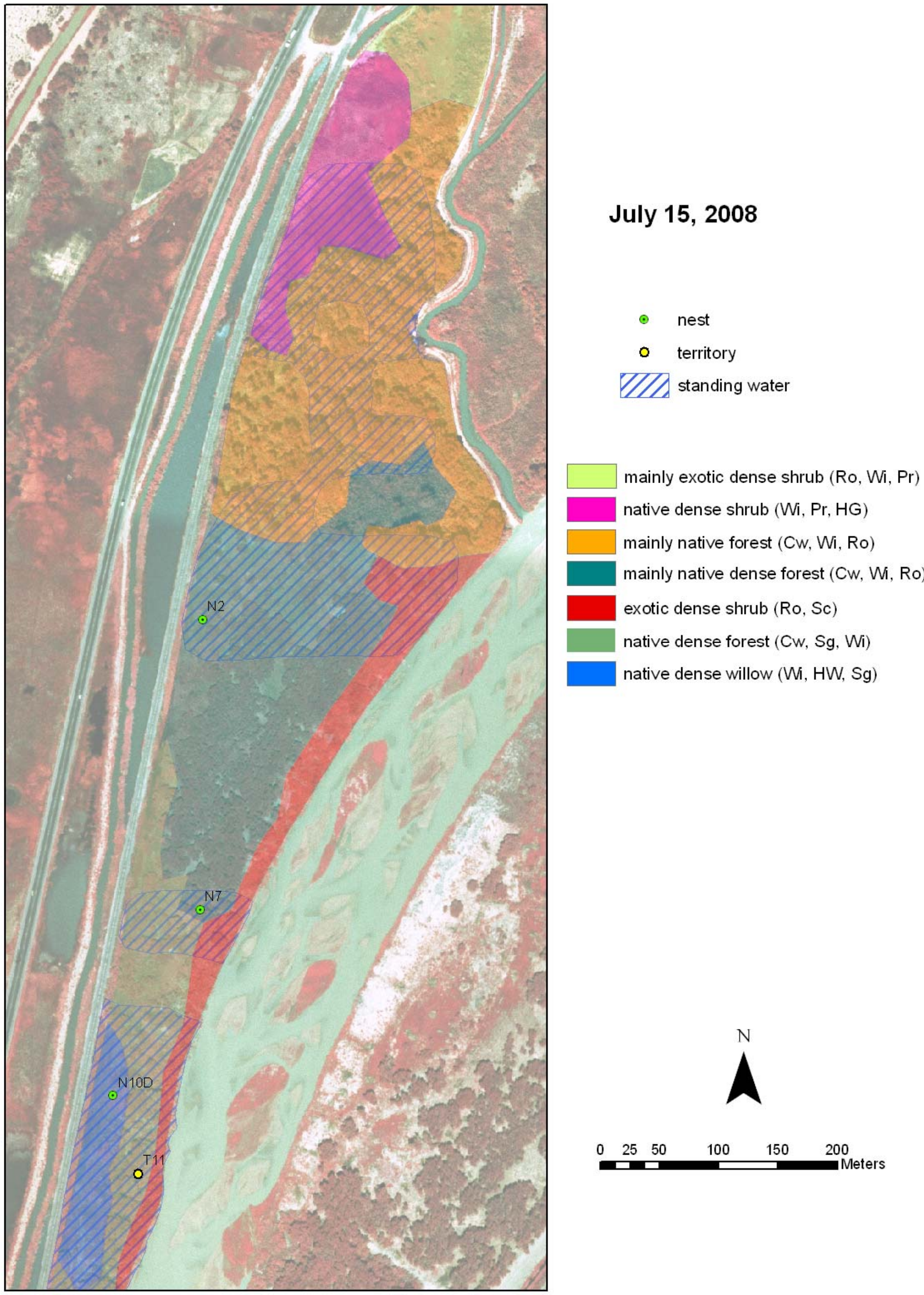


Figure 12. Water, SWFL territories, and nests on 7/15/2008.

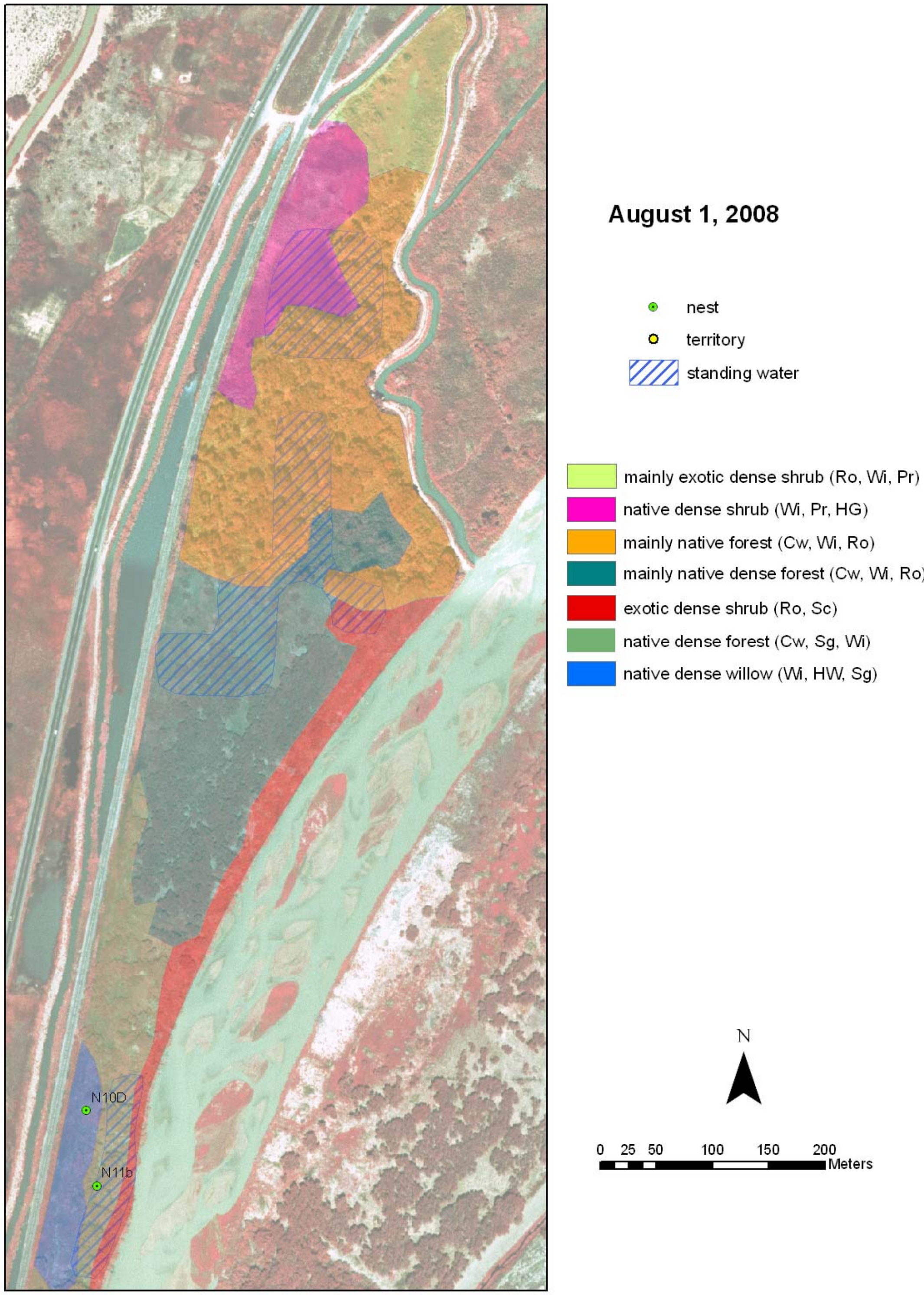


Figure 13. Water, SWFL territories, and nests on 8/1/2008.

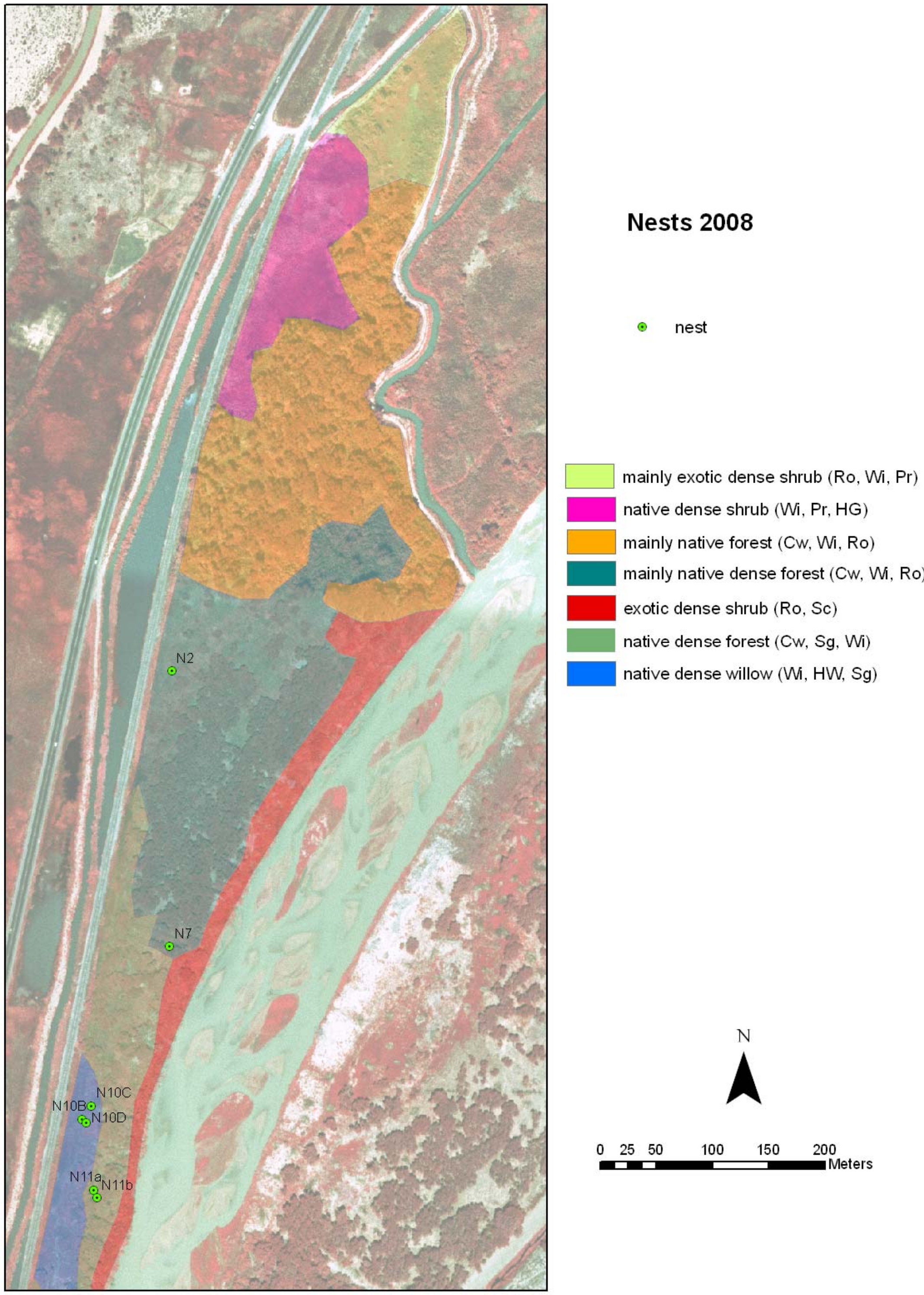


Figure 14. Nests in 2008 and vegetation type.

The two wettest MUs are situated in the lower elevation, southern half of the study area and have long habitat edges close to the river. Both are apparently influenced by groundwater flows coming from the river. Native Dense Forest comprises primarily native species of trees (cottonwood, Gooding's willow) and shrubs (coyote willow). The Mainly Native Dense Forest and Mainly Native Forest also regularly have had patches of wet soil. Mainly Native Forest is less dense and has less water in a typical year (e.g., 2007). Native Dense Shrub had small wet patches in 2007 that increased in size in this unusually wet year. Native Dense Willow has been variably wet, with 59% wet soils in 2006, dry soils at all three dates in 2007, and over 90% inundation in 2008.

Soil Moisture and Nesting

Soil Moisture and Territory Establishment 2008

Although 41 loggers were deployed in 2008, we recovered data from only 39 (Figure 2). In areas outside the nesting territories where we did not install loggers, we mapped standing water based on our notes. On 15 May, the entire study site was inundated at depths ranging from about 0.5 m to 1.3 m. At that time, five males were present. Two territories were in Mainly Native Dense Forest (turquoise), and three were in Native Dense Forest (green, Figure 8). By 1 June, most of the study area was still under water, although a few dry areas had appeared in the Mainly Native Forest (brown), north of SWFL territories (Figure 9). Seven males had established territories, two in Mainly Native Dense Forest, four in Native Dense Forest, and one in Native Dense Willow (blue), all inundated. The pair from territory 1 disappeared at the same time that a pair appeared in the south; timing suggests that they might have occupied territory 7. One migrant was present for a few days across the drain from Mainly Native Forest (brown), and another was present briefly on territory 8 in Native Dense Forest. By 15 June, wet areas were primarily south of the Mainly Native Dense Forest (turquoise), except for one wet patch on the eastern side (Figure 10). Six active territories remained, two in Mainly Native Dense Forest, three in Native Dense Forest, and one in Native Dense Willow. All territories except territory 2 in Mainly Native Dense Forest were still inundated. By 1 July, a new unpaired male had appeared in the far north, on the boundary of Mainly Exotic Dense Shrub (lime green) and Native Dense Shrub (pink), in a dry area. The two territories in Mainly Native Dense Forest were still active, and both were again inundated. Only one pair each remained in Native Dense Forest and Native Dense Willow, both territories wet (Figure 11). By 15 July, most of the southern part of the study area was still under water, including all four territories. The northernmost territory had been abandoned. The nests in territories 2 and 7 had fledged but the fledglings were still in the area (Figure 12). By 1 August, the water distribution was similar to that of 15 July, except for some drying in the Mainly Native Forest. Nests in territories 10 and 11were still active, and the fledglings from territories 2 and 7 had moved away from their territories (Figure 13). The first of August is relatively late to have two active territories at this site.

Table 8. Success of nests over wet versus dry soil, all years, nests for which we have data. All nests for each SWFL pair are included.

	Failed	Fledged
Wet	18	12
Dry	4	7

Soil Moisture and Nest Placement

Of 41 nests for which we have data on soil moisture near the nest, 30 (73%) were placed over water or saturated soil and 11 over dry soil (27%, Table 8). Of the nests over water, 18 failed (60%), and 12 fledged (40%). Seven of the 11 nests over dry soil fledged (64%). These differences are not significant (X^2=1.8, df=1, P=0.179).

Vegetation Types Chosen for Territories and Nests

Territory Vegetation 2006-2008

In 2008, SWFLs established four territories in Native Dense Forest, two territories in Mainly Native Dense Forest, one territory in Native Dense Willow, and one territory on the border between Mainly Native Forest and Native Dense Shrub. Native Dense Forest was the most popular vegetation type for territory establishment in 2008.

In 2006, after initial territory shifting early in the season, birds settled in Mainly Native Dense Forest (3), Native Dense Forest (2), and Native Dense Willow (2). In 2007, they established territories in Mainly Native Dense Forest (5) and Native Dense Forest (4). Mainly Native Dense Forest and Native Dense Forest have together held 83% of territories over the past three years.

Based on the relative area of each vegetation type in the study area, we calculated expected frequencies of territories in each vegetation type over the six years of the study. A goodness-of-fit test comparing observed to expected numbers of territories in each type allowed rejection of the null hypothesis of random territory placement relative to vegetation type (X^2=22.1, df=5, $0.001<P<0.005$). More territories were placed in Native Dense Forest and fewer in Native Dense Shrub and Exotic Dense Shrub than expected. The number of nests in Mainly Native Dense Forest (12) was similar to that expected (11.5), based on percent of the study area covered.

Nesting, Nest Success, and Vegetation Type 2003-2008

Over the six years of the study, SWFLs have nested preferentially in four of the six vegetation types: Mainly Native Forest, Mainly Native Dense Forest, Native Dense Forest, and Native Dense Willow (Table 9). SWFLs have never nested in Native Dense Shrub (pink), which has no overstory and contains significant proportions of common reed and herbaceous grassy vegetation. They have built only two nests in Exotic Dense

Shrub (Russian olive and saltcedar). Since 2005, they have not nested in Mainly Native Forest, the most popular habitat in 2003 and 2004.

Excluding Exotic Dense Shrub, SWFLs have nested successfully in only three vegetation types, with success rates of 40%, 67%, and 40% (Table 9). Birds have not nested in Mainly Native Forest since 2005, leaving Native Dense Forest and Mainly Native Dense Forest as the only two currently preferred and successful vegetation types. One of two nests placed in Exotic Dense Shrub was successful in 2005, but birds have not nested there since then. Two failed nests in Native Dense Willow were parasitized, two were abandoned, and one was depredated. Together, these two dense, mainly native habitat types have held 61% of nests and 74% of successful nests over the study. Thus, the vegetation types preferred for establishing territories and nesting also have the highest success rates. These types are also among the wettest types (see Soil Moisture and Vegetation, above).

Table 9. Nest success in each vegetation type, 2003-2007.

Vegetation	2003	2004	2005	2006	2007	2008	Total Nests	Success %
Native Dense Shrub							0	
Mainly Native Forest	2/4	1/5	1/1				10	40%
Mainly Native Dense Forest	0/2	2/3	1/2	2/2	1/1	2/2	12	67%
Exotic Dense Shrub			1/2				2	50%
Native Dense Forest		2/2	0/1	1/6	3/4	0/2	15	40%
Native Dense Willow			0/1*	0/1*		0/3	5	0%
% success	33%	50%	43%	33%	80%	29%	44	43%

*these nests were parasitized by BHCO.

Discussion

Between-year Soil Moisture Patterns

In 2006 and 2007, the southern part of the habitat had deeper water, larger wet areas, and more wet days than the northern part, but in 2006 the southern part did not become wet until later in the season. In 2000 and 2004, standing water was present in the south, but only early in the season. The exceptions to the pattern of standing water in the south occurred in 2003, when the entire site was completely dry, and 2005 and 2008, when the entire site was completely inundated for most of the season. Even in the very wettest years, the southern areas are the last to dry out. The southern part is lower in elevation - a contour line on the USGS topographical map passes between the north and south parts of the habitat. The southern section is apparently influenced by water levels in the river via lateral groundwater movement through a gravel substrate (John Sorrell pers. comm.). The northern section is not only higher but also wider and would therefore require greater groundwater movement to become saturated. The northern area is apparently influenced more by precipitation events than by lateral groundwater movement, as water stands in the northern section mainly after precipitation events.

Water and Vegetation

Water is presumably related to vegetation type, but it is difficult to define a causal relationship between vegetation type and presence of water. The four wettest vegetation types include exotic, mainly native, and native vegetation types. This suggests that the extent of soil saturation that occurs on the study site does not exclude either native or non-native species. The site has been completely inundated frequently enough to maintain riparian vegetation types, but beyond a threshold level, more or less water may not have discernible effects on vegetation composition. Soil moisture at the study site varies widely from year to year and over the breeding season, and vegetation composition changes over many years. These realities contribute to the difficulty of discovering direct relationships between soil moisture and vegetation composition.

Milford et al.'s (2005) vegetation map (revised for this project in 2007), classifies all except one MU as "dense." It is therefore difficult to infer anything about vegetation structure or density based on the map units. However, our vegetation density plots suggest that the wettest native vegetation type, Native Dense Forest, is also the densest, at heights relevant to SWFL nest construction.

Nesting Vegetation Type

SWFLs nest in a variety of dense riparian vegetation types (Sogge and Marshall 2000). Native-dominated vegetation can vary from monotypic, single-stratum to multi-species, multi-layered types with canopy and sub-canopy structure. Exotic-dominated types typically contain a saltcedar understory in a cottonwood-willow gallery forest or tall, mature saltcedar (Sogge and Marshall 2000). At our study site, the Native Dense Willow type is mainly monotypic, single-stratum willow with no overstory, and the three native forest types have native cottonwood overstory with coyote willow or coyote willow/Russian olive understory. All four types fit the description of suitable habitat, above. Exotic Dense Shrub, the only exotic-dominated MU at the study site, contains dense Russian olive mixed with saltcedar but does not fit the above description of exotic vegetation types used by SWFLs because it lacks tall overstory trees. Native Dense Shrub, containing willow, grasses, and reeds, lacks the necessary shrub density.

Over the four years of the study, SWFLs have never nested in Native Dense Shrub and have nested only twice (4.5% of 44 nests) in Exotic Dense Shrub. They have nested five times in Native Dense Willow, but all nests in that habitat have failed. However, Native Dense Willow is increasing in height and density, which may account for its increasing use. One pair nested there three times in 2008. Of all nests, 84% have been constructed in (often on the edge of) one of three native forest vegetation types. All three types have a cottonwood overstory with shrub understory of either native willows or a mix of willow and Russian olive. Thus, although monotypic and multi-species single-stratum native vegetation types and dense exotic types occur on the study site, the SWFLs at the Pueblo of Isleta have more often nested in vegetation types with a cottonwood overstory and dense willow understory. Preference for the denser forest types accords with our finding that vegetation at SWFL nests is significantly denser than that in other parts of territories.

Of the three forest types, Mainly Native Forest is the northernmost and typically the driest, Native Dense Forest the southernmost and wettest, and Mainly Native Dense Forest intermediate in both latitude and soil moisture. The northern type is drier and is classified on the map as less dense. In 2006 and 2008, only one pair established a territory in the northern forest habitat, and no pair nested there in 2007 or 2008. There has not been a nest in that type since 2005, as birds have settled further south in recent years. Only two vegetation types have been consistently preferred for the last five or six years. These are also the only two types with successful nests over the same period.

Nesting and Soil Moisture

From 2000 to 2007, the distribution of nests has shifted from north to south within the study site. In 2000, five nests were placed in the northern part, one in the center, and one in the south of the habitat. In 2003, all six nests were in the northern part of the habitat. In 2004 and 2005, birds constructed relatively more nests in the narrow, southern section, and territories were dispersed throughout the study site. In 2006, birds settled in the north but two moved south when northern territories remained dry. In 2007, birds avoided the most northerly, traditional territories and settled early in the season, leaving territories packed into the narrow southern section (see maps in Smith and Johnson 2008). In 2008, only one migrant and one unpaired male settled briefly in the northern part of the study area, and no pair nested there. All four nesting territories were in the wet, southern half of the study site (Figure 14).

We have suggested two likely explanations for the southerly shift (Smith and Johnson 2008). First, in 2006 and 2007, northern territories were drier than southern territories. Birds might have moved because they preferred moist soils and/or standing water. Second, the shrub layer in the south has steadily increased in height and density over the course of the study. These increases have likely been facilitated by seasonal availability of water in the south.

Increased vegetation density is apparently not the only reason for increased preference for southerly territories, because birds first settled, then moved out of northern territories (2006) and avoided them altogether (2007) when they were dry. The improved structure at southern territories apparently provided acceptable alternatives to the traditional northern part of the habitat when northern territories remained dry.

At the nest scale, 30 of 41 nests (73%) for which we have soil moisture data were constructed over standing water or wet soil. This finding is consistent with literature asserting a preference for nesting over saturated soil, but could also be explained by the prevalence of standing water and its co-incidence with preferred vegetation structure.

Soil Moisture and Nesting Success

Timing of standing water appears to be associated with nesting success at the site scale. In three of the six years we have been working at Isleta, the southern one-half to two-thirds of the site was covered in standing water at the time of territory establishment (2000, 2004, and 2007). Nest success was also highest in two of those three years (2004-50%, 2007-80%; Table 1). In 2000, we did not monitor nest contents for the entire nest cycle, but we did check nests from a distance well into the nesting period. It appeared that nest success would be high, with a possibility of up to 71% success. Thus, the pattern of standing water in the southern part of the study site during May and early June was associated with higher nesting success ("high," 50%, and 80%). The lowest success rate occurred when the entire site was flooded for most of the season (2008-29%). Success was also low in the years the site was entirely dry (2003 – 33%) or entirely dry early in the season (2006-33%). Intermediate success occurred in another year the site was completely flooded for most of the season (2005-43%). These results contrast with results at other sites along the Middle Rio Grande from Velarde to Elephant Butte Reservoir (Moore and Ahlers 2008; the majority of nests were from Elephant Butte). In that study, nests over flooded or wet soils that later dried had much lower fledging success and higher predation and parasitism rates than did nests that were flooded all season, saturated all season, or dry all season. This difference suggests that the POI site may be unique among Middle Rio Grande flycatcher breeding populations in the effects of water on nest success. More data are needed to investigate this apparent difference between the two studies.

The by-year summaries for the entire site, however, do not accord with the by-nest data. At the nest scale, a few more nests failed than fledged over wet soil, and a few more dry nests fledged than failed, but differences were not significant. Although it might appear that SWFLs strongly prefer to place nests over wet soil, most of the suitable habitat is often wet when birds are settling on territories. (In 2005 and 2008, the entire study site was inundated for most of the breeding season. In 2006, the dense, native vegetation that the flycatchers prefer was inundated by the time most nests were constructed. In 2004, the study site was partially flooded early in the season.) The lack of agreement between the site-scale and nest-scale data could mean that the presence of water increases nest success at the site scale, rather than at the nest scale. Perhaps the entire site produces more insects when it is wet early and dries later, thus benefiting birds irrespective of the presence of water under each nest. Sample sizes are still relatively small, which limits our ability to separate the importance of water and vegetation structure.

Nest failure was most often due to predation or abandonment (Table 4). Although water differences between years appear to be related to nesting success, the mechanism is not clear (Tables 1, 4). Predation may be correlated indirectly to water levels if adults forage further away from the nest in dry years and leave nests unattended for longer periods. Access of snakes or small mammals to nests is probably limited by deep standing water under nests, but this hypothesis does not explain the 29% predation rate in 2008, a year the entire site was completely inundated. Avian predators such as Cooper's hawks (*Accipiter cooperii*) could account for some nest predation. Starvation and abandonment could also increase if lack of water reduced insect abundance and thereby required birds to be away from nests for longer periods, but there is no apparent pattern relating abandonment to soil saturation over the years. Unexplained disappearances in 2004, 2005, and 2008 could have been due to other causes, which obscures understanding of the relationship between soil moisture and nest success. More research is needed to understand the mechanism by which flooding and its timing affect nesting success.

If the lack of water in the north caused the birds to move south, then it may also have increased their risk of BHCO parasitism. In 2005 and 2006, the southernmost nest was parasitized. Both nests were in an area (classified as Mainly Exotic Dense Shrub RO in Smith and Johnson 2007 but now classified as Native Dense Willow on revised maps) with little or no overstory and may have been more visible to cowbirds. In addition to the lack of dense vegetation above the nest, spatial aspects of southern territories might place them at increased risk of parasitism. The southern part of the habitat is much narrower than the north and is bounded by open habitat, unlike the north. BHCO parasitism rates have been shown to increase with the amount of edge habitat (Sedgwick and Knopf 1988), open area nearby (Brittingham and Temple 1983), and proximity of foraging areas for BHCO (Tewksbury et al. 2006). In addition, several prominent snags provide perches for BHCO above southern SWFL territories. In 2003, the parasitized nest was in the drier north and was visible from the nearby road. It is possible that reduced insect abundance associated with dry soil, in combination with high visibility, increased BHCO access to that nest.

Water or Vegetation?

Six years of data suggest that SWFL territory choice and nest placement are based on multiple interacting factors. Most SWFLs in this study have established nesting territories in (often on the edge of) three main vegetation types, all of which include a cottonwood overstory and a dense willow understory. Birds will apparently abandon territories in otherwise acceptable habitat if territories remain dry and if acceptable alternatives are available. The distribution of territories has also shifted from north to south over several years, apparently in response to lack of water on the traditional territory sites in the north. With abundant water in the southerly territories, the shrub layer, particularly coyote willow, has grown taller since the beginning of the study, thus providing more suitable nesting habitat in southerly territories. Birds did not settle in the north in 2008, in spite of the availability of inundated territories in the north. This suggests that southerly territories are increasingly preferred for their vegetation structure, and not just the presence of water at the time of territory establishment. In addition, if the presence of water early in the season increases insect abundance at the site scale, then birds may be choosing territories based on vegetation but benefiting from intermediate water levels via their effects on insect productivity.

Our nest vegetation data indicate that once SWFLs choose a territory, they then tend to place nests at sites having denser vegetation around and above the nest. Nests are constructed in various shrub species; the shrub species appears less important than density of vegetation at and above the nest. In addition, nests are typically placed over standing water or wet soil.

Our small sample of data on nest microclimate suggests that temperatures are cooler at nests than in surrounding vegetation. This is probably a logical consequence of birds placing nests in dense vegetation and is likely driven by predation pressures rather than physiology. However, in the hottest months, it is reasonable to expect that nestlings would experience heat stress if nests were not well shaded; dense vegetation may provide a secondary benefit by reducing heat stress.

Thus, in answer to the question of which is more important, water or vegetation, current evidence weakly suggests that vegetation type and structure are proximate cues for territory choice. However, it is possible that timing of inundation affects reproductive success within a season through its effects on insect availability. Water also clearly affects the development of suitable vegetation type and structure over years. To clarify the relative importance of these variables, we need more data on territory establishment from years when the site is not entirely inundated, in addition to information on the relationships between water and insect abundance and insect abundance and nesting success.

Management Recommendations

Native Dense Shrub (pink)

SWFLs have never nested in Native Dense Shrub (pink), which lacks an overstory layer and contains significant proportions of common reed and herbaceous grassy vegetation. Height and density of the willows in this MU, however, have increased over the years of the study. Although this area is not currently a high priority target for SWFL habitat management, this MU could develop into suitable habitat in time. Water delivery from the turnout could hasten this process.

Mainly Native Forest (brown)

Our first management recommendation is for the Mainly Native Forest vegetation type, situated in the northern part of the study site. This habitat has the basic structure favored by SWFLs, cottonwood overstory and shrub understory, but in places the shrub layer is sparse. We suggest that annual inundation in the early part of the nesting season would encourage development of the willow shrub layer and create saturated soils favored by the birds. The Pueblo of Isleta has already laid the groundwork necessary to implement this recommendation. The turnout gate is in place and a trench has been dug from the turnout to an appropriate point in the Mainly Native Forest habitat. We recommend that the Pueblo either make the trench wider and deep enough that water would easily flow the length of the trench or install PVC pipe at the appropriate angle to transport water from the turnout to the target area.

Native Dense Willow (blue)

The potential for Native Dense Willow, in the south of the study site, to develop into good nesting habitat is inherently limited by the low elevation and narrow width of the site. This low-lying area is strongly influenced by groundwater, and soils are typically quite muddy. Cottonwood trees on the east edge should be left in place to provide marginal overstory, and any Gooding's willow or cottonwood saplings at the site should be allowed to grow. We recommend that the tops of dead snags be cut off to eliminate BHCO perches.

Exotic Dense Shrub (red)

This extremely dense strip of Russian olive and saltcedar offers very little habitat potential in its present form. At minimum, we recommend monitoring this MU and minimizing its spread into the adjacent suitable habitats. The preferred action would be to remove the dense exotics and restore native willows and cottonwoods to this area. This area might also be made into suitable habitat by extensively thinning the exotics and encouraging a shrub layer of coyote willow. We recommend that we consult on any restoration in this or any other part of the study site, to avoid impacts to SWFL territories.

Mainly Native Dense Forest and Native Dense Forest (teal, green)

As long as Mainly Native Dense Forest and Native Dense Forest are partly or entirely inundated every year or two, this habitat will probably remain suitable for SWFL nesting. SWFLs have voted with their territory choices in favor of the current hands-off management practices in these habitats. However, if reduced precipitation and/or river volumes cause these MUs to stay dry all spring and summer, our recommendations would be similar to those for the Mainly Native Forest: inundate most of both habitats at least every two years and preferably every year. Some Russian olive trees occur in these habitats, but they are frequently used as nesting substrates. Unless the proportion of exotics increases in these habitats, we would not recommend removing them.

Future Work

A recent literature review of the water needs of the SWFL (Copeland et al. 2009) identified several information gaps:

1. *"Importance of duration of water on reproductive success (nest success, productivity, and breeding season female productivity)*
2. *Importance of duration of water for nest selection for late nests and re-nests*
3. *Importance of the amount of wet area in a territory on selection and reproductive success*
4. *Relationship between food availability and reproductive success*
5. *Relationship between food availability and water availability, annually and throughout the breeding season*
6. *Relationship between ground water tables, soil moisture, and the duration of water throughout the breeding season*
7. *Relationship between water availability and the duration of water on survival."*

Our work at the Pueblo of Isleta over the past six years, and especially the past three, has addressed numbers 1 and 2. We have also investigated relationships between the timing and amount of water and vegetation type and density. Results to date have suggested how favorable water management schedules for SWFLs at Isleta might look. However, to further test our hypothesis that the wet-early, dry-late soil moisture pattern is good for nesting success, we need more years of data on nesting success and soil saturation, particularly in atypical years. More data points should also clarify the relationship between nest success and placement over wet versus dry soil.

We have suggested that the relationship between water and nesting success might be mediated through increased insect availability in years with high early spring precipitation or runoff. In 2008, we planned to begin monitoring insect prey availability to look for associations with soil saturation and nesting success. The unusually widespread and prolonged flooding this year meant that there were no dry areas within the nesting colony to provide comparisons with flooded areas. Therefore, we did not sample insects. For future work, we want to compare insect abundance, territory establishment, and nesting success in dry versus wet areas of the nesting colony, dry versus wet periods of the season, and dry (railroad site) versus wet (traditional site) study sites. We also want to investigate if a relationship exists between water availability and predation, the primary cause of nesting failure at our study site.

Conclusions

After six years of monitoring SWFL nesting, four years of studying habitat preferences, and three years of mapping water distribution and vegetation, it appears that SWFLs at the Pueblo of Isleta fit the typical SWFL habitat profile surprisingly well. SWFLs at our study site have more often established territories in three vegetation types, all of which contain a cottonwood overstory and dense coyote willow and/or Russian olive understory. These map units are also consistently wetter than less preferred types. Within territories, SWFLs tend to nest on the edges of clumps, near open meadow habitat, and over wet soil. Nests are typically placed in vegetation that is denser than at other spots in the territory. Nests with low-density vegetation and nearby perches for BHCO appear to be at increased risk of nest parasitism.

Soil moisture patterns appear to be spatially associated with development of native shrub structure, as evidenced by the increasing height and density of willows in the wetter, southern MUs. Moisture thus affects territory establishment and nesting success via its effect on vegetation type and structure.

Nesting success appears to vary with the temporal and spatial distribution of standing water, and this effect occurs at time scales too short to be mediated through vegetation structure. Success has been higher in years having soils that are wet during territory establishment and dry by mid-June. Nests fail primarily due to predation, abandonment, and parasitism. If insect abundance is higher during wet periods, birds may need to spend more time foraging and less time covering or guarding nests during dry spells. If so, any of the above factors could be expected to increase during dry periods.

Three times as many nests were constructed over wet as over dry soil, but the percent of successful nests was not significantly different. The small size of our sample of nests over dry soil apparently limits statistical power. Future work should increase sample sizes.

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