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SCALE PERSPECTIVES IN HABITAT SELECTION AND ANIMAL PERFORMANCE FOR WILLOW FLYCATCHERS (*EMPIDONAX TRAILLII*) IN THE CENTRAL SIERRA NEVADA, CALIFORNIA

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Abstract. Habitat selection is often evaluated using a hierarchy of spatial scales, from coarse selection of general vegetation communities to fine selection of specific foraging or nesting locations. Rarely, however, are these differing scales examined to determine how they relate to habitat quality (as measured by animal performance). We examined how habitat selection at each of three scales (meadow, territory, and nest) constrained or influenced selection at other scales, and then assessed how these selections related to animal abundance, territory productivity, and nest success for Willow Flycatchers (*Empidonax traillii*) in the Sierra Nevada, California. During 1997 and 1998, we surveyed and monitored 104 meadows to document Willow Flycatcher abundance, territory, and nesting status. Vegetative and hydrologic variables were measured in association with all meadows, territories, and nest sites. We used multiple linear and logistic regression to determine which variables best predicted animal performance at each of the three spatial scales, and we used logistic regression to compare nest sites, territories, and occupied meadows with unused or adjacent areas at each scale. The patterns of selection were relatively consistent across scales, with riparian shrub cover a primary predictor of habitat selection for meadows, territories, and nest sites. At successively finer scales, Willow Flycatchers selected areas with higher riparian shrub cover. Increased shrub cover also predicted both Willow Flycatcher abundance and territory success, suggesting that the habitat characteristics selected by these birds also conferred high animal performance and thus habitat quality.

Key Words: animal performance, *Empidonax traillii,* habitat selection, habitat quality, meadow, reproductive success, riparian, *Salix,* Sierra Nevada, Willow Flycatcher.

Habitat selection occurs when there is a discrepancy between what is used by an organism and what is available (Johnson 1980). Habitat selection is an often-studied aspect of animal ecology. Because of the recent increase in preparation of habitat suitability indices, models, and recovery plans for endangered species, the accurate interpretation of what constitutes habitat has increased in importance (Verner et al. 1986, Hall et al. 1997). Many scientists have proposed that habitat selection should be viewed as a hierarchical process at multiple spatial scales (Johnson 1980, Hutto 1985; Wiens 1985, 1989b) in which an organism chooses habitat components at a number of scales; for example, meadow, territory location, nest location, and prey choice. These spatial scales exist in a hierarchy, such that selection at one scale is constrained by habitat selection at the scale above, and each choice constrains selection at the scale below (O'Neill 1989; Wiens 1989b, 1989c; Levin 1992). For example, organisms select territories in a non-random manner, which puts constraints on placement of nest or den sites.

Effective management may require more than simply exploring what is selected for use by an organism (Pullium 1988, Hall et al. 1997). We can most effectively determine which habitat components imply high habitat quality by viewing how selection at one scale constrains and influences selection at other scales, and then examining how these choices influence animal performance. For Willow Flycatchers (*Empidonax traillii*) we define animal performance as a measure of animal fitness that varies by spatial scale, including: relative abundance, territory/pair success, and nest success. Habitat quality is the relative ability of a given location to provide the conditions necessary for survival, reproduction, and persistence (Van Horne 1983, Hall et al. 1997).

We examined the relationship between selection and animal performance at multiple spatial scales for Willow Flycatchers in the central Sierra Nevada range. Our study took place along the zone of intergradation between two subspecies of Willow Flycatcher; *E. t. brewsteri* and *E. t. adastus* (Phillips 1948, Unitt 1987). These two subspecies are listed as endangered by the state of California, and designated as "sensitive" species in California by the U.S. Forest Service Region 5, and by the U.S. Fish and Wildlife Service Region 1. At this time it is unknown whether the birds at our study sites were *E. t. brewsteri, E. t. adastus,* hybrids between the two, or a combination.

The Willow Flycatcher is a neotropical migrant that winters from Mexico to northern South America, and breeds across North America (Bent 1942, Fitzpatrick 1980, Unitt 1987, Sedgwick 2000). Breeding Willow Flycatchers in the Sierra Nevada occupy wet meadows and occasionally riparian thickets from 600 to 2500 m in elevation (Serena 1982, Valentine et al. 1988, Harris et al. 1987, Flett and Sanders 1987, Bombay 1999). Historical accounts and museum records indicate that this species was locally common as recently as the 1940s within Sierra Nevada meadow systems (Ray 1903, 1913; Ingersoll 1913, Orr and Moffitt 1971, Serena 1982, Klebenow and Oakleaf 1984, Gaines 1992; Western Foundation of Vertebrate Zoology, unpublished nest records). The current Sierra Nevada Willow Flycatcher population is estimated at only 300 to 400 individuals based on surveys completed between 1982 and 1998 (Serena 1982, Harris et al. 1987, CDFG 1991, Bombay 1999, Stefani et al. 2001).

To facilitate meaningful conservation and management efforts for Willow Flycatchers and the meadows they occupy in the central Sierra Nevada, we examined flycatcher habitat selection and animal performance at three scales: the meadow, the territory, and the nest site. Our objective was to examine how habitat selection at each scale constrained or influenced selection at other scales (*sensu* Johnson 1980), and then to assess how these selections related to animal performance and therefore habitat quality (Van Horne 1983, Hutto 1985, O'Neill 1989; Wiens 1989b, 1989c; Levin 1992, Hall et al. 1997). Specifically, our goal was to create a hierarchical habitat model for the Willow Flycatcher in the central Sierra Nevada that (1) determined factors influencing habitat selection at the meadow, territory and nest site spatial scales, and (2) determined which habitat characteristics within these scales conferred high abundance and reproductive success.

STUDY AREA

Our study area included montane wet meadows within a 1.2 million-ha portion of the central Sierra Nevada (Fig. 1). This area included over one-third of the Willow Flycatchers known to exist within the Sierra Nevada at the time (Serena 1982, Harris et al. 1987, California Natural Diversity Database 1997, Stefani et al. 2001). Precipitation in the region falls mostly in the form of snow, with accumulations ranging from as little as 36 cm per year on the eastern slope, to 205 cm per year on the western slope.

The meadows within the study area were generally associated with streams or small headwaters rivers, but some also occurred along lake or pond margins, or were associated with springs and seeps at higher elevations (Ratliff 1982, Weixelman et al. 1999). Vegetation usually consisted of a variety of grasses, forbs, sedges (*Carex* spp.), and rushes (*Juncus* spp.) depending on elevation, slope, hydrology, substrate, and management history (Ratliff 1982, Weixelman et al. 1999, Dull 1999). Riparian deciduous shrubs were generally distributed in a patchy manner across meadows, or in some cases restricted to the edges of the water course. Willows, particularly *Salix lemmonii* and *Salix geyeriana,* were the dominant shrubs within open meadows in our study area, although other willow species, mountain alder (*Alnus tenuifolia*), creek dogwood (*Cornus sericia*), aspen (*Populus tremuloides*), gooseberries (*Ribes* spp.) and lodgepole pine (*Pinus contorta*) also occurred (Storer and Usinger 1963; Ratliff 1982, 1985; Weixelman et al. 1999).

METHODS

DISTRIBUTION AND ABUNDANCE OF WILLOW FLYCATCHERS

To assess habitat selection at the meadow scale we designated all meadows as occupied or unoccupied by Willow Flycatchers based on our survey results, with meadows being considered unoccupied if we did not observe at least one flycatcher. To assess animal performance we determined the relative abundance of Willow Flycatchers at each meadow. Relative abundance was defined as the percent of survey points where flycatchers were detected at a site.

We surveyed a total of 104 meadows during 1997 and 1998 to determine distribution and abundance of flycatchers relative to hydrologic and vegetative characteristics. Sites ranged from small meadows only a few ha in size to expansive riverine/meadow systems. Survey sites were limited to meadow and riparian communities, and included three subsets: (1) 28 meadows known to currently or historically support Willow Flycatchers based on surveys, journal articles, and nest records obtained from the Western Foundation of Vertebrate Zoology oological collection; (2) 66 meadows identified as having vegetation and hydrology with a potential to support flycatchers based on aerial photo analysis or field reconnaissance; and (3) a stratified random subset of 10 riparian or meadow sites between 600 and 2500 m in elevation and supporting some riparian deciduous shrubs (as delineated on U.S. Fish and Wildlife Service wetland survey maps or aerial photos).

We conducted surveys between first light and 10:00 hrs (PST), from 15 June through 31 July, in 1997 and 1998. These dates maximized the likelihood of detecting flycatchers, while minimizing chances of detecting migrants rather than breeders (Craig et al. 1992). We spaced survey points 100 m apart; at each point we first listened for spontaneous singing for 1 min, then played three to four bursts of a taped song and listened for responses. We repeated this process for a total of six minutes at each point. We conducted surveys once per site only.

MEADOW CHARACTERISTICS

We selected physical and biological variables measured at the survey sites (meadow scale) based on parameters that reflect structural and compositional aspects of meadow systems relevant to Willow Flycatchers, as indicated by previous research (Serena 1982, Flett and Sanders 1987, Valentine et al. 1988, Whitfield 1990, Sedgwick and Knopf 1992). We measured or estimated the following variables for each meadow surveyed: size of meadow (ha); elevation (m); total area of riparian shrub (m^2); percent of meadow with

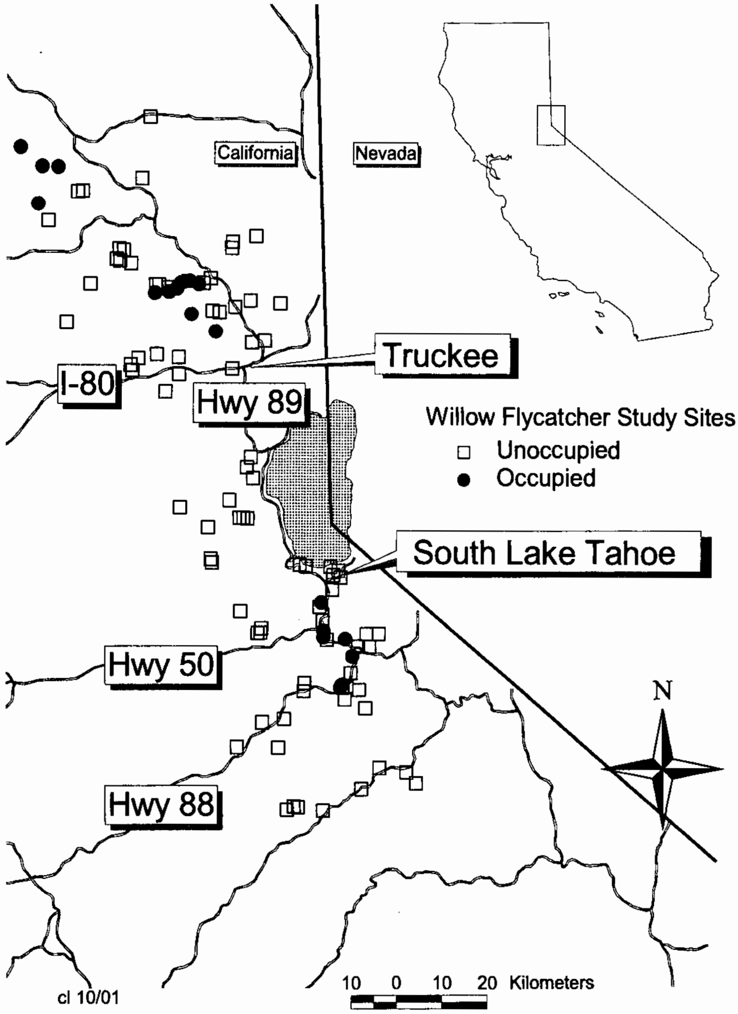

FIGURE 1. Locations of Sierra Nevada meadows surveyed for Willow Flycatchers in 1997 and 1998, and included as study sites.

riparian shrub matrix; proportion of riparian shrubs by species group; average shrub height (m); percent overstory canopy closure within the shrub matrix; dominant herbaceous vegetation (grass, forb, sedge, rush); presence/absence of standing or running water; percent of meadow covered by water, or with saturated soils; dominant type of water across the site and in the riparian shrub matrix (stream, seep, oxbow, in channel pool, snowmelt, pond, lake margin); average stream width (m); and presence/absence of beaver (*Castor canadensis*). Variables except for meadow size, elevation, and total riparian shrub were measured by ocular estimates during the flycatcher field surveys. We recorded elevation from topographic maps, and calculated meadow size and total area of shrub from aerial photos using a grid and photo scale for all survey sites. Approximately one third of the photos were taken in 1997, with the remainder taken between 1991 and 1995. Photo scale was generally designated as 1:12,000 (Range 1:16,000–1:8000); however, because photo scale varies within a flightline, we calculated individual photo scale using 7.5 min, 1:24,000 U.S. Geological Survey topographic maps.

TERRITORY SELECTION AND SUCCESS

To examine habitat selection at the territory scale we compared Willow Flycatcher territories to adjacent meadow areas. To assess animal performance we placed all territories in one of two categories depending on whether or not they produced successful nests.

We mapped flycatcher territories by observing individual males and marking the locations of their singing perches and frequently used foraging areas on aerial photographs. To delineate general territory boundaries, we completed an initial 1.5 hr visit at each territory, then refined our boundary maps during each subsequent monitoring visits (described below). We conducted observations between approximately 1 June and 31 August each year. Timing of territory mapping and nest searching took place between dawn and dusk.

We used standard nest searching techniques (Martin and Geupel 1993, Ralph et al. 1993) to determine reproductive status for all flycatcher territories. We observed each territory for 0.5–1.5 hr every two to seven days, until nests were found. We briefly visited each nest, at the same frequency, to determine if it was still active and if so, its stage (incubation, nestling, fledging). We considered territories successful if at least one nest therein fledged at least one flycatcher. We confirmed fledging when either fledglings were directly observed or adults were seen carrying food after the nest was empty (Vickery et al. 1992). We monitored each territory from its delineation until fledging, or until we observed that the territory was abandoned on three consecutive visits.

Territory Characteristics

We could not actually measure the availability of resources to Willow Flycatchers because we cannot know what is potentially accessible from the perspective of an organism (Johnson 1980; Wiens 1983, 1989a; Hutto 1990). Instead, we measured the abundance of a variety of resource variables and explored which variables were actually selected for use by individual flycatchers in their territories, and in what proportion relative to their abundance within meadows.

Because the abundance of Willow Flycatchers in the Sierra Nevada is already quite low, it is not reasonable to assume that: (1) all suitable meadows are saturated, or occupied; or that (2) unused meadows are unsuitable (Wiens 1983, 1989b; Capen et al. 1986, Noon 1986). Therefore we compared the abundance of specific habitat variables within 87 territories to their relative abundance within randomly selected adjacent plots in the same meadow, rather than comparing territories to areas defined as unsuitable or unused.

After territory boundaries were recorded and flycatcher fledglings had been out of the nest for approximately 10 days or nest failure had been documented, we collected vegetation and hydrology data for each territory. We used our territory mapping photos to locate the center point of the territory, and marked the point regardless of whether it fell within riparian shrub patches or the open meadow. We then centered a 60 m baseline over the territory center point; baseline direction was determined by adding a random number (between −15 and +15) to the compass bearing of the long axis of the territory. We also established four 20 m transects that alternated from right to left at 5, 20, 35, and 50 m along the baseline. After collecting data within each territory, we randomly selected a location 75 m from the territory center and constructed our comparison baseline and transects. The compass bearing for both baselines in each pair was the same.

We used the point intercept method to measure cover for individual woody plant species or herbaceous species groups (e.g., grasses, forbs, rushs, sedges), total plant and water cover, and percent cover by height class (USDI/USDA 1996, Kelly and Wood 1996, Elzinga et al. 1998). We collected data at 5-m intervals along the four transects and baseline (30 points), and recorded one hit for each species or species group touching the measuring rod in any or all of the following height classes: 0–1 m, 1.01–2 m, and >2 m. We used two measures of total percent shrub cover. In the first, we pooled all height classes so that one hit was recorded for each of the 30 point intercept locations if there was any shrub hit in any height class (x/30 points * 100 = percent cover for all height classes pooled). In the second measure, we recorded two-dimensional cover by recording the presence or absence of shrub hits for each height class at each point intercept. As a result we had three vertical points at each of 30 point intercept locations (x/90 points * 100 = percent cover across all height classes). To provide an estimate of vegetative dominance at the intercept point, we listed species in descending order by the estimated number of hits on the pole. At all points that intercepted riparian shrubs, we measured the maximum height (m) of the live growth of the shrub, and the shortest distance (m) from the outside edge of the shrub to the outside edge of its two closest shrub neighbors. In 1998, we added two additional vegetative variables to our territory analyses. The first was a measure of foliar density that was essentially a finer measurement of the vegetation hits on the vertical pole. We divided the 1-m intervals on the pole into 0.2-m intervals and recorded the number of these 0.2-m intervals (0–5) that had hits. We did this for both the 0–1 m and 1.01–2 m height classes. We also measured the average height of herbaceous vegetation found within a 0.5-m radius of the vertical pole (m).

We recorded water depth (m) and water type for all points that intercepted streambeds, oxbows, or obvious depressions that were holding water during the data collection period or that were known to have held water earlier in the flycatcher breeding season (based on personal observation or the presence of aquatic plants). Soil moisture was also recorded as a number ranging from 0 (no moisture) to 10 (saturated) as measured by a soil moisture meter.

Nest Site Selection and Success

We evaluated habitat selection by Willow Flycatchers at the nest scale by examining characteristics of 87 nest sites relative to the abundance of hydrological and biological variables within the territory. The measure of animal performance at this scale was nest success; a successful nest was defined as one that fledged at least one flycatcher, and an unsuccessful nest was one that fledged none.

Nest Site Characteristics

Nest-related habitat variables described three aspects of nest sites: (1) description of the actual nest, (2) location of the nest within the riparian shrub patch, and (3) the physical and vegetative description of the area within 12 m of the nest (to approximate the 0.04 ha nest area standard described by Noon 1981).

We measured the height and diameter (cm) of each nest, and the number and average diameter (cm) of the supporting branches. We recorded the placement of the nest relative to potentially important habitat features in the immediate vicinity of the nest, including: proximity to water (m), nest height from the ground (m), distance from nest to top of shrub (m), distance from nest to nearest shrub edge and patch edge (m), average distance from nest to shrub edges and patch edges (m), nest shrub height (m), nest concealment (0–4), and distance from the nest to nearest elevated perch, nearest shrub neighbors, and nearest tree (m). The variables we chose to characterize the general area surrounding the nest and to compare with the overall territory included: total percent cover by all riparian shrub species combined and by height class, percent cover from each riparian shrub species, dominant herbaceous vegetation (forb, grass, sedge, rush), type of water present (oxbow, stream, depression), mean depth of water (m), soil moisture (0–10), and average herbaceous height (m).

We set 12-m transects radiating away from each nest in each of the four cardinal directions (N, S, E, W), with point intercept locations every 2 m and at the nest location itself. Therefore, we recorded data at 25 points for each nest, following the territory scale protocol described above.

Data Screening and Preliminary Analyses

Prior to conducting multivariate analyses addressing each hypothesis, we performed preliminary data exploration (Hosmer and Lemeshow 1989) and removed all variables that were present in less than 5% of cases. We tested the remaining variables for normality using the Kolomogorov-Smirnov test, and then examined for skewness and kurtosis.

To reduce the number of variables included in the following multivariate analyses, for each hypothesis we first examined the results of the t-tests, Mann-Whitney tests, and Chi-Square contingency tables for the appropriate variables. We removed those variables with $P > 0.2$, then conducted bivariate correlations for all remaining variables and removed one variable from each pair with a Pearson's correlation coefficient ≥ 0.80, unless our knowledge of flycatcher biology suggested that both should be included (Hosmer and Lemeshow 1989). We based the selection of which correlated variable to retain on the member of the pair with the smallest P-value derived from t-tests or Mann-Whitney tests. In instances where P-values were similar or equal we retained the variable that we estimated to have the greater biologic importance and/or the one that would be easiest to interpret for management purposes. In addition, to avoid including variables with statistically, but not biologically, significant univariate relationships in our multivariate analyses, we removed variables if the absolute difference between group means was less than 3%. This helped us to protect against multivariate results being skewed by variables with large relative difference but small absolute difference (e.g., a cover variable with values of only 2% and 4% for used and unused sites, respectively), and therefore unlikely to be biologically meaningful. If after using these criteria, the number of variables in the final variable list was still >25% of the sample size included in the analysis, we removed those variables with P-values > 0.1. In the case of very small sample sizes, we considered results to be exploratory in nature (Johnson 1981).

We pooled our data across all years because sample sizes were too small in 1997 to permit statistically valid analyses. Additionally, lumping of years and sites was preferred because our ultimate goal was to build a model describing Willow Flycatcher habitat selection and animal performance at the study area scale (central Sierra Nevada).

Multivariate Analyses

In all but one multivariate analysis (animal performance at the meadow scale), we used forward stepwise logistic regression or logistic regression with forced variable entry. These methods were chosen because they are rigorous even with departures from parametric assumptions, and they allow the inclusion of both continuous and categorical variables in a single analysis (Brennan et al. 1986, Capen et al. 1986, Hosmer and Lemeshow 1989, Norman and Streiner 1994, Zar 1996, Morrison et al. 1998). Variables were entered into the forward stepwise models if the score statistic was <0.05 and removed from the models if the likelihood ratio was >0.10. Models with fewer variables are more likely to be numerically stable, and are more easily generalized than models with many variables (Hosmer and Lemeshow 1989). For this reason we manually restricted the addition of new variables in the stepwise logistic regression process unless the additional variables improved the overall percent correct classification of the model by at least 5%.

To interpret final logistic regression models, we examined the odds ratio of each variable, which indicates how much more, or less, likely it is for the outcome (i.e., occupied or unoccupied) to occur with a one unit change in the independent variable. In cases where a one unit change was thought to be biologically insignificant relative to flycatcher habitat decisions (e.g., a 1% change in shrub cover across an entire meadow), outcomes were also described relative to a 10 unit change.

In examining habitat selection at the three spatial scales, we tested the null hypotheses that selection of meadows, territories, and nest sites for use by Willow Flycatchers was not dependent on hydrologic and vegetative characteristics. For these three tests we compared occupied to unoccupied meadows, territories to adjacent meadow areas, and nest sites to territories, respectively.

Because we had unequal sample sizes for occupied ($N = 20$) and unoccupied meadows ($N = 81$), we first conducted forward stepwise logistic regression analyses on ten equal sample size subsets, by randomly subsampling the larger outcome group (unoccupied meadows). We then determined which variables appeared in the results of more than 50% of the subsets and entered those variables in the final logistic regression using forced variable entry.

To assess animal performance at the territory and nest scales our null hypotheses were that the success of territories and nests was not dependent on the relative abundance of hydrological and vegetative characteristics. For both scales we first used the forward stepwise procedure with the entire territory and nest datasets.

At the territory scale, we included duplicate vegetation data for territories if two years of observation existed. This created some risk of increased error because these two cases were not independent of one another. To check for bias related to non-independence, we used forced entry of the variables selected with the initial forward stepwise logistic regression model, and applied them to two independent samples of the territory data. For those territory locations with observations in multiple years we used only 1998 data for one test and only 1997 data for another test. Data from territory locations with only one year's worth of data (1997 or 1998) were included in both additional tests.

For the nest success analysis, the requirement of independence of all data points was not met because (a) in many cases the same territory produced more than one nest in a given year, and (b) some territory locations, with potentially the same male or female, produced nests in more than one year. For this reason, after building the forward stepwise model we used forced entry of variables to compare the model to those created by using independent subsets that eliminated all renests, and eliminated nests from 1998 or 1997 for those territory locations with two years of data.

To examine animal performance at the meadow scale we used stepwise linear multiple regression to evaluate whether relative abundance of flycatchers was significantly related to any of the biological and physical characteristics of meadows. In this test we used data only from those meadows currently occupied by Willow Flycatchers. Because the r^2 statistic tends to be an over estimate of the population parameter, we used adjusted r^2, which compensates for this optimistic bias (Norusis 1998).

RESULTS

Meadow Scale Habitat Selection

Data screening resulted in 17 variables for inclusion in the logistic regression procedure comparing unoccupied to occupied meadows. When we used these 17 variables to build logistic regression models by subsampling from the unoccupied meadow category, the following 12 physical and biological variables were included in at least one of the 10 models: total amount of riparian shrubs (ha); percent shrub matrix cover; dominance of forbs within the overall meadow (index: 0–4); dominance of grasses or forbs within the shrub matrix only (index: 0–4); shrub foliar density (index: 1–2); prevalence of small braided channels as a watersource (index: 0–2); prevalence of single large channels as a water source (index: 0–2); prevalence of small depressions or oxbows with standing water (index: 0–2); average primary channel width (index: 1–3); and meadow size. Only the first three of these variables were included in at least 50% the models and therefore we entered the three variables into the final logistic regression model.

The logistic regression model found that meadows were 3% more likely to be occupied with each 1% increase in the percent of the site with a riparian shrub matrix; this equals a 30% increase in likelihood of occupancy with a 10% increase in riparian shrub matrix (Table 1). Meadows were 17% more likely to be occupied

TABLE 1. Descriptive Statistics and Logistic Regression Results for Habitat Characteristics Distinguishing Between Meadows Occupied by Willow Flycatchers (N = 20) from Unoccupied (N = 81) Meadows[a]

	Descriptive statistics		Logistic regression			
Habitat variable	Occupied mean ± SD	Unoccupied mean ± SD	Coeff. (B) ± SE	Odds ratio	Wald statistic	P-value
Dominance of forbs within meadow	2.4 ± 0.8	3.4 ± 0.9			11.135	0.011
Forbs—low site dominance[b]						
Forbs—moderately low site dominance			−1.033 ± 1.452	0.36	0.506	0.477
Forbs—moderately high site dominance			−1.919 ± 1.380	0.15	1.934	0.164
Forbs—high site dominance			−5.297 ± 1.868	0.01	8.044	0.005
% riparian shrub matrix	60.3 ± 22.9	40.5 ± 25.3	0.031 ± 0.014	1.03	4.946	0.026
Total ha riparian shrubs	4.8 ± 2.7	3.0 ± 3.6	0.157 ± 0.090	1.17	3.037	0.081
Constant			−1.269 ± 1.541		0.678	0.410

[a] Model X^2 = 36.27, $P < 0.001$, forced variable entry.
[b] Reference category.

TABLE 2. RESULTS OF MULTIPLE REGRESSION COMPARING HABITAT CHARACTERISTICS TO RELATIVE ABUNDANCE OF WILLOW FLYCATCHERS IN OCCUPIED MEADOWS (N = 20)[a,b]

Habitat variable	Coeff. (B) ± SE	P-value
% overstory cover from trees	−0.257 ± 0.039	<0.001
Elevation	0.001 ± 0.001	<0.001
% riparian shrub matrix	0.004 ± 0.001	0.004
Mean riparian shrub height	0.162 ± 0.500	0.005
Constant	−1.423 ± 0.297	<0.001

[a] Forward stepwise multiple regression (entry: 0.05, removal: 0.10).
[b] Model Adjusted R^2 = 0.835, $P < 0.001$.

with each 1 ha increase in absolute area of riparian shrub. Interpretation of the categorical variable related to forb dominance is slightly modified because a reference category (low forb dominance) is involved. Forbs were negatively associated with Willow Flycatcher presence and therefore analysis of odds ratios showed that meadows where forbs had moderately low dominance, moderately high dominance, and high dominance were 2.8, 6.8, and 200 times less likely to be occupied than meadows where forbs had low dominance within the herbaceous layer (Table 1; χ^2 = 36.27, $P < 0.001$). We found that although these variables correctly classified 93% of unoccupied meadows, they only correctly classified occupied meadows 30% of the time; overall percent correct classification for both groups was 80%.

MEADOW SCALE ANIMAL PERFORMANCE

The following nine variables were included in the multiple regression analysis comparing Willow Flycatcher abundance to physical and biological variables in occupied meadows: elevation; mean riparian shrub height; percent overstory canopy cover; presence or absence of tree species other than lodgepole pine (0/1); percent mountain alder cover; sedge dominance within the meadow (index: 0–4); prevalence of lake margins as sources of standing water (index: 0–2); percent riparian shrub matrix cover; and percent of the shrub matrix formed by willow species.

Based on the multiple regression analysis, four variables were significant predictors of Willow Flycatcher relative abundance. Flycatcher relative abundance increased with increasing riparian shrub matrix, mean height of riparian shrubs, and elevation, but decreased with increasing overstory cover from trees (Table 2; Adjusted Model r^2 = 0.835; $P < 0.001$).

TERRITORY SCALE HABITAT SELECTION

Seventeen variables were included in the logistic regression analysis related to territory selection, including: percent *Salix geyeriana* cover in the 1.01–2-m height class; percent *Salix lemmonii* cover in the >2-m height class; percent cover from gooseberry; percent total cover from riparian shrubs (all height classes pooled); mean shrub height; shrub dispersion; percent shrub foliar density in the 0–2-m height class; mean height of herbaceous vegetation; percent cover from grasses, forbs, sedges, and rushes; percent of points dominated by grasses, forbs, and sedges; percent ground cover of standing and running water; and water depth.

In the final model, only total riparian shrub cover was a significant predictor of territory selection. An area was 11% more likely to be a territory for every 1% increase in total riparian shrub cover (Table 3; Model χ^2 = 66.49; $P < 0.001$), or 110% more likely if shrub cover increased by 10%. When examining the ability of this model to correctly predict areas used as territories, we found that total shrub cover correctly classified 80% of adjacent areas and 80% of territories; overall total correct classification was 80%. It is important to note that total shrub cover was highly correlated with two-dimensional shrub cover (r = 0.962, $P < 0.001$), and shrub cover in the 0–1-m (r = 0.912, $P < 0.001$), 1.01–2-m (r = 0.965, $P < 0.001$), and >2-m (r = 0.797, $P < 0.001$) height classes independently; therefore, it is difficult to be certain whether different portions of the shrub layer are more or less important to the species at the territory scale (Bombay 1999).

TERRITORY SCALE ANIMAL PERFORMANCE

Six variables were included in the logistic regression procedure comparing successful to unsuccessful territories: percent herbaceous cover from forbs; percent shrub cover in the >2-m height class; percent total shrub cover (all height classes pooled); percent shrub foliar density in the 0–1-m height class; and water depth for standing water only, and for standing and running water combined. Only total shrub cover was a significant predictor of territory success. With every 1% increase in total shrub cover, territories were 5% more likely to be successful (Table 4; Model χ^2 = 9.908; P = 0.002); a 10% increase in shrub cover improved the likelihood

TABLE 3. Descriptive Statistics and Logistic Regression Results for Habitat Characteristics Distinguishing Willow Flycatcher Territories (N = 66) from Adjacent Meadow Areas (N = 64)[a]

Habitat variable	Descriptive statistics: Territories mean ± SD	Descriptive statistics: Adjacent areas mean ± SD	Logistic regression: Coeff. (B) ± SE	Logistic regression: Odds ratio	Logistic regression: Wald statistic	Logistic regression: P-value
% shrub cover (height classes pooled)	48.4 ± 13.5	22.4 ± 17.1	0.100 ± 0.017	1.11	36.678	<0.001
Constant			−3.465 ± 0.621		31.129	<0.001

[a] Model χ^2 = 66.49, P < 0.001; forward stepwise variable selection.

success by 50%. Using only shrub cover this model correctly classified successful territories 70% of the time and unsuccessful territories 60% of the time; overall percent correct classification was 65%.

Because some territories had two years of data and were therefore represented twice within the preceding test, we repeated the logistic regression on two independent subsets using forced entry of total shrub cover. In subset one, the shrub cover correctly identified 36% of unsuccessful territories and 78% of successful territories, for an overall correct classification rate of 59% (Table 4; Model χ^2 = 2.514; P = 0.113). In data subset two, the original model correctly classified 66% of unsuccessful territories and 72% of successful territories, for an overall correct classification rate of 69% (Table 4; Model χ^2 = 10.481; P = 0.001).

Nest Scale Habitat Selection

Eleven variables were included in the logistic regression procedure comparing nest sites to territories: percent cover from sedges and forbs; percent of herbaceous layer dominated by grasses; percent cover in the 0–1-m shrub height class, and across all height classes (two dimensional); percent foliar density in the 0–1-m shrub height class; mean shrub height; mean shrub dispersion; percent ground covered by running water; and mean standing and running water depths. Only two variables were significant predictors of nest site selection. With every 1% increase in total shrub cover across all height classes (two dimensional), areas were 5% more likely to be nest sites. Nest sites were negatively associated with foliar density within the 0–1-m height class; therefore with each 1% increase in foliar density in the 0–1-m portion of the shrub layer, areas were 12% less likely to be selected as nest sites. (Table 5; Model χ^2 = 32.79; P < 0.001). Together these two variables correctly classified 61% of territories and 75% of nest sites 76%; overall percent correct classification for both groups was 69%.

Nest Scale Animal Performance

Seven variables were included in the logistic regression procedure comparing successful to unsuccessful nests: maximum live height of nest shrub; maximum dead height of nest shrub; mean distance from nest to shrub edge; distance from nest to nearest shrub patch opening; percent foliar density in the 0–1-m height class at the nest; distance from nest to nearest tree; and mean supporting branch diameter. Only distance from nearest tree was a significant predictor of nest success. With every 1 m increase in distance from the nearest tree (which ranged up to

TABLE 4. DESCRIPTIVE STATISTICS AND LOGISTIC REGRESSION RESULTS FOR HABITAT CHARACTERISTICS DISTINGUISHING SUCCESSFUL FROM UNSUCCESSFUL WILLOW FLYCATCHER TERRITORIES USING THE FULL DATA SET AND TWO INDEPENDENT SAMPLES

	Descriptive statistics		Logistic regression			
Habitat variable	Successful mean ± SD	Unsuccessful mean ± SD	Coeff. (B) ± SE	Odds ratio	Wald statistic	P-value
Model A: Full data set (N = 46; 42)[a]						
% shrub cover (height classes pooled)	51.7 ± 14.1	42.7 ± 13.1	0.051 ± 0.017	1.05	8.579	0.003
Constant			−2.310 ± 0.844		7.498	0.006
Model B: Subset 1 (N = 36; 28)[b]						
% shrub cover (height classes pooled)	50.5 ± 13.8	45.2 ± 12.8	0.031 ± 0.020	1.03	2.387	0.122
Constant			−1.213 ± 0.975		1.548	0.214
Model C: Subset 2 (N = 32; 32)[c]						
% shrub cover (height classes pooled)	53.5 ± 12.4	43.1 ± 12.6	0.068 ± 0.023	1.07	8.481	0.004
Constant			−3.279 ± 1.158		8.024	0.005

[a] Model A: X^2 = 9.908, P = 0.002; forward stepwise variable entry.
[b] Model B: X^2 = 2.514, P = 0.113; forced variable entry.
[c] Model C: X^2 = 10.481, P = 0.001; forced variable entry.

500 m), nests were 1% more likely to be successful (Table 6; Model χ^2 = 7.135; P = 0.008); with each 50 m increase, nests were 50% more likely to be successful. Although the model using this variable correctly classified nests as unsuccessful 84% of the time, the correct classification rate for successful nests was only 34%. Overall percent correct classification for both groups was 59%.

Because some nests occurred within the same territory in either the same year, separate years, or both, we repeated the logistic regression test on two independent subsets using forced entry of distance to nearest tree. In subset one, the original model correctly classified 84% of unsuccessful nests and 48% of successful nests, for an overall correct classification rate of 65% (Table 6; Model χ^2 = 10.092; P = 0.002). In data subset two, the original model correctly classified 88% of unsuccessful nests and 50% of successful nests, for an overall correct classification rate of 71% (Table 6; Model χ^2 = 10.897; P = 0.001).

DISCUSSION

We found that Willow Flycatchers showed consistent preference for areas with greater riparian shrub cover at all scales, and in our study area willow made up 85%, 98%, and 99% of riparian shrubs at occupied meadows, territories, and nest sites, respectively (Bombay 1999). Thus, Willow Flycatchers in the Sierra Nevada select meadows with a large proportion of area covered by a riparian shrub matrix, and within these meadows, flycatchers select territories in the areas with the most riparian shrubs. Again, within the constraints of the territory boundaries, flycatchers select nest locations with the highest total shrub cover across all three height classes. Interestingly, riparian shrub cover was also a good indicator of animal performance, and therefore habitat quality at meadow and territory scales. When examining both habitat selection and habitat quality, riparian shrub cover was most highly predictive at the territory scale; in fact, it was the only variable selected at this scale, while at the meadow and nest scale it contributed less towards model fit. Although consistently selected by our models, shrub cover was not the only variable of importance for flycatchers.

MEADOW SCALE HABITAT SELECTION

We found a consistent negative relationship between occupied meadows and the predominance of forbs within the herbaceous layer. The dominance of forbs within Sierra Nevada meadows is often related to lowered water tables, and is considered an indicator of early seral stage, or

TABLE 5. DESCRIPTIVE STATISTICS AND LOGISTIC REGRESSION RESULTS FOR HABITAT CHARACTERISTICS DISTINGUISHING WILLOW FLYCATCHER NESTS (N = 66) FROM TERRITORIES (N = 64)[a]

	Descriptive statistics		Logistic regression			
Habitat variable	Nests mean ± SD	Territories mean ± SD	Coeff. (B) ± SE	Odds ratio	Wald statistic	P-value
Shrub foliar density (0–1.0-m)	40.3 ± 6.5	47.5 ± 10.1	−0.110 ± 0.030	0.90	13.719	0.0002
% shrub cover (across height classes/3-D)	39.8 ± 15.8	31.2 ± 10.3	0.052 ± 0.014	1.05	12.718	0.0004
Constant			3.219 ± 1.340		5.768	0.0163

[a] Model $X^2 = 32.786$, $P < 0.0001$; forward stepwise variable selection.

the result of disturbance caused by human-associated uses (Ratliff 1985, Ratliff et al. 1987; Weixelman et al. 1997, 1999). The positive relationship between riparian shrub cover and Willow Flycatcher occupancy at the meadow scale suggests that a relatively abundant riparian shrub community is important at the meadow scale of habitat selection. This finding agrees with Bent (1942), Grinnell and Miller (1944), King (1955), Serena (1982), Harris et al. (1987), Sedgwick and Knopf (1992), and Sedgwick (2000).

Although our total percent correct classification for the logistic regression model at this scale was 80%, our model's ability to correctly identify occupied meadows was only 30%. This means that although we could identify unoccupied meadows most of the time (93%), we had very inconsistent results in predicting meadows that were selected by flycatchers. This suggests that the Willow Flycatcher population is now at such low numbers that it may not be fully occupying all areas that could support them. Alternatively, these inconsistent correct classification rates could mean that at the scale measured, differences in habitat variables between occupied and unoccupied meadows were not biologically significant.

MEADOW SCALE ANIMAL PERFORMANCE

In addition to more shrub cover, meadows with more Willow Flycatchers were characterized by having taller shrubs and being at higher elevations, compared to sites with fewer flycatchers. Taller shrubs suggest the flycatchers are using sites with more mature stands of riparian shrubs, with less intense grazing pressure or other disturbance factors, and/or sites with better growing conditions. Elevation is more difficult to understand since Willow Flycatchers were known to historically occur at lower elevations within our study area (Ray 1903, 1913; Klebenow and Oakleaf 1984). Perhaps higher elevation sites have undergone less dramatic habitat changes due to fewer types and intensities of human activities. Percent overstory cover from trees had a negative relationship with flycatcher abundance, suggesting that birds settled in greater numbers in broad open meadow systems with little encroachment from lodgepole pine, or with a smaller edge to interior ratio. This could indicate preference for less disturbed meadows with higher water tables, where lodgepole pine do not become established as easily, or wide open floodplain settings where there is less edge per hectare of meadow (Benedict 1984, Ratliff 1985, Kattelmann and Embury 1996, Dull 1999). Because this analysis was based on a small sample size of only 20 occupied meadows, inferences about animal perfor-

TABLE 6. DESCRIPTIVE STATISTICS AND LOGISTIC REGRESSION RESULTS FOR HABITAT CHARACTERISTICS DISTINGUISHING SUCCESSFUL FROM UNSUCCESSFUL WILLOW FLYCATCHER NESTS USING THE FULL DATA SET AND TWO INDEPENDENT SUBSETS

	Descriptive statistics		Logistic regression			
Habitat variable	Successful mean ± SD	Unsuccessful mean ± SD	Coeff. (B) ± SE	Odds ratio	Wald statistic	P-value
Model A: Full data set (N = 44; 43)[a]						
Distance to tree	82.4 ± 101.0	40.4 ± 35.8	0.009 ± 0.004	1.01	4.691	0.030
Constant			−0.500 ± 0.306		2.680	0.102
Model B: Subset 1 (N = 27; 25)[b]						
Distance to tree	113.7 ± 117.8	40.3 ± 37.8	0.014 ± 0.006	1.01	5.166	0.023
Constant			−0.830 ± 0.436		3.620	0.057
Model C: Subset 2 (N = 22; 24)[c]						
Distance to tree	126.4 ± 127.5	40.5 ± 37.8	0.014 ± 0.006	1.01	5.883	0.015
Constant			−1.109 ± 0.449		6.114	0.013

[a] Model A: X^2 = 7.135, P = 0.008; forward stepwise variable entry.
[b] Model B: X^2 = 10.092, P = 0.002; forced variable entry.
[c] Model C: X^2 = 9.869, P = 0.002; forced variable entry.

mance at this scale should be viewed as preliminary (Johnson 1981).

TERRITORY SCALE HABITAT SELECTION

Because flycatchers selected meadows with an extensive shrub matrix and a late seral herbaceous community, territory placement was confined by those conditions. We were surprised to discover that Willow Flycatcher territories did not have significantly more ground covered by water than adjacent areas, though Sedgwick and Knopf (1992) had similar results. Sedgwick and Knopf (1992) postulated that the lack of a significant difference was due largely to the overall mesic nature of the meadows being occupied by Willow Flycatchers. In our study area, occupied meadows had 57% of their area covered by standing water or saturated soils, while territories and comparison transects had 44% and 42% cover from standing water, respectively (Bombay 1999). It is possible that because selected meadows are wet, they are constraining territory choices to areas with relatively uniform mesic conditions.

TERRITORY SCALE ANIMAL PERFORMANCE

Willow Flycatchers selected territories with higher shrub cover than was present in adjacent areas, and within this constraint, territories with the highest levels of shrub cover provided the highest habitat quality. High shrub cover values across territories may allow for a greater choice of possible nest locations, and this could be important when multiple renesting attempts are needed (Martin 1992). Shrub cover and shrub configuration may also have implications relating to nest parasitism or predation, post fledging survival, thermal cover (for nests and adults), foraging efficiency, and territorial defense by males (King 1955, Norman and Robertson 1975, Anderson and Storer 1976, Freeman et al. 1990, McCabe 1991, Martin 1992, Sedgwick and Knopf 1992, Staab and Morrison 1999, Sedgwick 2000, Uyehara and Whitfield 2000). The importance of riparian shrubs to this combination of many life history factors may explain why increased shrub cover predicted increased territory success even though it did not predict individual nest outcomes.

Our ability to predict animal success was best at the territory scale with percent correct classifications for successful territories between 70–78%, and overall percent correct classification between 59–69%. As suggested by Laymon and Barrett (1986), this may indicate that the territory is a better scale for evaluating the physical and biological variables that drive animal performance and therefore habitat quality, particularly when developing management prescriptions.

Although the results varied somewhat between our original territory success model and the models based on two independent subsets, the general pattern of the relationship between successful and unsuccessful territories remained constant. This suggests that the use of the same territory locations by flycatchers between years did not overly bias the original model results.

Nest Scale Habitat Selection

Territory selection constrained nest placement to areas with high shrub cover. We found that two-dimensional shrub cover (percent cover across all height classes) was significantly higher in nest areas than across territories overall (40% and 31%, respectively). The negative association with foliar density (0–1 m) in nest areas is likely due to our observation that the amount of leafy vegetation is decreased in the lower interior portions of large shrub clumps (where nests are frequently placed) due to shading. Placement of nests based on these two variables may help minimize nest predation and parasitism (Sanders and Flett 1989, Martin 1992, Uyehara and Whitfield 2000), and buffer against mean nighttime low temperatures of 2.4°C (June through August, 1997–2001), as well as summer snowstorms and hailstorms (Ingersoll 1913, Sanders and Flett 1989, Western Regional Climate Center 2001).

Nest Scale Animal Performance

Nest success was negatively associated with proximity to the closest tree. This variable was much better at explaining unsuccessful nests than at predicting successful ones. Perhaps nests that are close to trees experience more predation pressure from the combination of meadow and edge predators, while nests far away still have predation from meadow predators, but have lower overall predation pressure without the edge predators (Wilcove 1985, Cain 2001). Additionally, trees may provide locations for visual predators to search for nests (Anderson and Storer 1976, Gates and Gysel 1978, Freeman et al. 1990, Rosenfield and Bielefeldt 1993). These factors may explain why only 59% of the successful nests could be predicted by distance to the nearest tree. Alternatively, poor correct classification rates could mean that at the scale measured, differences in habitat variables between successful and unsuccessful nests were not biologically significant.

Although the results varied somewhat between our original nest success model and the models based on two independent subsets, the general pattern of the relationship between successful and unsuccessful nests remained constant. This suggests that the use of similar nest locations by flycatchers between years and the use of data from multiple nest attempts did not overly bias the original model results.

Our model predicting nest success failed to select any habitat characteristics associated with the area directly surrounding the nest, most notably shrub cover. It is possible that the variables that we choose to measure, or the 12 m area that we examined around the nest site, were not appropriate for the assessment of nest outcome. Another scenario is that nest outcome may be largely affected by the level of chance involved in nest searching by predators, as well as fluctuations in predator populations and weather patterns (Martin 1992). Given this, it may take a larger sample size over more years to differentiate the effects of these variations from those of habitat characteristics.

CONCLUSIONS

Our findings indicate that although the variables we used to describe riparian shrub cover changed between scales (percent shrub matrix within meadow, percent cover within territory, and percent cover within 12 m of nest), shrub cover nonetheless remained linked to Willow Flycatchers across all scales. When considering that riparian shrub cover also predicted flycatcher abundance and territory success at the meadow and territory scales, our confidence in shrub cover as a measure of habitat quality is strong.

Based on the fact that animal performance was predicted by the same characteristic at two spatial scales, one might be inclined to assume that in the case of Willow Flycatchers in the Sierra Nevada, relative abundance alone could indicate habitat quality. Our model of individual nest success, however, did not select a shrub related variable, but rather distance to the nearest tree. Assumptions about habitat quality would be somewhat premature since only two (relative abundance, reproductive success) of Van Horne's (1983) parameters for habitat quality were included in our models. Only when long term results on survival and reproductive trends are applied to a habitat model can we be sure that relying on a single measure of both habitat selection and animal performance is adequate for habitat management of a population at risk (Van Horne 1983).

Although additional information is necessary to fully understand habitat selection and habitat quality issues for Willow Flycatchers, a 10% increase in riparian shrub cover resulted in 30, 110 and 50% increases in the likelihood of a meadow, territory, and nest area being selected by flycatchers, respectively. Additionally, territories were 50% more likely to produce successful nests with each 10% increase in riparian shrub cover. As a result, where the goal is to restore or maintain Willow Flycatcher habitat in montane settings, management efforts that at a minimum provide the conditions necessary for riparian shrub regeneration and recruitment appear warranted at this time.

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