HABITAT USE BY WESTERN POND TURTLES IN THE TRINITY RIVER, CALIFORNIA

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Abstract: Habitat associations of western pond turtles (*Clemmys marmorata*) were examined in a dammed and undammed tributary of the Trinity River in northwestern California to clarify the relations between habitat use and damming. The dammed tributary had more sedimentation, decreased water temperatures, increased canopy cover, and higher water velocities, all of which are potentially relevant to western pond turtles. The overall heterogeneity of aquatic habitats also was lower, possibly because of the dam. At both dammed and undammed sites, western pond turtles appeared to select for deep water with low velocities and the presence of underwater refugia. On the dammed tributary, western pond turtles were associated with basking structures, which may be particularly important because of the low water temperatures. On the undammed tributary, western pond turtles tended to be in slower-flowing portions of the river with denser canopy cover and higher water temperatures. Given the alterations of channel morphology and flow regimes associated with damming, the implications are that habitat suitability for western pond turtles is decreased. While damming may increase the amount of deep water along shores and promote formation of undercut banks, it eliminates low-velocity areas preferred by western pond turtles and lowers water temperatures. Habitat enhancement efforts should focus on restoring natural structura1 and hydrological features.

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Fossil remains suggest western pond turtles have probably existed in the western United States since at least the late Pliocene (Holland 1992). During the past 2-5 million years, this species has persisted through radical changes in the distribution of suitable habitats (Flint 1957, Levins 1968). However, some recent human-induced changes (Lord and Norton 1990), such as the modification of the Central Valley of California for agricultural use, have reduced populations to nonviable levels and thereby caused effective, if not complete, local extirpation (Jennings and Hayes 1994). Other changes have been less deleterious, allowing populations to persist with diminished abundance. Few populations, if any; have densities equivalent to their historic counterparts, and age structures of extant populations tend to be adult biased (Holland and Bury, in press).

Current disturbances with potential effects on western pond turtles include urban development, agricultural development, livestock grazing, gold mining, gravel mining, dams and water diversions, and timber operations. To evaluate the relative severity of these disturbances and to develop mitigition measures, biologists need to understand habitat requirements for this species. Holland and Bury (in press) provided descriptions of aquatic and terrestrial habitats used by western pond turtles, and Bury (1972) provided the only quantitative assessment of habitat associations to date by analyzing the habitat characteristics of Hayfork Creek, California, in relation to turtle abundance. However, his analysis was limited to pools and lacked the multivariate approach necessary to establish context across a range of available habitats. Management will be more effective if understanding of habitat use is broad enough to include the diversity of habitats used by western pond turtles. To predict the effects of proposed alterations, one needs well-delineated ranges of habitat values for microhabitats occupied by this species.

Western pond turtles are generalists relative to most other aquatic turtles, occupying a vari-

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ety of lentic, lotic, and even ephemeral waterways (Stebbins 1985). This flexibility and breadth of habitat use makes the task of quantifying habitat requirements particularly difficult and underscores the need for development of habitat models on an area-specific basis. A model developed at 1 site may not be applicable in another area for this species, particularly if the areas differ substantially in latitude or hydrologic regimes. With these considerations in mind, we initiated a study of habitat use by western pond turtles in the Trinity River Basin.

The mainstem (a dammed site) and south fork (an undammed site) of the Trinity River can be compared on the basis of their close proximity and similar features. Although the 2 sites differ in some geomorphological features such as proportions of confined bedrock versus alluvial channel, they are similar in flow volume, channel size, vegetation, and land-use history (California Department of Water Resources. 1982. South Fork Trinity River salmonid habitat enhancement studies, unpublished report. California Department of Fish and Game, Sacramento, California, USA; Trinity River Restoration Program. 1994. Restoration of the Mainstem Trinity River, unpublished report. U.S. Fish and Wildlife Service, Trinity River Fishery Field Office, Weaverville, California, USA). Comparison of habitat use by western pond turtles at these 2 sites can be used to determine the range and mean value of habitat attributes under different water-velocity regimes, potentially yielding data that provide evidence of, and insights into, shifts in habitat use as a result of dam-related modifications (e.g., Poff et al. 1997).

The Trinity River system is also unique in continuing to harbor relatively large populations of western pond turtles (R.A. Wilson et al. 1991. Trinity River riparian wildlife survey-1990, unpublished report. Trinity River Restoration Project, U.S. Bureau of Reclamation and U.S. Fish and Wildlife Service, Weaverville, California, USA). Evaluations of habitat suitability, particularly those that compare occupied and unoccupied sites, should be conducted in areas that are well-populated by the target species such that sufficient sample size is obtainable. In addition, the density of individuals relative to habitat availability is relevant. If this ratio is low, there is a risk of attributing unoccupied habitat to lack of suitability, when other factors may be responsible (i.e., inaccessibility to colonists or local extinction following a cataclysmic event). A high ratio of turtle density to habitat suitability could also obscure the criteria for suitability to the extent population pressures have forced individuals into marginal habitats.

Our research addressed 3 objectives: (1) available habitat on the mainstem of the Trinity River was compared to available habitat on the south fork site to ascertain whether differences could be detected that might be attributable to the dam; (2) habitat use by western pond turtles on the mainstem and south fork site was evaluated in relation to habitat availability; and (3), applying our knowledge of habitat associations, we hoped to make inferences about the consequences of dam-related alterations for western pond turtles.

STUDY AREA

Damming of the mainstem in 1963 resulted in numerous habitat alterations that included expansion and encroachment of riparian vegetation in response to absence of scouring flows during winter. A Geographic Information System (GIS) analysis found that riparian cover nearly tripled during the 27 years subsequent to dam construction (R. A. Wilson. 1993. Trinity River riparian vegetation mapping, unpublished GIS report. U.S. Bureau of Reclamation and U.S. Fish and Wildlife Service, Weaverville, California, USA). The established riparian vegetation traps sand and has promoted development of berms in the riparian corridor. Thus, the river has become channelized and has changed to a narrow, trapezoidal shape; shallow, edgewater habitats were replaced by deep, swift waters (Hampton 1995). Also, due to the reduction in winter flows, seasonally flooded marshes have been eliminated, and annual sediment transport is reduced such that pools have been filled with fine sediments (Petts 1984, Wilhams and Wolman 1984, Hampton 1995).

In contrast, the south fork site is likely to resemble the mainstem prior to the dams. The annual flow of the south fork site is approximately 1.1 million acre-feet (California Department of Water Resources. 1982. South Fork Trinity River salmonid habitat enhancement studies, unpublished report. California Department of Fish and Game, Sacramento, California, USA), while mainstem annual flow prior to the dam was approximately 1.2 million acre-feet (Trinity River Restoration Program. 1994. Restoration of the Mainstem Trinity River, unpub-

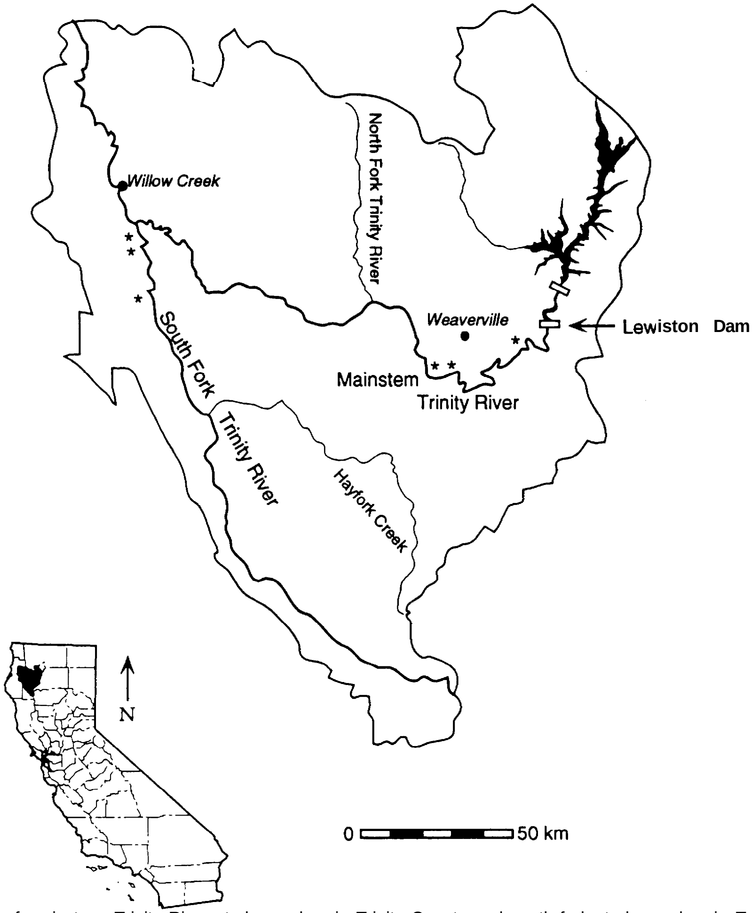

Fig. 1. Locations of mainstem Trinity River study reaches in Trinity County and south fork study reaches in Trinity and Humboldt counties, California (adapted from unpublished U. S. Fish and Wildlife Service figure). Reach locations are indicated with stars.

lished report. U.S. Fish and Wildlife Service, Trinity River Fishery Field Office, Weaverville, California, USA). Wide, shallow-water gravel bars alternate with riffles and deep pools on the south fork site, and mature riparian vegetation occurs in small patches on the outside of each riverbend. Because both shallow riparian edgewater areas and deep pools have been attenuated due to the dam, the mainstem is probably more homogeneous now than historically. Hence, depending on the magnitude of other site differences (unrelated to the dam), the south fork site may be more heterogeneous than the mainstem, and habitat use by western pond turtles on the south fork site might reflect selection from a larger variety of available habitat.

We gathered data along the mainstem and south fork site of the Trinity River in conjunction with mark-recapture sampling conducted during May-August 1993 (Reese 1996). We examined 3 study sites (stream reaches), each approximately 3 km in length. Stations were placed at intervals of approximately 250 m along each reach to provide a more fine-grained resolution system (Reese 1996). The mainstem reaches were between the Lewiston Dam and the confluence with the North Fork Trinity River, while the south fork site reaches were upstream and within 15 km of the confluence with the mainstem (Fig. 1). We chose reaches that contained a range of turtle densities, which implied a range of habitat conditions. The sampled reaches differed with respect to human settlement, width of valley floor, and density of riparian vegetation. The south fork reaches were all undammed and consequently were subject to natural flow regimes and fluvial processes.

METHODS

We collected habitat data during 2 mark-recapture sampling sessions at the mainstem site and 2 similar samplings at the south fork site in 1993. Turtles were captured underwater by snorkelers who searched the submerged banks and river bottom both manually and visually (Reese 1996). We measured habitat characteristics the first time each turtle was captured during the year. A floating rectangular quadrat measuring 3 x 6 m and divided into 9 subquads (1 x 2 m) was laid on the water surface with its center over the location where the animal was first sighted before capture, with the long side of the quadrat parallel to shore. The quadrat size was chosen with the intent of circumscribing the aquatic habitat flow types associated with western pond turtle locations; stretches of >6 m of shoreline tended to contain multiple flow types (e.g., pool, riffle, glide; for definitions see Reese 1996). Casual examination in the field revealed that a 6-m stretch of shoreline tended to contain only 1 or 2 habitat types but was long enough to accommodate basking logs and other large features.

We measured the following features within quadrats: shoreline vegetation type, flow types along a transect across the river, flow type in each subquad, water velocity, water depth, presence of basking sites, presence of cover objects, degree of bank undercut, water temperature, and percent canopy cover (for definitions and calculations of indices see Reese 1996). Some measured features yielded multiple variables for analysis. For example, because Bury (1972) indicated deep water might be important for western pond turtles, we used a "maximum depth" variable (maximum value of the 9 subquads) in addition to the "mean depth" variable. Because of an indication that slow-flowing water might be preferred (Bury 1972; Holland and Bury, in press), we used a "minimum flow" variable. Finally, because bank undercuts frequently serve as turtle refugia, and deeper undercuts may be more protective, we used a "maximum undercut" variable in addition to a "mean undercut" variable.

For every capture where a quadrat was characterized, we also characterized a random quadrat intended to represent the available habitat at each river site. We set the number of random quadrats to equal the number of individual captures within each sampled reach. We determined the placement of each random quadrat by using random numbers to select a survey station, a distance from the station, a direction (upstream or downstream), and a distance from shore. At both study sites, we constrained the distance from the station to 0-100 m so as to cover as much area as possible without overlap of downstream measurements from 1 station and upstream measurements from the next. The distance from shore was constrained to 0-4.0 m to match the actual area searched for turtles (Reese 1996). High-gradient riffles were excluded from the search effort because they were not safely swimmable by divers. However, riffles were not likely to harbor western pond turtles (personal observations; Holland and Bury, in press); hence, random quadrats that landed in riffles were removed and another set of random coordinates generated.

Comparison of Available Habitat on the Mainstem and South Fork Site

To compare habitat heterogeneity between the mainstem and south fork site, we examined the ranges of measured habitat variables. We predicted ranges of values for the south fork site would be larger, particularly for those variables likely affected by damming (i.e., mean water velocity, mean depth, water temperature, canopy cover). We examined the respective variabilities via principal component analysis (PCA) of all continuous variables. If necessary, variables were transformed to meet assumptions of normality. We then pooled mainstem values with south fork site values to create a single dataset for PCA (n = 177). We used the correlation matrix for the PCA, followed by a varimax rotation to achieve the best relative fit of the factors. We plotted the first 2 principal component factors (those representing the greatest variance) against each other and fitted the minimum convex polygon to the set of points for each site (see James and McCulloch 1990), which facilitated comparison of the spread of factor values at each site; a larger polygon indicated greater overall variability in habitat.

We used Hotelling's T^2 to determine whether available habitat on the mainstem differed from available habitat on the south fork site. Four of 93 quadrats on the mainstem and 1 of 84 quadrats on the south fork site had missing values for $\geq$1 variable(s) and were omitted from the analysis. To ascertain which variables caused the difference between sites in the multivariate model, we conducted individual *t*-tests (or Wilcoxon signed rank tests, depending on the distribution of each variable). The significance level was set at α = 0.05. The α was adjusted for multiple tests with the Bonferroni inequality (Stevens 1986). In this case, 13 variables were tested for differences between sites; thus, α = 0.05 was adjusted to α = 0.004. For *t*-tests of individual variables, we used the maximum number of quadrats (mainstem: *n* = 89-93; south fork site: *n* = 83 or 84).

Comparison of Habitat Use to Availability

For each study site, we used discriminant analysis (DA) to ascertain whether turtle-use quadrats could be distinguished from random quadrats on the basis of the measured habitat characteristics, testing the null hypothesis that turtles use habitat in proportion to availability. The DAs were accompanied by the Wilk's lambda test statistic, which identifies multivariate differences between means. Although many habitat characteristics varied daily and seasonally (e.g., water temperature, water velocity), concurrent measurements at capture sites and random sites allowed comparison of habitat values.

Prior to the DA, we used correlation analysis to identify redundancies among variables, especially those known to have a close relation (i.e., mean and maximum values of a habitat characteristic). If 2 variables were highly correlated ($r \leq$ -0.75 or $r \geq 0.75$) and both entered the model, we retained the variable that contributed the most discriminatory power. We used a stepwise procedure to select the subset of original variables most useful for discriminating random sites from those with turtles. Significance was α = 0.10 for entry of variables into the model because the moderate α protides a criterion more appropriate for the detection of ecological trends (Toft and Shea 1983, Toft 1991). In applied situations related to management of ecological systems, a Type II error is often more tangible and costly than making a Type I error (Toft and Shea 1983, Schrader-Frechette and McCoy 1993). A moderate significance level allows for more variables to enter each model and thus provides the best discriminatory power given a limited sample size (Costanza and Afifi 1979).

Where variables were nonnormally distributed, even after transformation, we conducted a nonparametric DA (kernel method; SAS 1989). We estimated kernel density via the Epanechnikov kernel, which is optimum in the sense of minimizing the smallest mean integrated square error achievable (Silverman 1986). This approach permits less rigid assumptions about the distribution of the observed data. The smoothing parameter (h) was chosen to minimize the mean square error, assuming a multivariate normal distribution (Silverman 1986). We allowed band widths to differ between the 2 groups (turtle, random). For parametric DAs, we used Bartlett's modification of the likelihood-ratio test (SAS Institute 1989) to test for heterogeneity among variance-covariance matrices, setting α = 0.05. Where matrices were heterogeneous, we generated quadratic as opposed to linear discriminant functions. For the DA, we substituted mean values for missing values for ≥ 1 variable(s) in 4 of 93 quadrats on the mainstem and 1 of 84 quadrats on the south fork site.

We used a jackknife procedure to evaluate the classification success of the parametric and nonparametric models (SAS Institute 1989). Cohen's Kappa (Titus et al. 1984) was then computed for each test to compare the classification success to chance. The significance level for performance was set at α = 0.05. Standardized structure coefficients are presented to indicate the relative contribution of each variable to the canonical discriminant function (Rencher 1992).

The DA was not suitable for examination of the noncontinuous variable, shoreline vegetation. Hence, the relation of shoreline vegetation to study site (mainstem or south fork site) was examined via a Pearson chi-square contingency table analysis (SAS Institute 1989). We tested the null hypothesis that study sites were indistinguishable with respect to distribution of vegetation types. We also examined the relation of vegetation to turtle-use quadrats versus random quadrats at each study site. The null hypothesis was that sites used by turtles have the same distribution of vegetation types as the overall distribution of vegetation types along the river. Where a relation emerged (P < 0.05), we then subdivided contingency tables into simpler 2 X 2 tables to ascertain where the significant differences in the table occurred (Zar 1984). We omitted from analysis 3 of 93 quadrats on the mainstem and 1 of 84 quadrats on the south fork site that had missing values for ≥ 1 variable(s). In addition, the unvegetated quadrats

Table 1. Range of values of random habitat measurements from the mainstem (n = 93) and south fork (n = 84) Trinity River, 1993.

Habitat feature	Minimum value		Maximum value		Range	
	Main	South	Main	South	Main	South
River transect (index)	135	120	370	380	235	260
Flow type (index)	1.0	1.0	3.8	4.0	2.8	3.0
Mean water velocity (m/sec)	- 17.7	-10.1	110.0	119.4	127.7	129.5
Mean water depth (cm)	11.7	2.2	236.1	200.0	224.4	197.8
Baskable bank (%)	0	0	44	44	44	44
Underwater cover (%)	0	0	100	100	100	100
Sand cover (%)	0	0	100	100	100	100
Water temperature (°C)	10	16	18	15	8	9
Canopy (%)	16.0	16.0	100.0	63.9	84.0	47.9
Small bask sites (index)	0.0	0.0	89.0	87.0	89.0	87.0
Large bask sites (index)	0.0	0.0	4.3	3.7	4.3	3.7
Mean undercut (cm)	0.0	0.0	53.3	23.3	53.3	23.3

were excluded from the mainstem analysis because this condition was uncommon along these reaches, and these cell counts for both quadrat types were negligible.

RESULTS

We captured 93 western pond turtles on the mainstem and 84 on the south fork site during the 1993 season, and we took 84 random quadrat measurements at each site. Two pairs of habitat variables were highly correlated (mean water velocity and flow index, maximum depth and mean depth), which were expected due to their close relations. We retained the single variable from each of these pairs with the best discriminatory power (see below).

Comparison of Available Habitat on the Mainstem and South Fork Site

The ranges of habitat values were greater at the mainstem study site for some variables and

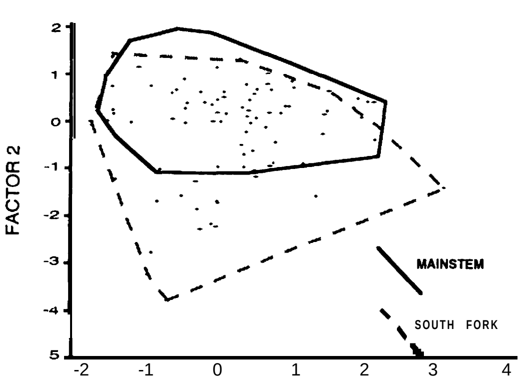

Fig. 2. Scatterplot of the first 2 principal components derived from measurements of habitat from the mainstem and south fork sites, Trinity River, 1993. Polygons represent the minimum convex polygon for each group.

greater at the south fork site for others (Table 1). Specifically, the mainstem site had a greater range of depths, canopy cover, basking sites, and undercuts. For all 4 of these variables, the greater range resulted primarily from greater maximum values on the mainstem. The south fork site had a greater range of flow types and water temperatures. The within-covariance matrices for the mainstem and south fork site random quadrats were different (χ^2_{10} = 78.04, $P <$ 0.001), indicating a difference in variability of the habitat values. The PCA of habitat values from the 2 study sites combined (n = 177) yielded 4 factors with eigenvalues >1. Factor loadings after varimax rotation indicated the first factor consisted primarily of flow index, average velocity, and river transect (Reese 1996); factor 2 was composed of the 2 depth measurements (mean, maximum). Factor 3 consisted of canopy cover, baskable bank, and water temperature (the last with a negative loading). Factor 4 included underwater cover, minimum flow, and sand (the later 2 with negative loadings). The first 2 factors explained 63% of the total variance in the dataset, and plotting these first 2 factors against each other revealed the south fork site was overall more heterogeneous with respect to the measured habitat characteristics than the mainstem site (Fig. 2). The south fork site differed from the mainstem with respect to mean values of the habitat characteristics (Hotelling's T^2 = 3.21; $F_{12,\ 159}$ = 42.49, P < 0.001). Mean water velocity, maximum water depth, and maximum undercut were excluded from analyses, because of their strong correlations to other variables (minimum water velocity, mean water depth, mean undercut). Of the

Table 2. Aquatic habitat variables at the mainstem and the south fork Trinity River, 1993. Mean and standard error are shown in actual measured units, although some variables were transformed prior to analysis.

Habitat characteristic[a]	Mainstem sites (n = 93) $\bar{x}$	SE	South fork sites (n = 84) $\bar{x}$	SE	Significance test results t	df	P
River transect (index)	212.6	4.0	201.4	5.7	2.20	147	0.030
Flow type (index)	1.8	0.1	1.6	0.1	1.90	175	0.060
Minimum water velocity (m/sec)	5.1	1.9	2.1	1.4	4.07	175	<0.001
Mean water depth (cm)	79.8	4.1	53.5	4.5	5.32	136	<0.001
Baskable bank (%)	10.3	1.6	8.8	1.6	0.65	174	0.517
Underwater cover (%)	27.3	3.0	26.1	3.4	0.51	175	0.609
Sand cover (%)	23.6	3.5	11.1	2.6	2.84	169	0.005
Water temperature (°C)	14.2	0.2	18.9	0.2	-17.72	164	<0.001
Canopy (%)	56.2	3.0	16.3	1.7	11.22	127	<0.001
Undercut (cm)[b]	7.9	1.2	1.6	0.5	-5.15	177	<0.001
Small basking sites (index)[b]	19.9	2.2	0.2	0.0	-5.82	177	<0.001
Large basking sites (index)[b]	0.2	0.1	0.5	0.1	0.92	177	0.354

[a] Hotelling's T^2 = 3.217; $F_{12, 159}$ = 42.49, P < 0.001 for the complete model.
[b] Habitat characteristics which did not meet the assumptions for parametric t-test; reported values are Z-scores for Wilcoxon 2-sample test (therefore n is reported in place of df) and is riot included in Hotelling's T^2.

13 variables remaining, 6 showed significant differences between the mainstem and the south fork site (Table 2). Water temperatures were 25% lower, bank undercuts 394% larger, and canopy cover 245% denser at the mainstem site. This site also had 49% deeper water and 143% higher minimum water velocities. There were more small basking objects at the mainstem site.

Shoreline vegetation type was associated with site (χ^2_3 = 78.73, P < 0.001; Fig. 3A). Thus, we rejected the null hypothesis that sites had identical distributions of vegetation. The frequencies of occurrence among vegetated types (Pacific willow [*Salix lasiandra*], white alder [*Alnus rhombifolia*], etc.) were not different (mature vs. immature: χ^2_1 = 0.14, P = 0.714; mature vs. mixed: χ^2_1 = 0.76, P = 0.384). The difference occurred between the vegetated and unvegetated types (i.e., gravel bar: χ^2_1 = 45.76, P < 0.001). Most of the south fork site samples were adjacent to unvegetated gravel bars, while the shoreline of nearly all mainstem samples had some riparian vegetation.

Comparison of Habitat Use to Availability on the Mainstem

For the mainstem DA, all measured variables met the assumption of normality and were ineluded in the stepwise process. The DA revealed turtle-use quadrats and random quadrats could be distinguished on the basis of habitat characteristics. The model that emerged was quadratic and was composed of the following variables: small basking sites, flow index, minimum water velocity, underwater cover, water depth, and baskable bank (Table 3). Specifically, there were more small basking structures and more baskable bank at turtle capture locales than at random locales. There were lower flow types and a lower minimum water velocity in turtle quadrats, and there were more underwater cover objects and deeper water in turtle quadrats than in random quadrats. This model was a highly significant discriminator between capture locales of western pond turtles and generally available habitat along the mainstem (Table 3). The jackknife procedure classified 80% of the observations correctly, and significantly better than chance (Cohen's kappa = 0.60, P < 0.001; Table 3).

Presence or absence of turtles in a quadrat on the mainstem was associated with shoreline vegetation (χ^2_2 = 6.80, P = 0.033; Fig. 3B). Turtles were found adjacent to immature and mixed assemblages in proportion to availability of these vegetation types (χ^2_1 = 0.04, P = 0.845); the mature vegetation type generated the significant difference (mature vs. mixed: χ^2_1 = 4.15, P = 0.033; mature vs. immature: χ^2_1 = 5.68, P = 0.017). Specifically, the random quadrats were most often adjacent to mature riparian vegetation (white alder-Fremont cottonwood [*Populus fremontii*] assemblages), while turtle-use quadrats were most often adjacent to immature riparian assemblages (Pacific willow dominant).

Comparison of Habitat Use to Availability on the South Fork Site

For the south fork site DA, the following variables (after transformation) did not meet

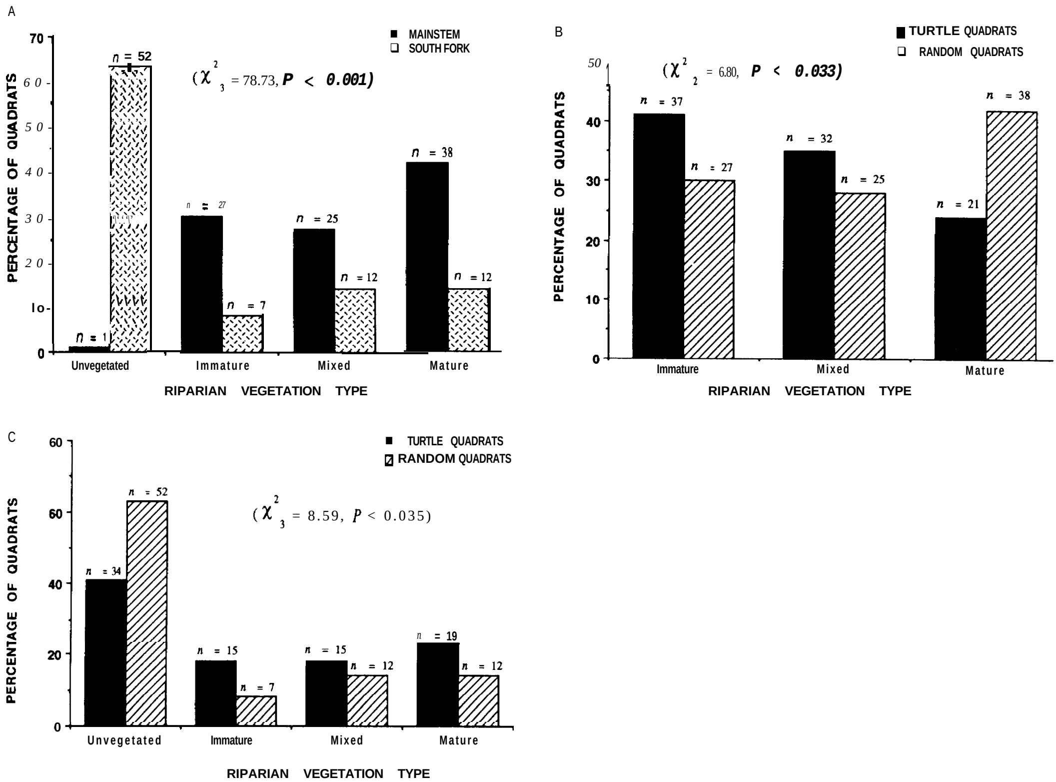

Fig. 3. (A) Distribution of random quadrats across shoreline vegetation types at the mainstem and south fork sites, Trinity River, 1993 (n = no. of quadrats). (B) Distribution of turtle habitat quadrats and random habitat quadrats across shoreline vegetation types at the mainstem Trinity River in 1993 (n = no. of quadrats). (C) Distribution of turtle habitat quadrats and random habitat quadrats across shoreline vegetation types at the south fork site Trinity River in 1993 (n = no. of quadrats).

Table 3. Two-group stepwise discriminant analysis of available habitat and used habitat for western pond turtles at the mainstem Trinity River, 1993. Means and standard error are in nontransformed units, although some variables were transformed prior to analysis. Standardized structure coefficients are presented for variables that entered the final model.[a] The final model had heterogeneous variance-covariance matrices.

Habitat characteristic	Turtle sites (n = 93) $\bar{x}$	Turtle sites SE	Random sites (n = 93) $\bar{x}$	Random sites SE	Standardized structure coefficient
River transect (index)	198.3	4.4	212.6	4.0	
Flow type (index)[b]	1.4	0.0	1.8	0.1	-0.307
Minimum water velocity (m/sec)	-1.3	1.0	5.1	1.9	-0.2615
Mean water depth (cm)[c]	88.8	4.3	79.8	4.1	+0.324
Maximum water depth (cm)[c]	128.5	5.1	110.5	5.3	
Baskable bank (%)	17.1	1.6	10.3	1.6	+ 0.322
Underwater cover (%)	50.5	3.2	27.3	3.0	+ 0.293
Sand cover (%)	24.9	3.7	23.6	3.5	
Water temperature (°C)	14.2	0.2	14.2	0.2	
Canopy (%)	66.3	2.8	56.2	3.0	
Small basking sites (index)	49.6	3.3	19.9	2.2	+0.637
Large basking sites (index)	0.8	0.1	0.2	0.1	
Mean bank undercut (cm)	11.0	1.7	7.9	1.2	
Maximum bank undercut (cm)	20.7	3.4	14.5	2.1	

[a] Wilk's Lambda = 0.597; $F_{1,185}$ = 18.68, P < 0.001; Jackknife success (%) = 80; Cohen's Kappa = 0.60, P < 0.001 for the complete model.
[b] Correlated with mean water velocity, which was removed from the model.
[c] Correlated pair, only mean water depth entered the model.

Table 4. Two-group nonparametric discriminant analysis of available habitat and used habitat for western pond turtles at the South Fork Trinity River, 1993. Standardized structure coefficients are presented for those variables that entered the model.[a]

Habitat characteristic	Turtle sites (n = 84) $\bar{x}$	Turtle sites SE	Random sites (n = 84) $\bar{x}$	Random sites SE	Standardized structure coefficient
River transect (index)	148.0	5.0	201.4	5.7	-0.318
Flow type (index)[b]	1.1	0.0	1.6	0.1	-0.311
Mean water velocity (m/sec)[b]	2.1	0.6	14.5	2.2	
Minimum water velocity (m/sec)	-1.9	0.5	2.1	1.4	
Mean water depth (cm)[c]	109.6	8.3	53.5	4.5	
Maximum water depth (cm)[c]	161.9	11.2	80.9	5.6	+0.411
Baskable bank (%)	12.7	1.9	8.8	1.6	
Underwater cover (%)	46.5	3.9	26.1	3.4	+0.483
Sand cover (%)	31.4	4.3	11.5	2.4	
Water temperature (°C)	20.2	0.3	18.9	0.2	+0.438
Canopy (%)	27.9	2.2	16.3	1.7	+0.313
Small basking sites (index)	0.3	0.1	0.2	0.1	+0.182
Large basking sites (index)	1.1	0.4	0.5	0.1	
Maximum bank undercut (cm)	5.3	1.5	4.1	1.4	+0.194

[a] Wilk's Lambda = 0.545; $F_{1,167}$ = 22.38, P < 0.001; Jackknife success (%) = 73; Cohen's Kappa = 0.46, P < 0.001 for the complete model.
[b] Correlated pair, of which only flow type entered the model.
[c] Correlated pair. of which only maximum water depth entered the model.

the assumption of normality required for the model: undercut, maximum undercut, small basking sites, and large basking sites. All 4 variables had high percentages of zero values (i.e., undercuts and basking sites were infrequent). A nonparametric DA (Epanechnikov kernel; h = 2.38) revealed turtle-use quadrats and random quadrats could be distinguished via the following habitat characteristics: river transect, underwater cover, canopy cover, small basking sites, water temperature, flow type, maximum water depth, and maximum bank undercut (Table 4). Specifically, the river transect and the habitat quadrats were composed of slower flow types at turtle locales than at random locales. There were more underwater cover objects, more basking sites, and deeper maximum undercuts in turtle quadrats. Turtle quadrats also had higher water temperatures, deeper water, and more canopy cover than random quadrats. This model was a highly significant discriminator between turtle capture locales and available habitat along the south fork site (Table 4). The jackknife procedure classified 73% of the observations correctly, and significantly better than chance (Cohen's kappa = 0.46, P < 0.001; Table 4).

Shoreline vegetation on the south fork site was different between turtle-use and random quadrats (χ^2_3 = 8.59, P = 0.035; Fig. 3C). The significant chi-square value was attributable to the unvegetated habitat type (grave1 bar) occurring with greater frequency than other types (χ^2_2 = 8.20, P < 0.017). Specifically, turtle-use quadrats were less frequently associated with unvegetated habitat than were random quadrats.

DISCUSSION

Habitat Use

On both the mainstem and the south fork site, the lower water velocities, deeper water, and more abundant underwater refugia of turtle-use quadrats compared to random quadrats was consistent with our observation that western pond turtles are relatively poor swimmers that rely on crypsis and use of refugia to escape from predators (see also Holland and Bury, in press). Use of deep pools with large woody debris, which provides cover, is Iikely to decrease the chance of turtles being detected by aquatic predators such as river otter *(Lutru canadensts)* and mink *(Mustela vison)*. These findings underscore the importance of maintaining deep, pooled habitats for this species on the Trinity River. Although deep waters have increased through damming of the mainstem, the trapezoidal shape of the channel promotes high velocities (Hampton 1995) that are likely to have reduced habitat suitability for western pond turtles.

The finding that turtles used areas containing more small basking objects and, on the mainstem, more baskable bank than randomly available indicates the importance of basking. Basking structures are critical for thermoregulation by turtles, particularly when water temperatures are low (Boyer 1965, Brattstrom 1965, Lefevre and Brooks 1995). Low water temperatures can mean turtles must spend more time basking to maintain body temperatures where physiological processes and resulting energetics are adequate for normal life functions like foraging, predator avoidance, and reproduction (see Lefevre and Brooks 1995). Consequently, stable and low water temperatures, like those produced by the dam, can have profound effects on the overall fitness of individual turtles and may ultimately influence the stability of the entire population. At the south fork site, basking structures are more scarce but may be less critical because of the higher water temperatures. The lower relative contribution of basking sites to the south fork model (compare standardized structure coefficients) supports this assertion.

The emergence of denser canopies as discriminators of habitat used by turtles at the south fork site may indicate vegetation canopy cover is important to western pond turtles. The result of the shoreline vegetation analysis shows that turtle locales were more frequently associated with vegetated banks than expected from availability. Areas of denser canopy could provide protection from predators (e.g., raccoons *[Procyon lotor]*, coyotes *[Canis latrans]*, and humans), whether via decreased accessibility (rock faces), decreased visibility (vegetation barriers), or increased camouflage (dappled shade). The conditions of patchy sunlight generated by vegetation cover may also moderate incidental solar radiation and allow turtles to thermoregulate effectively via small shifts in body position (Holland 1985).

Canopy cover at the mainstem site may not have emerged as a variable distinguishing turtle-use quadrats from random quadrats, because dense canopy was so widespread that it did not limit turtle distribution. The results of the shoreline vegetation analysis for the mainstem support this assertion. Nonvegetated shorelines were nearly absent, and turtles were associated more frequently with immature riparian vegetation than with mixed or mature types. Western pond turtles apparently select a moderate condition between the extremes of unvegetated gravel bars and advanced-stage riparian vegetation.

The significance of water temperature as a variable defining habitat used by turtles on the south fork site is unclear. Despite the colder water on the mainstem, turtle distribution appeared related to water temperature only on the south fork site. Perhaps there exists so little variation in temperatures along the mainstem that temperature is not useful for predicting turtle presence. Scarcity of basking structures on the south fork site also may force aquatic basking (see Holland and Bury, in press) such that turtles are more dependent on warm waters at this site. This issue certainly warrants further research. Finally, the emergence of the river transect and undercut variables in the south fork model indicates turtles used sections of the river with lower water velocities, deeper bank undercuts, or both, which are characteristics likely to provide refugia.

Effects of Damming

Dams and water diversions on rivers fragment aquatic habitat directly by acting as barriers to migration and indirectly by creating patches of unsuitable habitat (Petts 1984, Poff et al. 1997). The latter appears to have occurred on the mainstem Trinity River, where significant habitat alterations have occurred downstream of the Lewiston and Trinity River dams (J. F. Evans. 1980. Evaluation of riparian vegetation encroachment-Trinity River, California, unpublished report 0520-R5-78. U.S. Forest Service, Trinity River Basin Fish and VVildlife Task Force, Weaverville, California, USA). Such habitat fragmentation can increase stress on populations of species already reduced in number. Stretches of such unsuitable habitat are likely, on a large scale, to reduce the continuity of western pond turtle populations. For exampIe, impoundments on streams inhabited by the flattened musk turtle *(Sternotherus depressus)* in Alabama created areas of deep lentic waters not only unsuitable for this species, but impoundments also served to segregate the suitable habitat on either side of streams. Due to increased isolation, these musk turtle populations were then potentially subject to numerous threats including loss of genetic variability, abnormal population structure, stochastic factors, and susceptibility to disease (Dodd 1990).

Our analysis of available habitat on the 2 study sites is consistent with previous accounts of dam-related changes in habitat along the mainstem Trinity River (Hampton 1995). Relative to the south fork site, the mainstem has denser shoreline canopy cover, a result consistent with known encroachment of riparian vegetation onto previously unvegetated gravel bars. Indeed, analysis of shoreline vegetation confirmed random mainstem quadrats were significantly more likely to be vegetated than random quadrats at the south fork site. Vegetation promotes formation of berms that are then subject to undercutting, which creates the deeper undercuts along the mainstem channel. The higher minimum water velocities and mean water depths at the mainstem site are probably attributable to the elimination of slow-flowing edge-water habitats on this fork. By definition, a more trapezoidal channel has deeper water adjacent to the shoreline. The cooler mainstem water may be the result of artificial flow regimes associated with the dam, which have caused substantial decreases in summer water temperatures (U.S. Fish and Wildlife Service. 1995. Unpublished data from Trinity River flow evaluation, water years 1942-1946, 1959-1961, 1964-1983, 1987-1992. Lewiston gauging station, mainstem Trinity River, Trinity County, California, USA). Outflow is released from the base of the reservoir, thereby tapping deep, cold water instead of the warm upper layer. Also, the greater abundance of small basking material on the mainstem is likely related to the patches of woody debris that accumulate from dense shoreline vegetation without natural flushing flows.

The difference in heterogeneity of depth, canopy cover, undercut, and basking sites between the mainstem and south fork site was primarily attributable to higher maximum values of these variables at the mainstem site. These higher values may be the consequence of decreased water volume and lack of seasonal flushing flows on the mainstem (see above). The smaller range of water velocities and temperatures in the mainstem are consistent with the postulated decrease in heterogeneity of aquatic habitats. A natural alternation of pools and riffles is more likely to provide a wide variety of water velocities and temperatures than a straightened, trapezoidal channel. Indeed, overall heterogeneity was higher on the undammed south fork site, as we hypothesized.

MANAGEMENT IMPLICATIONS

These results serve to clarify aquatic habitat use by this cryptic species in the Trinity River basin. Favorable western pond turtle habitat is characterized by deep, slow-flowing pools with underwater cover and emergent basking sites, warm water, or both. Although dams increase the amount of deep water and promote formation of undercut banks, they compromise habitat suitability by eliminating slow-flowing water and lowering water temperatures. Given that deep water with refugia is available in a naturally flowing river as part of dynamic channel morphology, dams are likely to decrease overall habitat suitability for western pond turtles. There is evidence that changes in the mainstem Trinity River as a result of damming may have affected recruitment of juveniles, which are particularly dependent on slow-flow areas (Reese 1996, Reese and Welsh 1998). Some of the effects of altered flow regimes we did not address (i.e., sedimentation) may prove beneficial in the short run (e.g., by providing substrate that turtles burrow into for cover), but detrimental in the long run (e.g., by filling deepwater pools and crevices, which reduces cover and interstitial invertebrate fauna; Holland and Bury, in press).

Managing land to promote western pond turtle survival throughout its range has become increasingly important as this species experiences local extirpations and range contractions (Holland and Bury, in press). Our results suggest managers should focus on preserving and restoring structural features such as cover objects and basking logs on riverine systems. They also should work to maintain natural flow regimes with their associated consequences for water temperatures, water velocities, and water depths (Poff et al. 1997). Future research should consider the potential of fisheries mitigation measures (e.g., artificial high flows, mechanical manipulations of shorelines) to enhance habitat suitability for western pond turtles on the Trinity River.

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