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Vegetation Patterns and Abundances of Amphibians and Small Mammals Along Small Streams in a Northwestern California Watershed

Abstract

Our goal was to describe and evaluate patterns of association between stream size and abundances of amphibians and small mammals in a northwestern California watershed. We sampled populations at 42 stream sites and eight upland sites within a 100-watershed in 1995 and 1996. Stream reaches sampled ranged from poorly defined channels that rarely flowed to 10-m-wide channels with perennial flow. The majority of reaches flowed only intermittently. Aquatic vertebrates were sampled by conducting area-constrained surveys, and terrestrial vertebrates were sampled along three 45-m-long transects using cover boards, drift fence/pitfall trap arrays, and two types of live trap. Vegetation characteristics were strongly associated with measures of stream size, especially channel width. Compared to upland sites, mean numbers of plant species in the herbaceous layer were significantly greater along streams with active channel widths as small as 0.9-1.3 m. Larval Pacific giant salamanders (*Dicamptodon tenebrosus*) were found only in stream reaches with continuous flow or in channels ≥2.4-m wide, and larval tailed frogs (*Ascaphus truei*) were found only at sites with continuous or nearly continuous flow. Allen's chipmunks (*Tamias senex*) and deer mice (*Peromyscus maniculatus*) occurred at nearly every site sampled but were more abundant at reaches along larger streams than at reaches along smaller streams or at upland sites. None of the vertebrate species evaluated was significantly associated with intermittent streams having channels less than about 2-m wide and drainage areas less than about 10 ha. Our results provide additional information on the ecological role of small, intermittent streams.

Introduction

Most of the research on riparian wildlife habitat associations in the western United States has been conducted along relatively large, permanently flowing streams or rivers, and many of the studies have been conducted in arid or semiarid regions. Under these conditions riparian vegetation is typically structurally and compositionally distinct from upland vegetation, as are wildlife communities (Anderson and Ohmart 1977, Szaro 1980, Szaro and Jakle 1985, Thomas et al. 1979, Tubbs 1980). In moist coniferous forests in the Pacific Northwest, vegetation along small streams is typically less distinct from upland vegetation. Some studies of bird or small mammal communities along small perennial streams in the Pacific Northwest found significantly greater species richness and total abundance in riparian habitat compared to upland habitat (Cross 1985, Doyle 1990), but other studies did not (Gomez and Anthony 1998, McComb et al. 1993a, McGarigal and McComb 1992). Each of these studies found compositional differences between riparian and upland habitats: certain species were associated with riparian habitats and others with upland habitats. Few studies have compared patterns of wildlife habitat use or characteristics of wildlife communities among different-sized streams in the Pacific Northwest. Lock and Naiman (1998) found that bird species richness and abundance were significantly greater along larger rivers (67-140 m in width) than along smaller rivers (12-21 m in width) on the Olympic Peninsula in Washington.

Because they have small drainage areas, small streams in the upper-basin portions of the channel network typically flow only intermittently (Montgomery and Buffington 1998). Also, in many parts of the Pacific Northwest, precipitation is highly seasonal, and many stream channels stop flowing during periods of little precipitation. Very little has been published on wildlife habitat use along intermittent streams. Under the Record of Decision for the Northwest Forest Plan, intermittent streams are included in a system of riparian reserves and require buffer strips unless watershed analysis can show buffers are unnecessary (USDA Forest Service and USDI Bureau of Land Management 1994). In the Record of Decision, intermittent streams are defined as "...any nonpermanent flowing drainage feature having a definable channel and evidence of annual scour or deposition." On 13 national forests in Oregon and Washington, channels classified as intermittent

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comprised an average of about two-thirds of estimated total channel length (USDA Forest Service et al. 1993:Table V-G-4). Although forested areas along small intermittent streams influence a variety of ecological processes (USDA Forest Service et al. 1993), information on the value of these habitats for wildlife will add to our understanding of the ecological role of these streams and help guide policy related to intermittent streams.

In this study we evaluate associations between stream size and patterns of occurrence and abundance of amphibians and small mammals within a watershed in northwestern California. Sample sites ranged from small, poorly defined channels where surface water rarely flowed, to channels up to 10-m wide with surface water continuously present. We especially wanted to determine if there were species associated with small intermittent streams. This was a descriptive and correlative study within a single watershed. We report results of statistical tests to facilitate description and interpretation of pattern, not to make statistical inference to other watersheds. We first evaluate associations between stream size and vegetation characteristics across the range of sample sites. Next, we describe patterns of occurrence of aquatic vertebrates. Finally, we evaluate associations between stream size and patterns of occurrence and abundance of terrestrial vertebrates.

Study Area

We conducted our study within the Pilot Creek watershed, located in the North Coast Ranges geographic subdivision of northwestern California (Hickman 1993, Welsh 1994). The watershed lies within the Six Rivers National Forest and straddles Humboldt and Trinity Counties (Figure 1). The watershed is located about 55 km inland from the Pacific Ocean and drains into the Mad River about 130 km above its mouth. Pilot Creek drains an area approximately 100 km^2. Franciscan Formation sedimentary rocks and schist underlie most of the watershed. The watershed is far enough inland that it rarely receives summer fog; summers are hot and dry (total precipitation in June, July, and August averages about 4 cm). Average annual precipitation is about 200 cm. Areas between about 600 and 1,350 m receive a mixture of snow and rain during the winter, and areas above 1,350 m typically hold snow throughout the winter (USDA Forest Service 1994).

Vegetation in our study area was classified as mixed-evergreen forest (Sawyer et al.1988). Stands in which we worked were unmanaged and dominated by conifers about 80-100 years old and large-diameter (>100-cm diameter at breast height), old trees with fire scars. The dominant tree species was Douglas-fir (*Pseudotsuga menziesii*). Other common tree species included white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), canyon live oak (*Quercus chrysolepis)*, black oak (*Q. kelloggii*), and big-leaf maple (*Acer macrophyllum*). The forest understory was relatively open; common shrubs included hazelnut (*Corylus cornuta*), ground rose (*Rosa spithamea*), and California blackberry (*Rubus ursinus*). Common ground-cover plants included western sword fern *(Polystichum munitum*), Oregon-grape (*Berberis aquifolium*), hound's tongue (*Cynoglossum grande)*, snowberry (*Symphoricarpos* sp.), yerba de selva (*Whipplea modesta*), starflower (*Trientalis latifolia*), bedstraw (*Galium* sp.), and Hooker's fairy-bell (*Disporum hookeri*).

Methods

We attempted to reduce environmental variation due to sources other than stream size by restricting potential sample sites to areas with the same bedrock and similar elevation, forest cover, and geomorphology. We first used geologic maps to constrain potential sample sites to parts of the watershed underlain by Franciscan Formation sedimentary rocks (primarily sandstone and shale). We restricted potential sample sites to an elevation range of about 1,000 to 1,300 m and to areas dominated by mature conifer forest that had not been previously logged.

Within these potential sample areas we traversed stream channels with at least some sign of fluvial deposition or scour to identify potential sample sites in spring 1995. We identified channel segments ≥75-m long at which a habitat patch ≥75-m wide on at least one side of the channel met the following criteria: slope, aspect, and vegetation were relatively homogeneous; there was no evidence of recent disturbance; and hillside slope was ≤60%. Potential sample sites also had to be separated by ≥125 m. The above conditions greatly restricted the number of potential sites, so we sampled all 42 stream sites that met these criteria. During spring 1996 we also identified 15 potential upland sites. Upland sites had to meet the above habitat conditions and be located ≥125

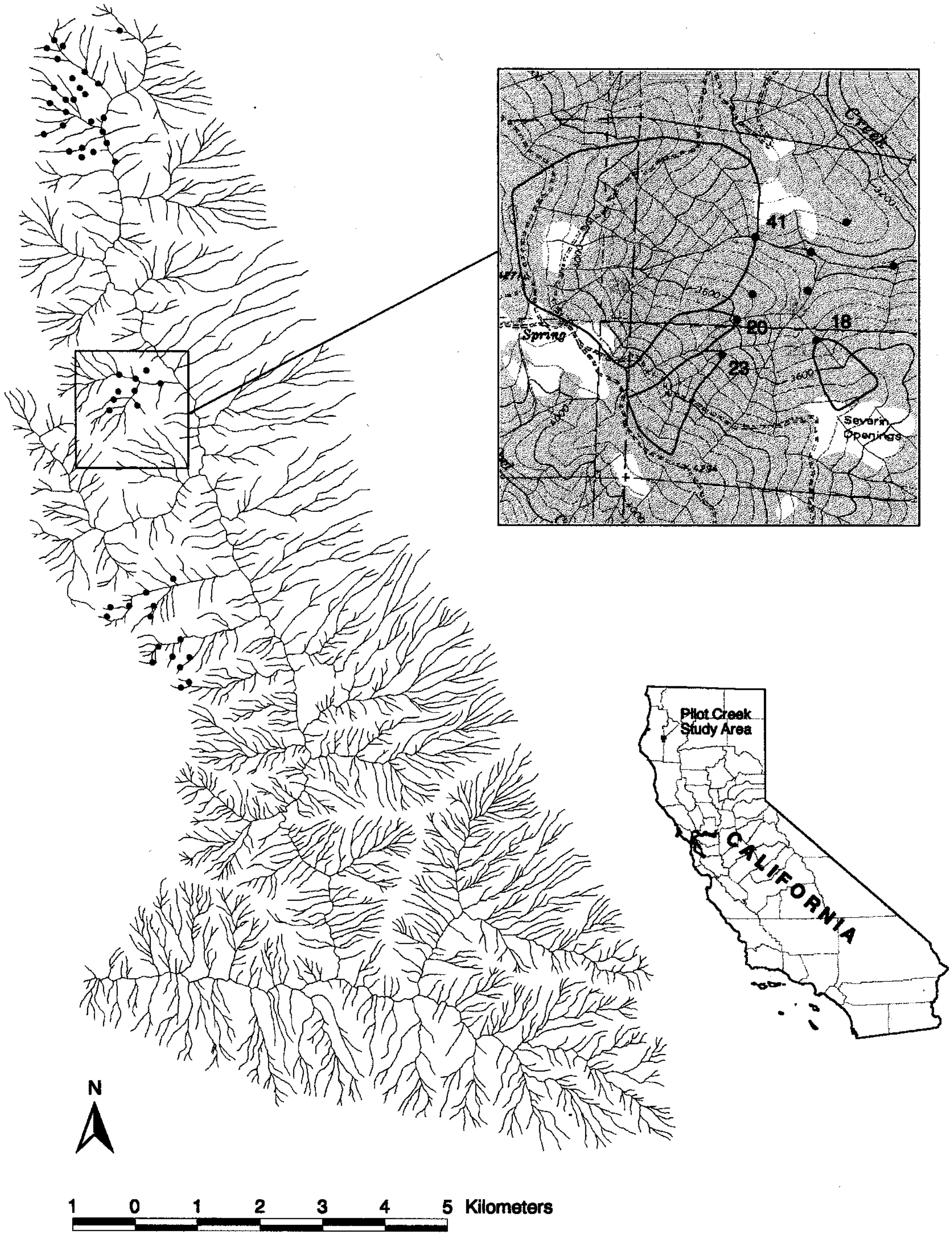

Figure 1. Map showing locations of Pilot Creek watershed and sample sites within the watershed. Stream layer includes channels drawn by a geographer based on crenulations in contour lines from a 7½-minute topographic map. Inset shows example of drainage-area boundaries of four stream sites.

m from any stream channel. We randomly selected eight of these 15 sites to sample in 1996.

At each of the 42 stream sites and eight upland sites, we established three parallel transects, each 45-m long. The riparian transect was located adjacent to the edge of the active channel, the midslope transect 15 m above the riparian transect, and the upslope transect 25 m above the midslope transect (40 m above the riparian transect). Transect length and spacing was the same for upland sites, even though the relative positions of riparian, midslope, and upslope transects were irrelevant.

We used three measures to describe stream size or flow. First, we determined average channel width by measuring the width of the active channel at 20 systematically located points along the 45-m length of channel adjacent to the riparian transect in August 1995. We recorded a zero for channel width at a point if there was no fluvial deposition visible. Second, we estimated the percentage of the 45-m channel length covered by water using a point-intercept method. We determined presence of surface water at 20 systematically located points in 1995 and at 45 systematically located points in 1996. Percent water cover was estimated three times in 1995 from August to September and five times in 1996 from May to September. Third, we estimated drainage area for all 42 stream sites. We used a global positioning system (GPS) to accurately locate positions of stream sites and a geographic information system (GIS) to create a map with three layers of information: a contour coverage, a stream-channel layer created by a geographer based on contour crenulations, and the stream-site point locations. We then drew watershed boundaries above each stream site based on contour lines and estimated drainage area by obtaining the area calculation for each of these polygons using Arc/Info (Environmental Systems Research Institute 1998).

Vegetation was sampled during late June and early July 1996. Species and diameter at breast height (dbh) were recorded for all trees within an area 4-m wide by 45-m long along each of the three transects. Shrub cover was estimated along each 45-m-long transect using the line-intercept method. We recorded all logs (≥1.0-m long and 10-cm wide) that crossed each transect and measured their diameter at the point of intersection. Ground cover was estimated visually in eight 0.75- by 0.75-m square plots systematically positioned along each transect. We also identified vascular plants within an area 4-m wide by 45-m long along each transect. Plant taxonomy follows Hickman (1993).

We conducted stream surveys to sample aquatic vertebrate populations at each of the 42 stream sites. These were area-constrained surveys conducted within the active channel along the 45-m length adjacent to each riparian transect. Two to three people slowly and systematically walked up the channel searching for amphibians on the channel bed and under rocks greater than about 10 cm in diameter that could be easily reached and moved. We conducted three surveys at each site in 1995 (10-16 August, 22-29 August, and 6-14 September) and three in 1996 (13-16 May, 12-19 June, and 12-18 July).

We used one cover board array, two drift fence/pitfall trap arrays, four Sherman live traps (8 by 9 by 23 cm), and two Tomahawk live traps (13 by 13 by 41 cm) systematically positioned along each transect to sample populations of small terrestrial vertebrates (Figure 2). Individual cover boards were 25 by 15 by 2 cm and placed in a three by three array (gaps between boards were 1-5 mm) at the midpoint of each transect. Drift fences were 5-m long and made by stapling fiberglass screening to wooden stakes. At each end of the drift fence was a pitfall trap with a cover board on top. Pitfall traps were made by taping together two number 10 coffee cans and inserting a plastic sleeve to reduce escapes.

During the summers of 1995 and 1996 we sampled vertebrates during four sample periods, each 3 trap-nights long (the 42 stream sites were sampled in both 1995 and 1996, and the 8 upland sites were sampled only in 1996). Because we could not sample all sites simultaneously, we sampled half of the sites one week and the other half the following week. In 1995 sample periods began 25 July, 8 August, 21 August, and 6 September. In 1996 sample periods began 30 May, 9 July, 6 August, and 16 September. To increase captures of salamanders we also sampled once each year during the fall after the first substantial rains fell. We checked only pitfall traps and cover boards during the fall sample periods (Sherman and Tomahawk live traps were not used). In 1995 we kept pitfall traps open for 15 nights beginning 13 November, and in 1996 we kept pitfall traps open for 21 nights beginning 29 October

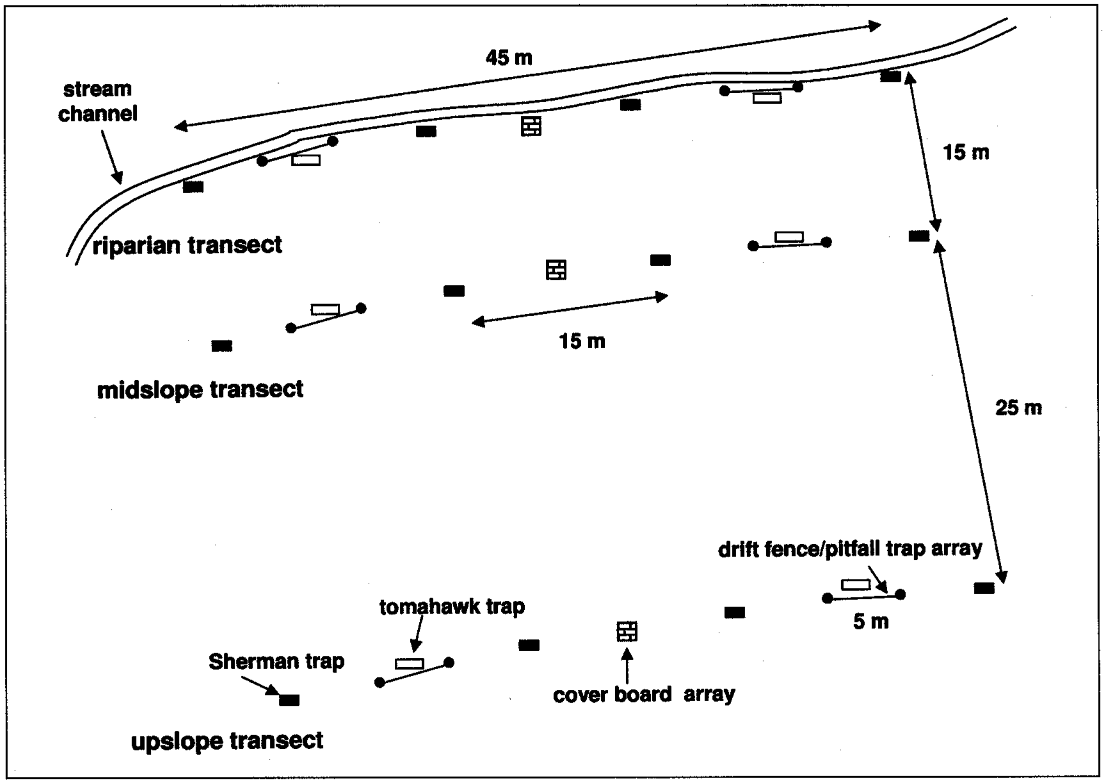

Figure 2. Example of sampling design at a stream site.

(date of trap closure was determined by onset of freezing temperatures).

Small mammals were individually marked by ear tagging or toe clipping, and salamanders were marked by toe clipping. Sex, weight, and reproductive status were recorded for all small mammals captured; sex and snout-vent length were recorded for salamanders. Mammalian taxonomy follows Wilson and Ruff (1999).

Analyses

We computed Spearman ranked correlation coefficients between each of 15 vegetation variables and the three measures of stream size across the 42 stream sites. Next, we performed all-possible-multiple regression to determine the level of association between stream size and vegetation characteristics. We used the coefficient of determination (R^2) and adjusted R^2 to assess level of association. We selected the model with the greatest adjusted R^2 (adjusted R^2 is adjusted downward for the number of parameters in the model.) The uniqueness index (Hatcher and Stepanski 1994) was used to rank relative importance of variables in each model. For the above analyses, values for vegetation variables were calculated using the average between values on the riparian and midslope transects. We excluded upslope transects for these analyses because our objective was to evaluate association between stream size and vegetation characteristics near the stream, not to evaluate variation in vegetation among transects.

We also selected three of the 15 vegetation variables to examine variation in plant diversity among transects and among stream-size groups: number of tree species, number of species in the shrub layer, and number of species in the herbaceous layer. To help interpret these patterns, we used a repeated-measures analysis of variance (ANOVA) design to test for effects due to channel width, transect (riparian, midslope, and upslope), and the interaction between channel width and transect (SAS Institute Inc. 1997:PROC MIXED). We ranked the 42 sites by channel width and divided them into six groups of equal sample size. (Sites were split into six groups so that sample size [n = 7] was similar to the number of upland sites.) The eight upland sites were included as a seventh group. Because sample sites were clustered within three areas within the watershed (Figure 1), we also included a blocking variable with three values. Channel-width, transect, and the interaction between channel-width and transect were fixed effects, block was a random effect, and transect was the repeated measure; individual sites were subjects in the model. If the effect due to transect or the interaction between channel width and transect was significant, we followed up by testing for a significant transect effect in each channel-width group. We also used Dunnett's test (SAS Institute Inc.1997) to compare the mean value (averaged across transects) for each channel-width group to the mean value for the upland sites.

We also evaluated a 2 X 4 contingency table for each plant species found at >5 sites to test for association between occurrence (present or not present) and stream-size category (upland sites and three groups of stream sites defined by channel width). We divided stream sites into three groups instead of six for these tests to reduce the number of cells with expected frequencies less than five. For the same rationale discussed above, we considered only riparian and midslope transects in determining occurrence at a particular site.

For aquatic vertebrates, we simply described where species occurred in relation to channel width, drainage area, and percent water. For terrestrial vertebrates, we evaluated patterns of occurrence and abundance across the range of sample sites. We evaluated patterns of occurrence and abundance for species that were captured frequently at many sample sites. For species that were captured at >5 sites but were not captured frequently at any site, we evaluated only patterns of occurrence. We did not evaluate patterns of occurrence or abundance for species captured at fewer than six sites. Similar to the analysis described above for plant species, we evaluated a 2 X 3 contingency table for each species found at >5 sites to test for association between occurrence and stream size (three groups of stream sites defined by channel width). A species was considered present at a site if it was captured at least once in either 1995 or 1996. We did not include upland sites in these tests because sampling effort was less.

We used capture rate of individuals as a measure of abundance. Capture rate was calculated separately for 1995 and 1996 for each site using the following formula:

$$\text{capture rate} = I \times 100(T - S/2),$$

where I = number of individuals captured, T = number of traps multiplied by number of nights traps were open, and S = number of traps sprung by all causes (Nelson and Clark 1973). Because numbers of captures were relatively low, we estimated abundance using the average capture rate for 1995 and 1996.

To evaluate associations between patterns of abundance of terrestrial vertebrates and stream size, we first computed Spearman ranked correlations between abundance and stream size across the 42 stream sites. Next we used ANOVA to compare mean abundance for each of the most common species among seven groups: the group of eight upland sites and the six groups of stream sites classified by channel width. Channel width was a fixed effect and block was a random effect. Dunnett's test was used to compare means for the six channel-width groups to the mean for the upland group.

Similar to the analysis comparing vegetation characteristics among transects and channel-width groups, we used ANOVA to compare capture rates of common species among riparian, midslope, and upslope transects. We used the same model design described above for vegetation. Capture rate was calculated the same way it was to estimate abundance, except instead of using the number of individuals captured per unit, we used the total number of captures (included recaptures of same individuals) per transect per unit for each species. We assumed that capture rate calculated this way provided an index of the amount of time species spent in the immediate vicinity of each transect. We were only interested in tests of the transect effect and the interaction effect between channel width and transect. We rejected all null hypotheses at an alpha level of 0.05.

Results

Stream Size

Width of the active channel varied from 0.1 to 10.5 m, drainage area from 2 to 579 ha, and percent water (averaged across the five sample periods in 1996) from 0 to 100% (Table 1). Channel reaches sampled varied from colluvial reaches to cascade,

TABLE 1. Active channel width, drainage area, and percentages of 45-m-long channel reaches covered by water for each of the 42 stream sites. Dates are the midpoints of the period during which all 42 sites were sampled (periods averaged 7 days and ranged from 4 to 9 days). Maximum numbers of larvae of *Dicamptodon tenebrosus* (DITE) and *Ascaphus truei* (ASTR) found in each channel segment in 1995 or 1996 are also listed.

Site	Channel width (m)	Drainage area (ha)	Percent Water								DITE	ASTR
			1995			1996						
			14 Aug	26 Aug	11 Sep	15 May	16 Jun	16 Jul	11 Aug	22 Sep		
1	0.1	2.1	0	0	0	0	0	0	0	0	0	0
2	0.1	2.4	0	0	0	0	0	0	0	0	0	0
3	0.1	8.5	0	0	0	0	0	0	0	0	0	0
4	0.2	2.8	0	0	0	0	0	0	0	0	0	0
5	0.3	3.9	0	0	0	0	0	0	0	0	0	0
6	0.5	4.0	0	0	0	0	0	0	0	0	0	0
7	0.7	3.8	0	0	0	0	0	0	0	0	0	0
8	0.9	2.8	50	75	70	100	100	100	49	62	0	0
9	0.9	13.6	0	0	0	78	33	0	0	0	0	0
10	1.1	4.2	15	15	20	78	53	22	13	11	0	0
11	1.2	3.1	0	0	0	11	9	0	0	0	0	0
12	1.2	4.6	0	0	0	69	27	0	0	0	0	0
13	1.2	6.9	0	0	0	0	0	0	0	0	0	0
14	1.3	16.1	95	65	55	100	100	84	56	40	0	0
15	1.4	4.2	5	0	0	42	20	2	2	2	0	0
16	1.4	8.3	100	100	100	100	100	100	100	100	1	0
17	1.7	6.3	0	0	0	91	36	4	0	0	0	0
18	1.7	10.5	0	0	0	56	7	0	0	0	0	0
19	1.8	8.1	0	0	0	100	76	4	0	0	0	0
20	1.8	12.2	0	0	0	100	84	13	0	2	0	0
21	1.8	7.8	0	0	0	36	24	0	0	0	0	0
22	1.9	9.7	15	5	0	100	93	22	7	2	0	0
23	1.9	11.7	0	0	0	18	2	0	0	0	0	0
24	2.0	13.2	0	0	0	82	49	9	4	4	0	0
25	2.0	16.2	10	0	0	100	96	51	13	20	0	0
26	2.0	23.0	55	30	10	100	100	98	27	22	0	0
27	2.1	19.4	5	10	0	100	69	31	13	11	0	0
28	2.4	28.1	70	70	65	100	100	98	82	84	27	0
29	2.9	16.2	0	0	0	100	84	13	2	2	0	0
30	3.0	14.2	70	55	30	100	100	93	58	56	26	0
31	3.1	44.9	20	15	10	100	91	44	-	42	1	0
32	3.1	61.4	100	85	80	100	100	100	93	76	38	7
33	3.6	112.9	0	0	0	100	100	38	0	4	2	0
34	3.9	71.9	5	10	5	100	100	51	0	2	7	0
35	5.3	101.8	35	25	25	100	100	60	33	33	15	0
36	5.4	200.4	100	95	90	100	100	100	80	78	29	0
37	5.5	108.6	100	100	90	100	100	100	98	91	23	3
38	6.4	381.8	85	55	30	100	100	100	87	80	50	1
39	7.5	504.4	100	100	100	100	100	100	100	100	55	5
40	7.9	543.6	100	90	70	100	100	100	93	100	58	2
41	8.2	95.5	0	0	0	100	0	0	0	0	0	0
42	10.5	578.6	100	100	100	100	100	100	100	100	39	1

step-pool, or plane-bed alluvial reaches (Montgomery and Buffington 1998). Colluvial reaches were at the uppermost part of the channel network, and although they contained fluvial deposition from episodic discharge events, we did not observe surface water at these sites during any of the sample periods (sites 1-7, Table 1). By the last sample in 1995, 67% of the 42 stream sites were completely dry or nearly dry (≤10% water), and 57% were dry or nearly dry by the last

TABLE 2. Spearman ranked correlation coefficients between three measures of stream size and capture rates of vertebrate species. Asterisk indicates correlation was significantly different than zero at an alpha of 0.05.

Variable	Channel width	Drainage area	Percent water
Channel width	1.00	-	-
Drainage area	0.92*	1.00	-
Percent water	0.74*	0.75*	1.00
Ensatina eschscholtzii	-0.22	-0.14	-0.11
Sorex trowbridgii	0.04	0.19	0.17
Tamias senex	0.67*	0.63*	0.63*
Peromyscus maniculatus	0.52*	0.48*	0.44*
Clethrionomys californicus	0.11	0.22	0.00

sample in 1996. All 42 sites sampled were confined (constrained) reaches (Gregory et al. 1991) with adjacent hillslopes coming down to the edge or near the edge of the active channel. Channel width was strongly correlated with drainage area (Table 2). Correlations between channel width and percent water and between drainage area and percent water were less, but also significant.

Vegetation

Correlations with the 15 vegetation variables were generally similar among the three measures of stream size (Table 3). Sample sites at stream locations with wider channels, larger drainage areas, and more continuous water flow had significantly greater basal areas of big-leaf maple and Pacific yew, shrub cover of hazelnut, numbers of species in the shrub and herbaceous layers, ground cover of forbs, and significantly less basal area of incense cedar and fewer small logs. Multiple regressions indicated that there was strong association between stream size and vegetation characteristics. Eighty percent of the variation in channel width was explained by a nine-variable model, 58% of the variation in drainage area was explained by a seven-variable model, and 64% of the variation in percent water cover was explained by an eight-variable model (Table 4). Shrub cover of hazelnut was the most important variable in models

TABLE 3. Spearman ranked correlation coefficients between three measures of stream size and vegetation variables measured at 42 stream sites. Asterisk indicates correlation was significantly different than zero at an alpha of 0.05.

Variable	Channel width	Drainage area	Percent water
Basal area of big-leaf maple	0.56*	0.53*	0.40*
Basal area of Douglas-fir	-0.06	-0.08	-0.27
Basal area of Pacific yew	0.57*	0.56*	0.51*
Basal area of white fir	-0.25	-0.12	-0.19
Basal area of incense cedar	-0.37*	-0.32*	-
Basal area of canyon live oak	-0.15	0.04	0.09
Basal area of snags	-0.09	-0.07	-0.06
Number of tree species	0.23	0.35*	0.29
Shrub cover of hazelnut	0.47*	0.57*	0.41
Number of species in shrub layer	0.67*	0.76*	0.59*
Percent ground cover of grass	-0.03	-0.16	-0.02
Percent ground cover of forbs	0.41	0.45*	0.55*
Number of species in herbaceous layer	0.55*	0.51*	0.45*
Number of logs ≤18 cm in diameter	-0.40*	-0.44*	-0.44*
Number of logs >18 cm in diameter	0.28	0.34*	0.26

TABLE 4. Results of all-possible-subsets multiple regression using three measures of stream size as response variables and 15 vegetation variables as potential predictor variables (n = 42 stream sites). Variables are presented in rank order of importance in the model.

Response variable	*R2*	Adjusted *R2*	Predictor variables
Channel width	0.80	0.75	Shrub cover of hazelnut, basal area of big-leaf maple, number of logs >18-cm diam., basal area of white fir, basal area of Pacific yew, ground cover of forbs, number of species in herbaceous layer, basal area of snags, number of species in shrub layer
Drainage area	0.58	0.49	Shrub cover of hazelnut, number of logs >18-cm diam., basal area of snags, number of species in shrub layer, basal area of white fir, basal area of big-leaf maple, basal area of live oak
Percent water cover	0.64	0.55	Basal area of white fir, number of tree species, shrub cover of hazelnut, logs >18-cm diam., basal area of incense cedar, logs ≤18-cm diam., basal area of Douglas fir, number of species in herbaceous layer

for channel width and drainage area and third most important in the model for percent water.

Number of tree species did not differ significantly among channel-width groups, but numbers of species in the shrub and herbaceous layers did (Figure 3). Averaged across transects, mean number of species in the shrub layer was significantly greater than the mean for upland sites in the three largest channel-width groups. Mean number of species in the herbaceous layer was significantly greater than the mean for upland sites in all but the 0.1-0.7-m channel-width group. Although the overall transect effect was significant for numbers of species in the shrub and herbaceous layers, only one of the tests comparing means among transects within individual channel-width groups was significant. For both variables, mean values were less for upslope transects than for riparian transects.

Of the 48 plant species tested, 23 showed a significant association between occurrence and stream size (Appendix). (With 48 significance tests, two to three Type I errors [rejecting the null hypothesis of no association when the null hypothesis is true] are expected with an alpha of 0.05.) Occurrences of most of the species with significant

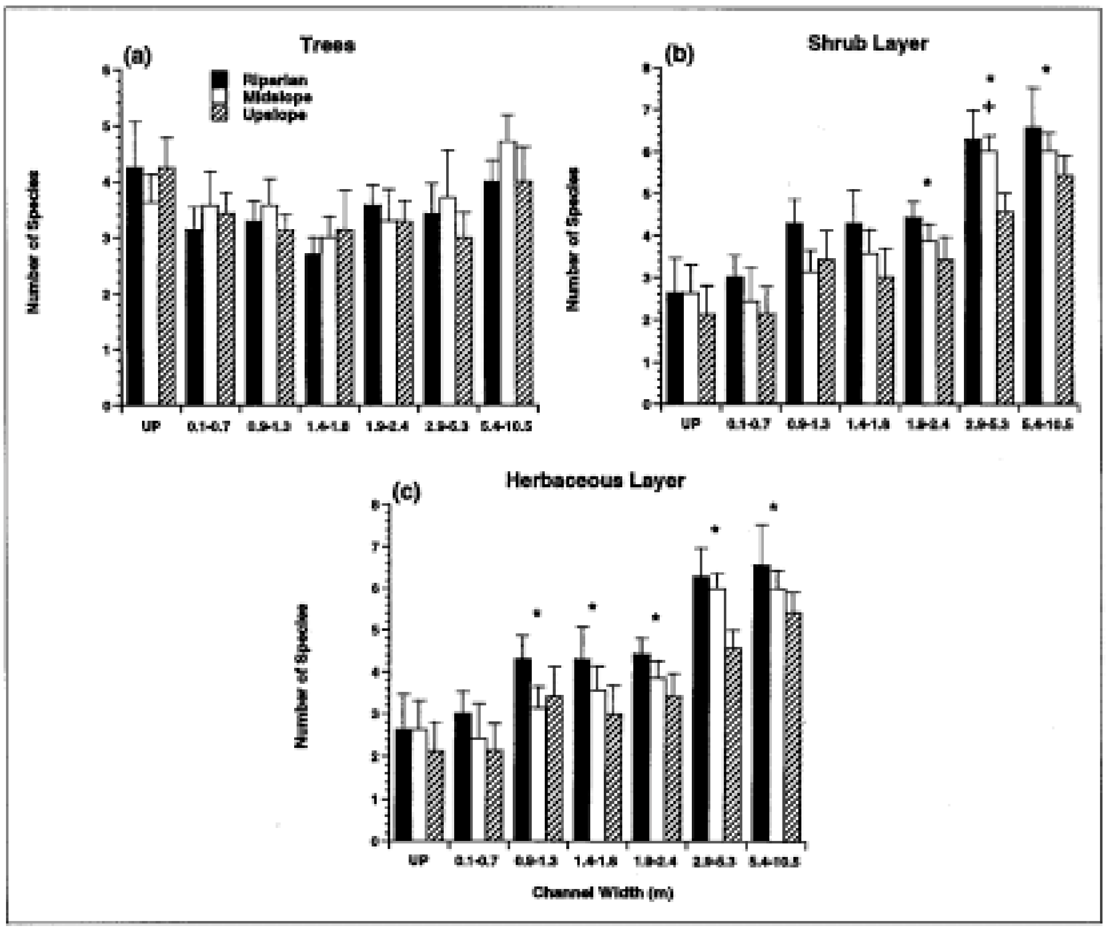

Figure 3. Means and standard errors for three measures of plant diversity. Values were averaged across eight upland sites (UP) and seven stream sites in each of six channel-width groups. Asterisks indicate groups that differed significantly from upland sites (averaged across transects). Plus symbols indicate groups in which there was a significant difference among transects. *P* values for effects due to channel width (CW), transect (TR), and the interaction between channel width and transect (CW*TR) from ANOVA tests are listed below. (a) Number of tree species: CW = 0.19, TR = 0.60, CW*TR = 0.69; (b) Number of species in shrub layer: CW = <0.01, TR = <0.01, CW*TR = 0.93; (c) Number of species in herbaceous layer: CW = <0.01, TR = 0.01, CW*TR = 0.62.

tests were associated with larger streams. Although white alder (*Alnus rhombifolia*) is not listed in the Appendix because it was included in a sample at only one site (site 38), this tree occurred only along the banks of wide-channel reaches with large drainage areas.

Vertebrates

Other than rainbow trout (*Salmo gairdneri*), which was observed only at sites 38, 39, 40, and 42, we observed two species of vertebrates with an aquatic life stage: Pacific giant salamanders (*Dicamptodon tenebrosus)* and tailed frogs (*Ascaphus truei*). Larvae of *D. tenebrosus* were found at each site with a channel width ≥2.4 m except sites 29 and 41 (Table 1). Although site 41 had a wide channel and large drainage area, stream flow readily went subsurface above this site and left the channel dry for most of the summer. *Dicamp- tenebrosus* was found at only one site with a channel width <2.4 m. One larva was found at site 16, which was located downstream of a perennially flowing spring. *Dicamptodon tenebrosus* was able to persist within disjunct pools in stream reaches where significant portions of the channel dried up during the summer (e.g., sites 33 and 34). We found larvae of *A. truei* at only six sites; each site had continuous or nearly continuous flow year round. Although we did not find any *A. truei* larvae at site 16, we did capture an adult in one of the pitfall traps along the riparian transect.

We found no significant association between stream size and occurrences of 11 species of terrestrial vertebrates that were captured at >5 of the 42 stream sites (Table 5): ensatina (*Ensatina eschscholtzii*), northern alligator lizard (*Elgaria coerulea*), Pacific shrew (*Sorex pacificus*), Trowbridge's shrew (*Sorex trowbridgii*), American shrew mole (*Neurotrichus gibbsii)*, northern flying squirrel (*Glaucomys sabrinus*), Allen's chipmunk (*Tamias senex*), deer mouse (*Peromyscus maniculatus*), western red-backed vole (*Cleth- californicus*), Sonoma tree vole (*Arbori- pomo*), and creeping vole (*Microtus oregoni)*. Although the test was not significant (P = 0.13), *S. pacificus* was captured at seven of 14 sites in the largest channel-width group and at only two of 14 sites in the smallest channel-width group. *E. eschscholtzii*, *S. trowbridgii*, *T. senex*, and *P. maniculatus* were captured at all or nearly all sample sites.

TABLE 5. Numbers of stream sites at which vertebrate species were captured at least once in 1995 or 1996. Fourteen sites were sampled in each of three channel-width groups. None of the 2 x 3 contingency tables testing for association between occurrence and stream size was significant at an alpha of 0.05.

	Channel Width (m)		
Species	0.1-1.3	1.4-2.4	2.9-10.5
Ensatina eschscholtzii	14	14	14
Elgaria coerulea	6	10	7
Sorex pacificus	2	5	7
Sorex trowbridgii	14	14	14
Neurotrichus gibbsii	4	6	6
Glaucomys sabrinus	4	4	1
Tamias senex	13	14	14
Peromyscus maniculatus	14	14	14
Clethrionomys californicus	7	8	10
Arborimus pomo	3	1	3
Microtus oregoni	5	5	4

We evaluated abundance patterns of five species: *E. eschscholtzii, S. trowbridgii, T. senex, P. maniculatus,* and *C. californicus.* Abundances of *T. senex* and *P. maniculatus* were significantly correlated with channel width as well as with drainage area and percent water cover (Table 2). Consistent with these results, abundances of only *T. senex* and *P. maniculatus* differed significantly among channel-width groups (Figure 4). Mean abundance of *T. senex* was significantly greater in the two largest channel-width groups than mean abundance at the eight upland sites (Figure 4c). Mean abundance of *P. maniculatus* was significantly greater in two of the three largest channel-width groups (Figure 4d).

There was a significant transect effect for *E. eschscholtzii* and *T. senex,* as well as a significant interaction between channel width and transect for *T. senex* (Figure 5). Mean capture rate of *E. eschscholtzii* was similar among the three transects in the smallest channel-width group, but in all other groups mean capture rate was less on the riparian transect compared to the midslope and upslope transects. For *T. senex* mean capture rate was similar among the three transects in the two smallest and the largest channel-width groups, but greater on the riparian transect than the midslope and upslope transects in the 1.4-1.8, 1.9-2.4, and 2.9-5.3-m channel-width groups.

Discussion

Unlike most studies of riparian wildlife habitat associations, the majority of stream reaches we

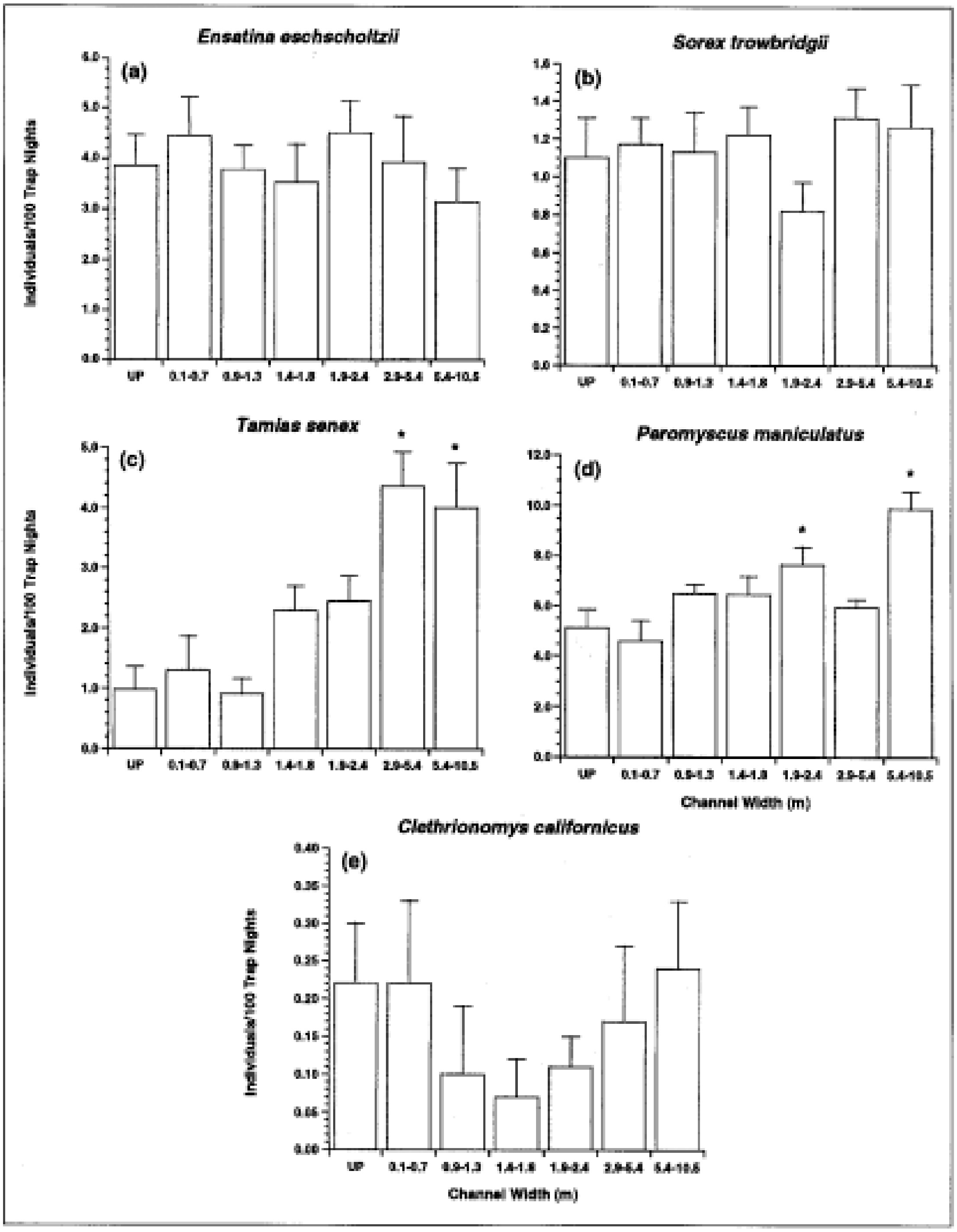

Figure 4. Means and standard errors of estimates of abundance for five species of terrestrial vertebrates. Values were averaged across eight upland sites (UP) and seven stream sites in each of six channel-width groups. Asterisks indicate groups that differed significantly from upland sites. *P* values for effect due to channel-width from ANOVA tests were (a) 0.61, (b) 0.10, (c) <0.01, (d) <0.01, (e) 0.63.

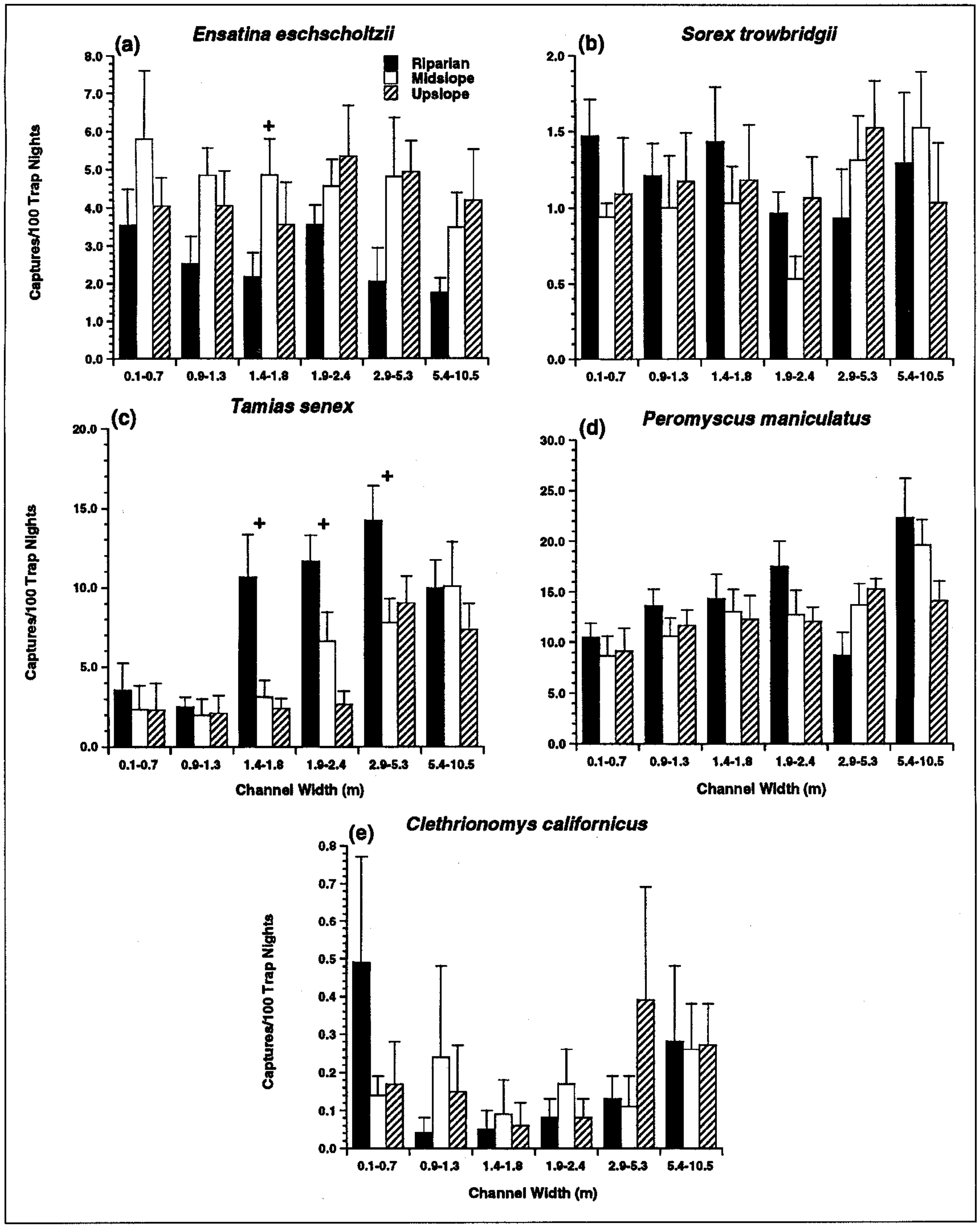

Figure 5. Means and standard errors of capture rates for five species of terrestrial vertebrates along riparian, midslope, and upslope transects. Values were averaged across seven stream sites in each of six channel-width groups. Plus symbols indicate groups in which there was a significant difference among transects. *P* values for effects due to channel width (CW), transect (TR), and the interaction between channel width and transect (CW*TR) from ANOVA tests are listed below. (a) CW = 0.65, TR = <0.01, CW *TR = 0.91; (b) CW = 0.16, TR = 0.47, CW *TR = 0.59; (c) CW = <0.01, TR = <0.01, CW*TR = 0.01; (d) CW = 0.01, TR = 0.16, CW*TR = 0.07; (e) CW = 0.64, TR = 0.95, CW*TR = 0.33.

sampled flowed only intermittently. In addition, our sample sites were located along confined reaches where vegetation near the channel is typically relatively similar to upslope vegetation (Gregory et al. 1991). In contrast, unconfined reaches are typically associated with distinct riparian plant communities with greater diversity of structure and composition than nearby hillslopes (Gregory et al. 1991, Naiman et al. 1998). Even though we only sampled along relatively small, confined stream reaches, we found strong associations between vegetation attributes and stream size and significant differences between vegetation along streams and vegetation at upland sites. Particularly interesting was the finding that mean number of plant species in the herbaceous layer along streams with channel widths as small as 0.9-1.3 m was significantly greater than the mean for upland sites, even though many of these reaches were dry for most of the summer. Other studies found that vegetation along small, perennial streams in the Pacific Northwest was distinct from upland vegetation (Cross 1985, Doyle 1990, Gomez and Anthony 1998, McComb et al. 1993a, McGarigal and McComb 1992), but we know of no studies that described vegetation along small, intermittent streams similar to those we sampled.

Factors that influence vegetation patterns in riparian zones include water availability, disturbance regime, and levels of solar radiation. Availability of water is greater than in upland habitats due to both the presence of water in the channel and the migration of groundwater into the rooting zone of riparian vegetation as it percolates toward the channel (Bilby 1988, Naiman et al. 1998). Nutrients carried by the groundwater also become available to riparian vegetation in this manner (Lowrance et al. 1984). High frequency of disturbance from flooding typically leads to a high diversity of microsites and greater plant diversity in riparian zones compared to upland sites (Gregory et al. 1991, Naiman et al. 1998). The effects of disturbance, however, are more pronounced along unconfined reaches and along larger streams and rivers. The presence of streams and stream size also affect levels of solar radiation reaching understory vegetation by providing a break in the forest canopy above the channel (Gregory et al. 1991). Other factors being equal, wider channels provide larger breaks in the canopy and thus wider zones adjacent to the channel edge where solar radiation can reach the forest understory. The level of solar radiation reaching the forest understory is influenced by channel orientation (direction) and canopy height and density, but in relatively dense coniferous forests like those in the Pilot Creek watershed, increased light reaching the forest floor may have great influence on understory vegetation patterns. Perhaps this is one reason why our multiple-regression analyses indicated that vegetation was more strongly associated with channel width than drainage area or percent water.

In the Pilot Creek watershed larvae of *A. truei* were found only at sites where surface water flowed continuously or nearly continuously throughout the year, but *D. tenebrosus* larvae occurred at sites where large sections of the channel dried up during the summer. *Ascaphus truei* is adapted for life in fast-flowing streams, and is known to be associated with cold, perennial forest streams throughout its range (Nussbaum et al. 1983, Stebbins 1954a, Welsh 1990). Tadpoles adhere to smooth rocks in fast-flowing sections of streams and feed primarily on diatoms, which they scrape off of rock surfaces. Unlike *A. truei* tadpoles, larvae of *D. tenebrosus* can move across land between isolated pools or sections of stream (Welsh 1986). Larvae of *D. tenebrosus* typically hide under rocks or logs in pools or slow-moving sections of streams and emerge at night to feed along the bottom (Nussbaum et al. 1983, Parker 1994).

Although *T. senex* and *P. maniculatus* were captured at nearly every site, they were more abundant along larger streams than at upland sites and smaller streams. Both species are omnivorous with varied diets that differ greatly with location, season, and year, but plant parts (leaves, flowers, fruits, and seeds) are the primary components of the diets of both *T. senex* (Gannon and Forbes 1995; Tevis 1953, 1956) and *P. maniculatus* (Gunther et al. 1983, Jameson 1952, Tevis 1956, Williams 1959). One hypothesis to explain why these two rodent species were more abundant along larger streams is that these habitats provided greater availability of food and thus higher quality habitat because of the greater amounts and variety of shrub- and ground-level vegetation. For these species, vegetation provides food directly in the form of leaves, flowers, fruits, and seeds, and indirectly by influencing the biomass and composition of arthropod communities. Studies have shown that capture rates of *P. maniculatus* were significantly greater along streams compared to upland habitats in Oregon (Cross 1985, Doyle 1990), but other studies have found no significant difference in abundance between riparian and upland habitats (McComb et al. 1993a, 1993b; Gomez and Anthony 1998). We know of no published studies that compared abundance of *T. senex* between riparian and upland habitats.

Parts of understory plants are not primary foods of the three species whose abundance patterns were not significantly associated with stream size: E. *eschscholtzii* (Gnaedinger and Reed 1948, Nussbaum et al. 1983, Stebbins 1954b), *S. trowbridgii* (Verts and Carraway 1998), and *C. californicus* (Maser and Maser 1988, Maser et al. 1978, Ure and Maser 1982). Capture rates of *E. eschscholtzii* were found to be significantly greater in upland habitats than in riparian habitats in Douglas-fir and red alder (*A. rubra*) forests in Oregon (McComb et al. 1993a, 1993b). Doyle (1990) found that capture rates of *S. trowbridgii* were significantly greater in riparian habitats than in upland habitats, but McComb et al. (1993a) found that capture rates were significantly greater in upland habitats, and other studies found no significant differences between riparian and upland habitats (Cross 1985, McComb et al. 1993b, Gomez and Anthony 1998). Several studies found that capture rates of *C. californicus* were significantly greater in upland habitats than in riparian habitats (Doyle 1990, McComb et al. 1993a, Gomez and Anthony 1998).

Although we only sampled along small, confined stream reaches in the Pilot Creek watershed, we did find associations between stream size and vegetation patterns and between stream size and occurrence and abundance patterns of vertebrates. Some of the vertebrate species evaluated occurred primarily at or were more abundant at stream reaches that either flowed continuously or were greater than about 2-m wide (drainage area greater than about 10 ha). None of the vertebrate species we evaluated was significantly associated with intermittent stream reaches smaller than this.

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Appendix

Numbers of sites at which plant species were found along the riparian or midslope transect, Sample sites are classified into upland sites (UP) and three channel-width groups (*n* equals number of sample sites in each group). Only species found at >5 sites are listed. Species whose contingency table indicated significant ($P < 0.05$) association between occurrence and stream size are identified with asterisk.

		Sample Area			
			Channel-Width Group(m)		
		UP	0.1-1.3	1.4-2.4	2.9-10.5
Layer	Species	(*n* = 8)	(*n* = 14)	(*n* = 14)	(*n* = 14)
Tree	*Calocedrus decurrens*	4	8	6	2
	Abies concolor	6	13	9	12
	Pseudotsuga menziesii	8	14	14	14
	*Taxus brevifolia**	0	0	0	7
	*Acer macrophyllum**	1	2	6	13
	*Corpus nuttallii**	1	0	0	7
	Quercus chrysolepis	7	13	13	13
	Quercus garryana	1	1	3	2
	*Quercus kelloggii**	7	5	4	5
Shrub	*Corylus cornuta**	4	8	10	14
	*Vaccinium ovatum**	0	0	1	9
	Ribes sp.	0	1	2	5
	Amelanchier alnifolia	2	2	3	2
	Rosa spithamea	7	13	13	14
	*Rubus parviflorus**	0	2	4	9
	*Rubus ursinus**	2	8	8	14
	Spiraea sp.	1	3	3	2
Herb	*Pteridium aquilinum*	0	1	1	4
	*Polystichum munitum**	1	8	11	10
	*Petasites frigidus**	0	0	0	6
	*Berberis aquifolium**	6	8	14	14
	*Vancouveria hexandra**	0	2	3	13
	Cynoglossum grande	4	9	12	6
	Symphoricarpos sp.	6	11	14	14
	Chimaphila umbellata	0	0	2	4
	*Pyrola picta**	5	2	4	8
	Nemophila sp.*	0	0	7	0
	*Whipplea modesta**	4	6	7	13
	Phlox adsurgens	0	4	2	2
	Claytonia perfoliata	0	3	2	1
	*Trientalis latifolia**	4	7	8	14
	Fragaria virginiana	1	6	5	9
	Galium sp. 1*	2	9	12	12
	Galium sp. 2	1	2	3	3
	*Tellima grandiflora**	0	0	6	3
	Viola glabella	2	5	8	9
	*Viola sheltonii**	1	8	7	2
	Iris fernaldii	5	6	3	5
	*Disporum hookeri**	5	8	11	14
	Erythronium californicum	0	3	3	5
	*Smilacina racemosa**	2	3	13	14
	*Smilacina stellata**	0	0	1	5
	Cephalanthera austiniae	5	6	5	2
	*Corallorhiza maculata**	5	6	4	1
	Corallorhiza mertensiana	2	1	1	4
	Unknown orchid	2	3	8	5
	Unknown grass 1	7	10	12	14
	Unknown grass 2	2	4	1	1