147

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DAM-SITE SELECTION BY BEAVERS IN AN EASTERN OREGON BASIN

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ABSTRACT.—We compared physical and vegetative habitat characteristics at 14 dam sites occupied by beaver (*Castor canadensis*) with those at 41 random unoccupied reaches to identify features important to dam-site selection in the Long Creek basin, Grant County, Oregon. Stream reaches with dams were shallower and had a lower gradient than unoccupied reaches. Beaver did not build dams at sites with a rock substrate. Bank slopes at occupied reaches were not as steep as those at unoccupied reaches; and occupied stream reaches had greater tree canopy cover, especially of thinleaf alder (*Alnus tenuifolia*), than did unused reaches. A discriminant model using transformations of bank slope, stream gradient, and hardwood cover classified all beaver dam sites correctly and 35 of 41 random sites as unoccupied sites. The 6 misclassified sites had rock substrates.

We also tested four habitat suitability models for beaver in this basin. Three models produced significantly different ($P < .05$) scores between occupied and random unoccupied reaches, suggesting that they might have some utility for this region.

Beaver (*Castor canadensis*) have long been recognized as having a significant effect on riparian ecosystems. Through alteration of stream flow, they impact soil moisture, biomass distribution, soil redox potential, pH, and plant-available nitrogen in riparian areas (Naiman et al. 1988). Creation of pool habitat is important to some salmonids (Gard 1961) and other pool-inhabiting animals, particularly in areas lacking pools formed by naturally occurring, coarse woody debris. Pool habitats can be particularly important for some species in arid regions where water levels decrease substantially during the summer. As central-place foragers, beaver also create early seral-stage patches that add to habitat complexity and may influence the diversity of terrestrial organisms (Naiman et al. 1988). Beaver management represents a low-cost alternative to intensive riparian rehabilitation activities, such as cabling coarse woody debris in streams, but its success depends on the ability of land managers to predict where beaver are likely to build dams and thus create pools.

Not all portions of all streams are suitable beaver habitat. Allen (1983) developed a habitat suitability index (HSI) model for evaluating lacustrine, riverine, and palustrine habitats for beaver. A similar model was developed by Urich et al. (1984) in Missouri. Howard and Larson (1985) in Massachusetts and Beier and Barrett (1987) in northern California used multivariate techniques to identify habitat features associated with beaver-occupied reaches. Slough and Sadlier (1977) developed a land capability classification system for beaver in British Columbia based on regression relationships. However, no models have been developed for beaver in arid habitats, and none of the existing models have been tested on independent data from arid habitats.

Our objectives were (1) to locate all beaver dams in a third-order basin representative of arid habitat in eastern Oregon, (2) to identify habitat features potentially important to beaver, (3) to develop a habitat classification model for beaver in the basin, and (4) to test four existing habitat classification models.

STUDY AREA

The Long Creek basin drains approximately 490 km^2 of Grant County, Oregon (Fig. 1). Elevations range from 760 to 1900 m. Average annual precipitation is 30–35 cm with most of that occurring in the winter. Temperatures range from about −10 to +30 C (Franklin and Dyrness 1973).

The area is dominated by shrub-steppe vegetation typical of arid eastern Oregon in the Blue Mountains physiographic region (Franklin and Dyrness 1973). Sagebrush (*Artemisia* spp.) dominates, with junipers (*Juniperus* spp.) and ponderosa pine (*Pinus*

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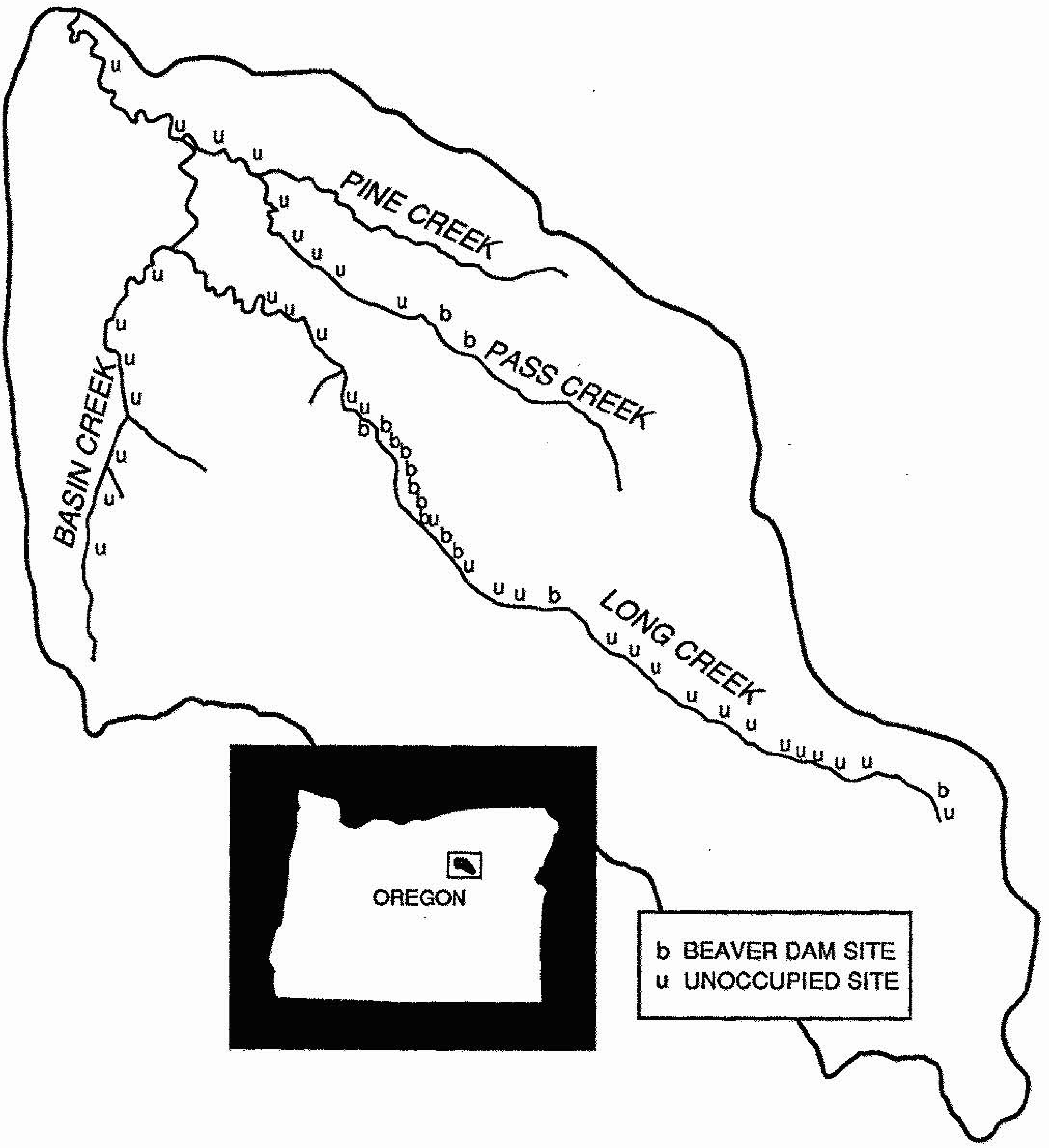

Fig. 1. Location of Long Creek basin, Grant County, Oregon, and distribution of beaver dams (b) and random unoccupied reaches (u) in the basin.

ponderosa) occurring in the higher elevations. Riparian vegetation is primarily thinleaf alder (*Alnus tenuifolia*), willow (*Salix* spp.), hawthorn (*Crataegus* spp.), and cottonwood (*Populus trichocarpa*). The dominant land use is grazing, and the land is privately owned except for the portion of the upper basin in the Ochoco National Forest.

Methods

On 2 September 1988 we examined 98 km of perennial streams in the Long Creek basin from the air at an altitude of 200–300 m. This included 48 km of Long Creek, 21 km of Pass Creek, 11 km of Pine Creek, 15 km of Basin Creek, and 3 km of unnamed streams. Thirty sites showing signs of possible beaver activity (ponds, pools, or felled trees) were marked on a topographic map and then visited on the ground. Fourteen of the possible beaver sites were actually occupied by beaver. The others were either natural pools or human-induced disturbances or structures. In September 1988 we recorded habitat characteristics at the occupied sites and at 16 randomly selected unoccupied reaches. Random reaches were selected by drawing random numbers to identify points that corresponded to distances in meters from the mouths of the streams. These reaches happened to be skewed toward the lower basin; so an additional 25 randomly selected unoccupied reaches were visited in March 1989 to obtain a better representation of riparian habitat available throughout the basin, resulting in a total of 41 unoccupied reaches.

Twenty-two habitat characteristics, including those used in previous studies, existing models, and some that were potentially important in this basin, were measured at each dam site ($n = 14$) and each unoccupied reach ($n = 41$) (Table 1). Stream variables were measured immediately below the dam at occupied sites or at the randomly selected point on unoccupied reaches. Terrestrial habitat was measured at two 40-m-diameter plots per site. Plots were established on both sides of the stream and were immediately adjacent to the dam at occupied sites or to the streambank at unoccupied reaches. Values for the two plots were averaged to characterize each site. Hall (1970) found that 90% of woody food was cut within 30 m of the stream edge, and Johnston and Naiman (in press) reported that most foraging occurred within approximately 35 m of the stream. Therefore, we assumed that 40-m-diameter plots adequately sampled terrestrial habitat for beaver. Additional variables were measured to characterize dam sites: dam height (cm), pond surface area (m^2), average basal diameters of woody stems (by species) cut by beaver, and percentage of available woody stems (by species) that had been cut by beaver.

Univariate comparisons were made between occupied and unoccupied reaches with a t test. Linear correlation between all combinations of pairs of variables was conducted. For pairs with $r > .80$, only the variable that seemed most biologically meaningful to beaver dam building in this basin was retained for subsequent analysis. Continuous variables were examined for normality using the W statistic (SAS Institute, Inc. 1982: 580). Nonnormal data were subjected to square root or logarithmic transformations to address assumptions behind parametric analysis. Any variables, either raw or transformed, with $W < 0.7$ (max $= 1.0$) were excluded from multivariate analyses. Based on these criteria, 10 of the original 20 continuous variables were retained for analysis. The subset of these

TABLE 1. Variables measured at 14 beaver dam sites and 41 unoccupied random stream reaches in the Long Creek basin, Grant County, Oregon, 1988–1989.

Variable	Method
Stream gradient (%)	Average of gradient upstream and downstream from dam or at a random point on unoccupied reaches measured with a clinometer.
Stream width (m)	High-water width immediately below dam or random point.
Stream depth (cm)	High-water depth immediately below dam or random point.
Floodplain width (m)	Width of area dominated by alluvial soils at the dam or random site.
Bank slope (%)	Average of bank entrance angle on both sides of the stream measured with a clinometer.
Bank type	Classified as predominantly dirt or small cobble (<20 cm diameter), cobble (>21 cm diameter), or solid rock.
Distances (m)	Distance to nearest road, building, or bridge.
Drainage area (km^2)	Area drained above a dam or random point.
Plant cover (%)	Ocular estimates averaged over two 40-m-diameter plots (see text) for grasses and sedges, forbs, thinleaf alder, willow, hawthorn, cottonwood, juniper, and other conifers (mostly ponderosa pine).
Hardwood	The sum of alder, willow, hawthorn, and cottonwood covers.
Shrub	The cover of all stems <1 cm diameter.
Total canopy	The sum of hardwood and conifer covers.
Grazing pressure	Classed as low (<25% stems eaten), medium (25–50% stems eaten), high (50–75% stems eaten), or very high (>75% stems eaten).

TABLE 2. Average (SE) habitat characteristics measured at beaver dam sites and unoccupied reaches, Long Creek basin, Grant County, Oregon, 1988–1989.

Habitat characteristic	Transformation	W	Occupied ($n = 14$)	Unoccupied ($n = 41$)	$P < t$
Stream gradient (%)	log	.840	2.3(0.2)	6.4(0.5)	.0001
Stream width (m)	log	.936	3.9(0.8)	3.3(0.3)	.5386
Stream depth (cm)	none	.899	5.4(0.6)	13.4(1.1)	.0001
Floodplain width (m)	log	.947	13.5(2.4)	12.0(1.4)	.5894
Bank slope (%)	sqrt	.939	11.1(2.6)	24.1(2.5)	.0009
Road distance (m)	none	.753	539 (113)	654 (68)	.3880
House distance (m)	none	.490	843 (84)	936 (24)	.2995
Bridge distance (m)	none	.473	864 (76)	903 (40)	.6332
Drainage area (km^2)	sqrt	.921	192 (23)	170 (22)	.5864
Plant cover (%)					
Grass	none	.952	54.6(5.0)	42.4(3.4)	.0669
Forb	sqrt	.894	16.8(2.3)	8.3(1.6)	.0067
Thinleaf alder	none	.631	11.2(3.7)	3.0(0.8)	.0452
Willow	none	.280	4.3(3.6)	0.9(0.3)	.3579
Hawthorn	none	.423	5.5(2.2)	1.1(0.7)	.0836
Cottonwood	none	.281	0.0(0.0)	0.0(0.0)	1.000
Hardwood	log	.904	21.0(7.1)	5.0(1.3)	.0001
Shrub	none	.650	23.1(6.7)	6.3(1.5)	.0313
Juniper	none	.198	3.6(3.6)	0.5(0.2)	.4040
Other conifer	none	.385	2.1(2.1)	1.4(0.4)	.7298
Total canopy	none	.630	26.7(8.0)	6.9(1.5)	.0001

10 variables best able to separate occupied from unoccupied reaches was selected by stepwise discriminant analysis. A classificatory model for the original data set was developed from this subset with canonical discriminant analysis.

Discrete data are reported as frequencies with chi-square goodness of fit analyses conducted for among-class comparisons. Values from random unoccupied reaches were used to establish expected frequencies.

From our data we evaluated the effectiveness of four existing habitat suitability models: (1) the U.S. Fish and Wildlife Service (USFWS) HSI model (Allen 1983), (2) the Missouri HSI model (Urich et al. 1984), (3) the Massachusetts model (Howard and Larson 1985), and (4) the Truckee River model (Beier and Barrett 1987). A new version of the Missouri HSI model includes beaver in the list of species evaluated. Scores were recorded for each occupied and unoccupied reach and then compared with a *t* test for each model. We assumed that a significant difference ($P < .05$) in scores between occupied and unoccupied reaches indicated potential utility for a model in Long Creek basin.

RESULTS AND DISCUSSION

Beaver dams were not abundant in the basin. We found an average of one beaver dam per 7 km of stream, but the distribution of the dams was highly clumped in the middle of the basin (Fig. 1). In a study covering a comparable area (600 km^2) and stream length (153 km), Beier and Barrett (1987) recorded 43 active beaver colonies in a Sierra Nevada basin. Other investigators have reported beaver dam densities of one per 0.1–3.6 km (Beier and Barrett 1987, Naiman et al. 1988).

Physical Habitat Relationships

Dam heights ($\overline{x} = 55$ cm) and pond surface areas ($\overline{x} = 167$ m^2) were highly variable (CV = 62% and 88%, respectively). Beaver dams occurred exclusively at sites with dirt rather than bedrock or cobble-dominated banks, whereas only 37% of the unoccupied reaches had dirt banks. Because beaver in this basin denned in banks or lodges adjacent to the banks, dirt substrates were probably a requisite for adequate dens.

Immediately below the dam, streams were shallower, had a gentler gradient, and had a gentler bank slope than at unoccupied reaches (Table 2). The features of dirt banks with gentle slope, low stream gradient, and relatively shallow water were best met in the middle of the basin. Further upstream the gradient was steep. Downstream the water was deep and would probably result in volumes that could wash out dams during high flows. All unoccupied reaches downstream from the occupied sites were dominated by bedrock. Drainage basin area, stream width, and floodplain width did not differ between occupied and unoccupied reaches (Table 2).

Distances to features that might have affected the likelihood of dam placement, such as bridges, roads, or buildings, did not differ between occupied and unoccupied reaches. Beaver will apparently live in close proximity to humans and human-made structures if all habitat requirements are met.

Vegetative-Habitat Relationships

Beaver cut exclusively hardwoods at the dam sites. Use of thinleaf alder (+6%), willow (−9%), and hawthorn (+3%) was nearly in proportion to availability (0% = use in proportion to availability). However, percent cover of a site by thinleaf alder was higher on occupied than on unoccupied stream reaches (Table 2). Because thinleaf alder was a dominant plant along the riparian area, hardwood cover and total canopy cover were higher on occupied than on unoccupied reaches. Alder also dominated the shrub category (stems <1 cm dbh); thus, shrub cover differed between occupied and unoccupied reaches. Cover by other potential food and dam-construction plants (willow and hawthorn) was highly variable among sites and so did not differ between occupied and unoccupied reaches, nor did cover by conifers (Table 2). Cover by forbs was higher on occupied than on unoccupied reaches, probably resulting from the higher water table around dam sites. Grass cover at dam sites did not differ from that at unoccupied reaches.

Assuming that this basin is typical of many in eastern Oregon, then beaver were most abundant prior to intensive beaver trapping in the late 1800s and early 1900s, followed by grazing of the area (Finley 1937). Kindschy (1985) reported that grazing can adversely affect beaver habitat in the region by reducing willow abundance. Grazing pressure was rated as low to none at 64% (9 of 14) of beaver dam sites and 49% (20 of 41) of unoccupied stream reaches ($X^2 = 0.73$, $P > .2$). Although we did not detect any association between grazing and dam-site selection, vegetation responses may have been obscured by historic cutting patterns of beaver, length of pond occupancy, and previous grazing practices (Kindschy 1985, Johnston and Naiman, in press). Many of the preferred food species may have been eliminated from the area prior to this study.

Habitat Classification

Bank slope, stream gradient, and hardwood canopy cover best separated ($P < .0001$, Pillai's trace = 0.62) occupied from unoccupied reaches. The model was:

$$\text{Response Variable} = 3.753 - [(\sqrt{\text{Bank slope}} * 0.272) + (\log_{10} \text{Stream gradient} * 5.239) - (\log_{10} \text{Hardwood cover} * 1.273)].$$

With zero as a decision level, negative values of the response variable were classified as beaver dam sites, and positive values were classified as random unoccupied reaches. Low values for bank slope and stream gradient and high values for hardwood cover produced negative values. The model correctly classified all dam sites and 35 of the 41 (85%) unoccupied reaches. Misclassified unoccupied reaches were dominated by either bedrock or cobble. Therefore, when all sites except those with dirt banks were deleted from the data set prior to running the model, classification was 100%. The accuracy of this model in other drainage basins of this size in eastern Oregon is unknown, but it seems likely that these habitat characteristics would influence beaver dam building elsewhere in the region.

Assessment of Existing Models

The only model that produced scores that did not differ significantly between occupied and unoccupied reaches was the Massachusetts model (Table 3). This model was designed for use in small watersheds (<750 ha) in the northeastern United States and included variables that did not pertain to conditions in eastern Oregon (soil-drainage class and abandoned-field proximity). The other three models produced scores that differed between occupied and unoccupied reaches ($P < .006$), suggesting that they can provide an index to beaver habitat quality in this basin.

Beier and Barrett (1987) used stream depth (a classificatory variable in their study) and stream gradient to identify beaver-occupied and unoccupied reaches in the Truckee River basin, California. When we assessed these

TABLE 3. Average (SE) scores for four models tested with data from beaver-occupied and random unoccupied reaches, Long Creek basin, Grant County, Oregon, 1988–1989.

Model	Occupied (n = 14)	Unoccupied (n = 41)	$P < t$
Massachusetts[a]	0.56(0.14)	0.52(0.06)	0.813
Truckee River[b]	1.44(0.05)	0.39(0.14)	0.001
Missouri HSI (original)[c]	0.67(0.03)	0.55(0.02)	0.006
(modified)	0.69(0.03)	0.54(0.02)	0.006
USFWS HSI (original)[d]	0.39(0.06)	0.20(0.03)	0.005
USFWS HSI (food)	1.46(0.23)	0.49(0.09)	0.001
USFWS HSI (water)	0.50(0.00)	0.43(0.02)	0.02
USFWS HSI (modified)	0.79(0.11)	0.29(0.05)	0.001
USFWS HSI (food)	1.46(0.23)	0.49(0.09)	0.001
USFWS HSI (water)	1.00(0.00)	0.78(0.05)	0.003
This study	−1.51(0.12)	1.34(0.23)	0.001

[a]Howard and Larson (1985)
[b]Beier and Barrett (1987)
[c]Urich et al. (1984)
[d]Allen (1983)

variables on the Long Creek basin data, stream gradient drove the model. The stream-depth variable was not sensitive to conditions at Long Creek. Beaver habitat suitability increased with stream depth in the Truckee River basin, but we found an opposite relationship in the Long Creek basin.

The Missouri HSI model produced acceptable results in eastern Oregon, but weaknesses were apparent. For example, this model places high habitat suitability value on stream sections with steep banks, whereas beaver in the Long Creek basin selected gentle bank slopes for dam placement. Reversing the suitability index scores for this variable made the model more sensitive to conditions in the Long Creek basin. A variable describing the proximity to croplands did not pertain to Long Creek basin and was eliminated. Making these alterations, however, changed the scores of the original model by only 0.02 units.

The USFWS HSI model produces life-requisite values between 0 and 1 for both food and water. The HSI is the minimum of these two values. The water life-requisite value is based on suitability indices (SI) for water level fluctuation and stream gradient. All sites measured in the Long Creek basin were classified as having moderate fluctuations in water level that could have influenced lodge entrances (SI = 0.5); so this variable was not sensitive to conditions at occupied and unoccupied reaches. Stream gradient was a better predictor of occupied reaches. Eliminating the variable for stream-level fluctuation from the model resulted in average life-requisite scores for water of 1.0 on occupied reaches and 0.78 on unoccupied reaches (Table 3). Average HSI scores for occupied reaches increased from 0.39 to 0.79 as a result of this change, while scores at unoccupied reaches did not change appreciably (0.20 to 0.29). We do not suggest changes in the calculation of the life-requisite value for food (and dam-construction material) because that score differed significantly between occupied and unoccupied reaches (Table 3).

Assessing Site Suitability

Williams (1965) indicated that in addition to sufficient food, suitable habitat for beavers requires a channel gradient < 15% and stable water levels. In riverine habitats, stream gradient is the most significant factor determining the suitability of habitat for beaver (Slough and Sadlier 1977). Gradient was considered an important habitat feature by Retzer et al. (1956), Slough and Sadlier (1977), Allen (1983), Urich et al. (1984), Howard and Larson (1985), Beier and Barrett (1987), and Naiman et al. (1988). Gradients on beaver-occupied reaches in the Long Creek basin ranged from 1.5 to 4.0%, while those on unoccupied reaches were as high as 12%. Excluding all stream segments with gradients >12% could facilitate identification of suitable dam-building segments along Long Creek and its tributaries. At most sites, gradients >7% are probably only of marginal value (Retzer et al. 1956). However, gradient alone is probably not the best indicator of dam-site

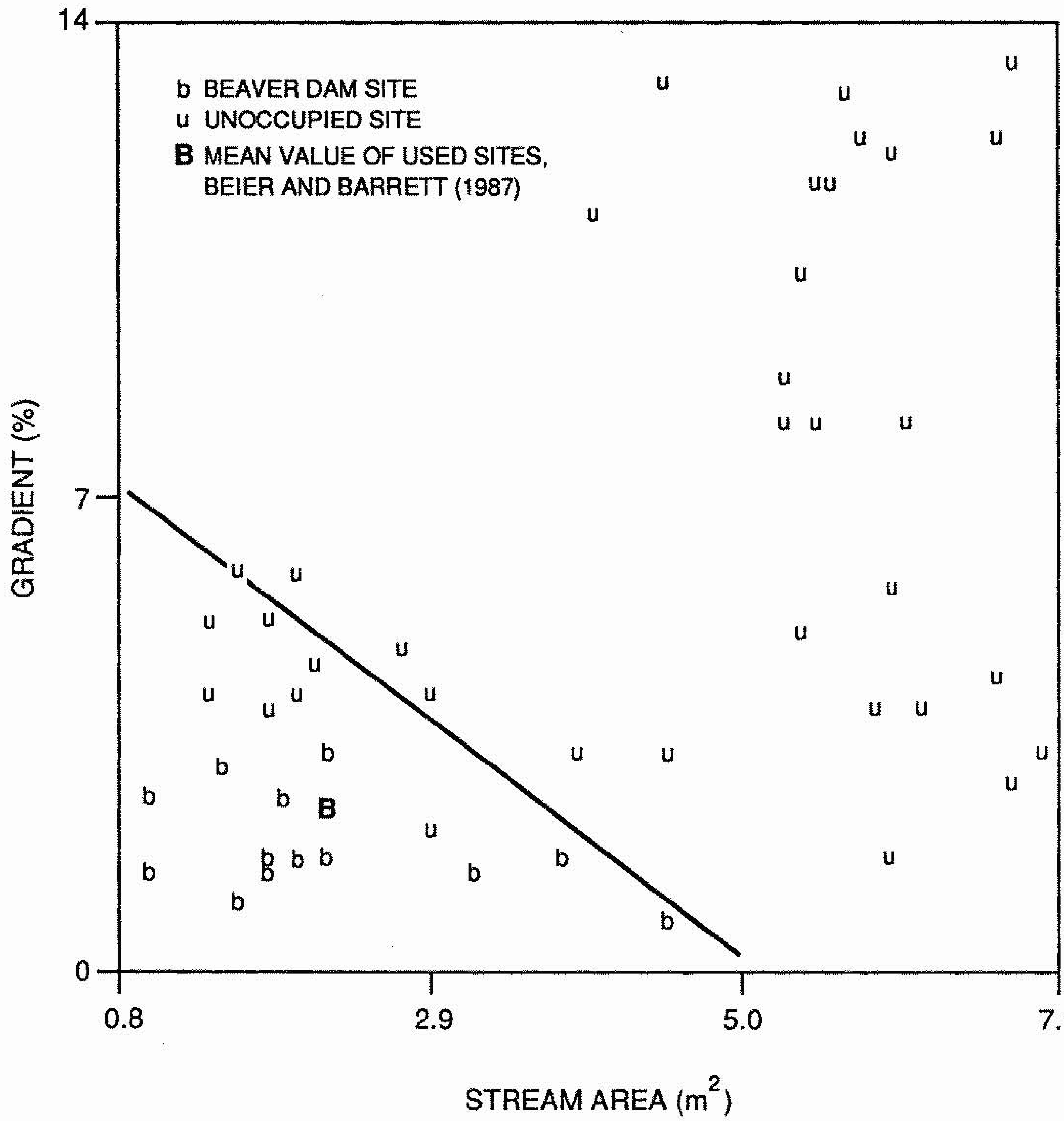

Fig. 2. Relative stream gradient diagram (stream gradient relative to stream cross-sectional area). Five random unoccupied reaches fell below 0.8-m^2 cross-sectional area. Values from random unoccupied reaches below the diagonal line were classified as unusable beaver habitat because of stream substrate or food availability (see text).

suitability. The relationship between gradient and dam building is influenced by the cross-sectional area of the stream because small, high-gradient streams can be dammed (up to a point), but large, high-gradient streams cannot. Similarly, large streams of low gradient can be dammed, but again only up to a point (~5-m^2 cross-sectional area on Long Creek). Our data support this concept, as does the mean value from active colony sites (B, Fig. 2) in the Truckee River basin (Beier and Barrett 1987). Although stream depth, width, and drainage area above the dam were important features in other studies (Howard and Larson 1985, Beier and Barrett 1987), the degree to which these variables indicate habitat quality for beaver is largely dependent on the length of stream sampled and the location of sampling in the watershed. In first- and second-order streams, these variables must be sufficiently large to provide adequate water for beaver (Howard and Larson 1985). In large streams, depth and width have a negative association with dam building because the force of the water can prevent dam persistence during high flows. Sampling a wide range of stream sizes resulted in a Gaussian distribution of these factors with similar means for occupied and unoccupied reaches (due to the location of beaver dams in the central basin), but the range of values for width and depth is narrower for occupied than for unoccupied reaches. Using relative stream gradient (cross-sectional stream area at a given gradient) overcomes this problem.

Substrate type can also be used to further refine selection of potential dam sites. Approximately 63% of Long Creek and its tributaries passes through substrates of rock or large cobble that seem to restrict dam construction. Slough and Sadlier (1977) reported that beaver in their study area did not use lakes with rocky margins.

Bank slope is another physical feature that seems important to dam-site selection. Urich et al. (1984) considered steep banks important to beaver in Missouri, probably because they offer suitable locations for dens along large streams. In our study and that of Beier and Barrett (1987) beaver were associated with gentle bank slopes. The influence of bank slope on habitat suitability may be a locally important variable and should not be universally included in habitat models.

An adequate and accessible supply of food and dam-construction materials must be present for establishment of a beaver colony (Slough and Sadlier 1977). On our study area, sites with <7% hardwood tree cover were unlikely to be dam sites (based on a 95% confidence interval). Denney (1952) summarized the food preferences of beaver in North America and reported that aspen (*Populus tremuloides*), willow, cottonwood, and alder were most often selected. The food species present may be less important in determining habitat quality than are physiographic and hydrologic factors (Jenkins 1981, Allen 1983). If food is not adequate, but the geomorphic features already described for dam placement are met, then the land manager can encourage the growth of food and dam-construction materials by restricting grazing of the riparian area, by artificial regeneration of the trees and shrubs, or both. Once a dam is built, forb abundance will probably increase (Table 2), resulting in improved food quantity and quality in the summer (Jenkins 1981).

CONCLUSIONS

For streams similar to those in the Long Creek basin, we suggest that land managers may evaluate the potential for beaver dam establishment using either the Allen (1983) HSI model modified for eastern Oregon conditions or the Beier and Barrett (1987) model. The discriminant model that we developed provided excellent classification of the original data and used habitat features identified by other investigators as important to beavers, but it has at least two weaknesses. First, variable transformations obscure direct relationships between beaver and the habitat characteristic (the square root or logarithm of a variable may not be as meaningful as the original value). Second, the model has not been tested on an independent data set.

An alternative to using the Allen (1983) or Beier and Barrett (1987) models is to use the following logic-based decision tree. A stream segment may support beaver: (1) if the relative stream gradient falls in the domain below the diagonal line in Figure 2, (2) if the stream substrate is not rock or cobble, and (3) if the hardwood cover is >7%. If hardwood cover is <7%, then the land manager has the option of improving the section of stream habitat by encouraging woody plant growth. To increase the volume of pool habitat in a stream by encouraging beaver, the land manager should identify reaches with adequate geomorphic characteristics, reestablish hardwoods (if necessary), and minimize trapping of beaver until the population is well established. For suitable stream sections, this approach would be more economical than adding logs or similar instream structures that could be better used elsewhere.

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