

BEAVER HABITAT USE AND IMPACT IN TRUCKEE RIVER BASIN, CALIFORNIA

PAUL BEIER, Department of Forestry and Resource Management, University of California, Berkeley, CA 94720
REGINALD H. BARRETT, Department of Forestry and Resource Management, University of California, Berkeley, CA 94720

Abstract: Stepwise logistic regression was used to identify factors important for habitat use by beavers (*Castor canadensis*) on streams. Increasing stream width and depth and decreasing gradient had the strongest positive effects on habitat use; food availability variables added little explanatory power. Some abandoned colony sites appeared to have been located on physically unsuitable habitat, whereas others appeared to be physically suitable sites abandoned due to resource depletion. The fact that few unused or uncolonized reaches were misclassified as suitable habitat suggests that suitable habitat has been saturated. Impact of beaver on woody plants was assessed for 8 forage species. Local extinction of quaking aspen (*Populus tremuloides*) and black cottonwood (*P. trichocarpa*) occurred on 4–5% of stream reaches. Willow (*Salix* spp.) showed good vigor despite heavy use in most reaches.

J. WILDL. MANAGE. 51(4):794–799

Multivariate wildlife-habitat relationships models are often used to identify actually or potentially suitable habitat for various species, or to identify those factors that are important in habitat selection (Shugart 1981). Retzer (1955), Slough and Sadler (1977), and Howard and Larson (1985) have used quantitative techniques to relate beaver occurrence, persistence, and density to various physical and vegetative characteristics.

Wildlife managers have long been concerned with the loss of aesthetic value and impacts on stream channels due to destruction of riparian vegetation by beaver (Bump 1941, Munther 1981). Hall (1960) reported that beaver will deplete aspen in the immediate vicinity of a colony. However, there has been little quantitative documentation of the role of these animals in the loss of riparian vegetation (Kindschy 1985).

Our objectives were to: (1) develop a model to identify the physical and vegetative characteristics of habitat colonized by beavers, and validate the model on a set of stream reaches not used in model development; (2) use the model results to suggest causes for colony abandonment, and evaluate whether beaver have saturated suitable habitat during the 40 years since introduction; and (3) describe the impact of beavers on woody vegetation.

This research was supported by the Calif. Dep. Fish and Game and the Calif. Agric. Exp. Stn. Proj. 4326-MS. J. S. Slaymaker assisted in most of the fieldwork. M. L. Morrison, R. A. Lancia, S. H. Jenkins, and W. M. Block provided helpful criticisms of the manuscript.

STUDY AREA

The Truckee River Basin lies within Sierra, Nevada, Placer, and El Dorado counties, California, and Washoe County, Nevada. Our study covered the Truckee River and its tributaries from the confluence with Deer Creek downstream to Verdi, Nevada. This encompassed an area of approximately 600 km², with 153 km of streams ranging from 1,485 to 2,750 m in elevation. Beavers were introduced into the area during 1938–46 and have since established colonies throughout the basin (P. Beier and R. H. Barrett, unpubl. data).

The dominant vegetation of the area is mixed conifer forest with an overstory of white fir (*Abies concolor*); Jeffrey (*Pinus jeffreyi*), ponderosa (*P. ponderosa*), Washoe (*P. washoensis*), and lodgepole (*P. contorta*) pine; and a shrub component including greenleaf (*Arctostaphylos patula*) and whiteleaf (*A. viscida*) manzanita, snowbrush (*Ceanothus velutinus*) and squawcarpet ceanothus (*C. prostratus*), pale serviceberry (*Amelanchier pallida*), rose (*Rosa* spp.), and Sierra gooseberry (*Ribes roezlii*). The mixed conifer forest is replaced in higher elevations by a forest dominated by Shasta red fir (*Abies magnifica*), western white pine (*P. monticola*), and lodgepole pine, with squawcarpet as a dominant shrub; and in lower elevations by open stands of Jeffrey pine and an understory including big sagebrush (*Artemisia tridentata*), antelope bitterbrush (*Purshia tridentata*), and herbaceous plants. Stream banks were characterized by deciduous riparian vegetation consisting of aspen, cottonwood, willow, mountain alder (*Alnus in-*

Table 1. Habitat variable means by beaver usage group for 214 reaches in the Truckee River Basin, California and Nevada, 1985. (Significant differences between adjacent \bar{x} 's denoted by * [<0.10], ** [<0.05], or *** [<0.01].)

Variable	Active colony (Group 1)		Abandoned colony (Group 2)		Used, no colony (Group 3)		Unused (Group 4)
Stream gradient (%)	1.16	***	4.22	*	5.75	***	12.53
Bank slope ^a	1.22		1.38	*	1.82		2.03
Bare soil (%)	4.3		4.0	**	7.0		6.7
Stream width (m)	8.1	***	5.9		4.9	***	1.4
Stream depth ^b	2.44	*	2.13		1.85	***	0.85
Elevation (m)	1,704	***	1,836		1,869	***	2,085
Riparian zone width (m)	33.4		38.2	*	17.2		19.1
Litter cover (%)	1.0		1.3		2.9	*	5.9
Aspen ^c	0.4	*	0.7		0.8		0.6
Alder ^c	1.7		1.9		2.0		1.9
Cottonwood ^c	1.2	*	0.8		1.0	***	0.4
Willow ^c	2.3		2.3		2.2		2.1
Lodgepole pine ^c	0.9		0.9		0.8		0.9
Jeffrey pine ^c	1.2		1.0		0.9		0.9
Fir ^c	0.4	**	0.7		0.9	***	1.5
Dogwood ^c	1.0		1.0		1.3		1.2
Grasses/forbs ^d	2.3		2.5	***	2.1		2.1

^a Slope class: 1 = 0–30, 2 = 31–40, 3 = 41–60, and 4 = >60%.

^b Depth class: 1 = 1–23, 2 = 24–46, 3 = 47–76, and 4 = >76 cm.

^c Abundance index: 0 = absent, 1 = 1–5, 2 = 6–20, and 3 = >20 trees or shrubs in riparian zone/100 m of stream length.

^d Abundance index: 0 = absent, 1 = rare, 2 = moderate, and 3 = abundant.

cana), gray dogwood (*Cornus racemosa*), bitter cherry (*Prunus emarginata*), and lodgepole pine.

METHODS

Each stream was divided into sampling units approximately 700 m in length. For each such reach, 6 physical and 11 vegetation variables were estimated between 5 May and 20 August 1985 (Table 1). Presence of active beaver colonies, sign of abandoned colonies, and current and past beaver cutting of 8 species of woody plants were also recorded. Four categories of vegetation use were recognized: light cutting, moderate cutting, heavy cutting with vigorous resprouting/recruitment, or heavy cutting with declining plant vigor (defined as poor recruitment/resprouting and displacement of most plants by individuals of other species).

Each stream reach with perennial water was classified into one of 4 groups based on beaver usage: (1) ≥ 1 active colony present; (2) sign of ≥ 1 abandoned colony; (3) some past or present beaver usage, but no sign of past or present colony; and (4) no sign of past or present beaver use. A reach was assigned to Group 1 if it contained both active and abandoned beaver works so that temporarily unused dams would not cause a site to be classed as abandoned.

Most habitat parameters were estimated by interval level variables with only 4 possible states,

and these variables were not normally distributed. The continuous variables were also significantly non-normal (Kolmogorov-Smirnov tests, $P < 0.01$); gradients, for instance, had a strongly bimodal distribution, and were skewed to the right (Table 2). Box's M-statistic indicated that group variances were heterogeneous ($P < 0.01$). The departure from normality persisted when the variables were log- or square-root-transformed, and neither transformation reduced Box's M-statistic. Therefore, stepwise logistic regression (SLR) (Engelman 1985) was used in a series of pair-wise contrasts to identify variables influencing habitat use by beavers. SLR is a classification procedure well-suited for use with dichotomous and discontinuous explanatory variables (Walker and Duncan 1967, Cox 1970) and is appropriate even when the conditions of normality and homogeneous variances are not met (Anderson 1972, Press and Wilson 1978).

Pair-wise contrasts between usage groups 1 and 2, and between groups 2 and 3, were used to suggest causes for colony abandonment. Pair-wise contrasts among all colonized reaches (groups 1 and 2 combined) and all uncolonized reaches (groups 3 and 4 combined), and among all used reaches (groups 1, 2, and 3 combined) and unused reaches (Group 4), were used to evaluate habitat saturation.

Variables that differed ($P < 0.10$) among the

Table 2. Number of reaches with perennial water classified by stream gradient and beaver use for all reaches in the Truckee River Basin, California and Nevada, 1985.

Gradient (%)	Active colony (Group 1)	Abandoned colony (Group 2)	Used, but no colony (Group 3)	Unused (Group 4)	Total
0-2	48	26	18	0	92
3-5	1	4	2	6	13
6-8	1	7	7	13	28
9-11	3	3	10	22	38
12-14	0	2	5	12	19
15-17	0	2	0	11	13
>17	0	1	2	8	11
Total	53	45	44	72	214

groups being contrasted were candidates for entry into the logistic functions. At each step the variable with the largest estimated coefficient was included until the significance of the *F*-statistic of each remaining variable was >0.10 . To avoid the problem of multicollinearity (Williams 1983), minimum tolerance was set at 0.60 (equivalent to a max R^2 of 0.40 with the other variables in the equation). However the latter constraint did not affect selection of variables because the *F*-to-enter criterion was most limiting in all cases. For each contrast, approximately half the cases were randomly selected for model development, and the other half (exact percentage varied due to the random nature of the selection process) were used for model validation. Prior probabilities were based on the proportion of cases falling into each group. The relationship between each coefficient and its standard error was used to standardize coefficient size for purposes of comparing variables included in the functions.

RESULTS

Habitat Use

Within the 214 reaches with perennial water, pairs of usage groups differed significantly with respect to all variables except abundance values for willow, alder, lodgepole pine, and dogwood (Table 1). On average, reaches with more intense beaver usage had flatter gradients, wider and deeper streams, gentler banks, less litter cover, and less fir. The differences in stream gradient were most striking (Table 2). Stream gradient, width, and depth appeared in the logistic functions in the greatest frequency and with the largest coefficients (Table 3).

Reaches with abandoned colonies had signif-

Table 3. Statistics for variables included in logistic functions contrasting reaches grouped by beaver use in the Truckee River Basin, California and Nevada, 1985. Approximately half the reaches were randomly selected to develop each function.

Group comparison ^a Variable	Coefficient	CI ^b	Tolerance
Group 1 (<i>N</i> = 29) vs. Group 2 (<i>N</i> = 20)			
Stream width	0.031	2.60	0.69
Stream gradient	-0.184	-2.13	0.69
Group 2 (<i>N</i> = 26) vs. Group 3 (<i>N</i> = 22)			
Grasses/forbs	0.720	3.25	0.75
Bare soil	-0.143	-2.32	0.79
Stream gradient	-0.162	-2.19	0.91
Groups 1 and 2 (<i>N</i> = 50) vs. groups 3 and 4 (<i>N</i> = 68)			
Stream gradient	-0.168	-4.00	0.62
Bare soil	-0.213	-3.26	0.99
Stream depth	0.900	4.07	0.62
Groups 1, 2, and 3 (<i>N</i> = 66) vs. Group 4 (<i>N</i> = 40)			
Stream gradient	-0.266	-4.53	0.63
Stream depth	2.053	4.53	0.63

^a Group 1 = active colony sites, Group 2 = abandoned colony sites, Group 3 = used but not colonized, and Group 4 = no beaver use.

^b CI = coefficient index (coefficient/SE of the coefficient).

icantly steeper stream gradients, more fir, more aspen, and less cottonwood and were narrower in stream width, shallower in stream depth, and higher in elevation than reaches with active colonies (Table 1). Of these, stream width and gradient were included in the logistic function contrasting reaches with active vs. abandoned colonies (Table 3). The logistic function correctly classified 75% of the reaches with active colonies and 44% of the reaches with abandoned colonies. The abandoned sites, misclassified as active colony sites, had significantly less aspen, fir, and willow than the correctly classified abandoned reaches and significantly less willow than the correctly classified reaches with abandoned colonies (*t*-test, $P < 0.10$).

Reaches that showed sign of beaver use but no sign of past or present colony (Group 3) had significantly steeper stream banks, steeper gradients, more bare ground, lower abundance of herbaceous plants, and narrower zones of riparian vegetation than reaches with abandoned colonies (Group 2) (Table 1). In contrasting groups 2 and 3, SLR selected stream gradient, percent bare ground, and abundance of herbaceous vegetation (Table 3) and correctly classified 63% of the reaches with abandoned colonies and 45% of the uncolonized-used reaches.

Colonized reaches (groups 1 and 2 combined) differed significantly ($P < 0.10$) from uncolonized reaches (groups 3 and 4 combined) with

respect to all variables except abundance values for alder, aspen, lodgepole pine, and dogwood. SLR selected 3 of these variables: stream gradient, stream depth, and percent bare ground (Table 3). The logistic function correctly classified 77% of the colonized reaches and 87% of the uncolonized reaches.

Used reaches (groups 1, 2, and 3 combined) had significantly gentler gradients and banks, wider and deeper streams, less litter cover and fir, and more cottonwood and willow than unused reaches (Group 4). Stream gradient and stream depth were included in the logistic function (Table 3), which correctly classified 91% of the used reaches and 94% of the unused reaches.

Impact on Woody Vegetation

In 32% of the 63 reaches where beaver and aspen coexisted, aspen had been used to the point that most stems had died or were declining in vigor (Table 4). On three of these reaches no living aspen remained, although beaver-cut stumps indicated that aspen had been present. In contrast, cottonwood and willows were used to the point of vigor decline in 16–17% of the reaches where they co-occurred with beaver, including 3 reaches in which cottonwood had become locally extinct (Table 4). Mountain alder had declined in vigor in 3 reaches. White fir, lodgepole pine, and Jeffrey pine were also cut, but never to the point of vigor decline.

DISCUSSION

Habitat Use

Stream gradient, stream depth, and stream width were clearly the most important factors related to beaver habitat use, based on the frequency of their inclusion in the functions and the magnitude of their coefficients. Retzer (1955), Slough and Sadlier (1977), and Howard and Larson (1985) similarly found that gradient and stream width were the most important physical variables related to colony density on streams.

Low stream gradients are probably important because they allow beavers to greatly increase their safe foraging area by dam-building, because steep topography hinders the establishment of a food transportation system (Slough and Sadlier 1977), and because flood damage to dams and food caches is more likely on higher-gradient streams (Taylor 1970). Stream depth and width are highly correlated ($r^2 = 0.83$ in this study). Deep and wide streams are important because a higher-volume channel offers

Table 4. Response of quaking aspen, black cottonwood, willow, and mountain alder to beaver usage for 142 reaches with past or present beaver use in the Truckee River Basin, California and Nevada, 1985.

Species	N ^a	% of reaches showing			
		Local extinction	Declining plant vigor	Good vigor, >light cutting	Good vigor, light cutting
Aspen	63	5	27	43	25
Cottonwood	84	4	12	62	23
Willow	142	0	17	51	32
Alder	118	0	3	47	50

^a No. of reaches on which the species was present.

more escape cover, more secure sites for underwater food caches, and a more reliable source of water for impoundments, especially during drought years (Howard and Larson 1985).

Bare soil and abundance of herbaceous plants were also chosen by the classification functions although with less frequency and smaller standardized coefficients than the previously discussed variables. Beavers prefer herbaceous vegetation over woody forage during seasons when herbaceous food is available (Jenkins 1981), and the increased likelihood of colonization in reaches with abundant herbaceous plants may reflect this fact. However, this difference, and the decrease in percent bare ground on colonized reaches, may also be responses to beaver occupancy, rather than factors to which beavers respond in selecting habitat. Removal of over-story woody vegetation allows herbaceous plants to increase their ground cover, and beaver impoundments increase soil moisture, which stimulates further plant growth.

Vegetation variables added little explanatory power to the functions. In part this is because beavers alter their habitat so that the observed species abundances may bear little relation to what was present when a colony was established. However, width of riparian vegetation, which was intended to index the total potential food supply, also failed to help explain beaver habitat use. Howard and Larson (1985) used aerial photographs taken prior to beaver occupancy to measure total hardwood and softwood abundances, and similarly found that food availability variables added little explanatory power. Jenkins (1981:577) similarly concluded that beaver are so highly opportunistic in food selection that "prediction of likely areas of beaver impact by evaluation of food resources may be problematic."

Colony Abandonment

Evidence of beaver activity in summer is sometimes cryptic (S. H. Jenkins, pers. commun.) and some active colonies may have appeared abandoned, introducing error into the active vs. abandoned logistic function and decreasing classification success. However, the significant univariate differences, and the importance of stream gradient and width in differentiating between reaches with active vs. abandoned colonies, suggest that abandoned sites are often located on marginal habitat and are not simply good colony sites at which resources have been depleted. The poor success of SLR in discriminating between abandoned colony sites and used but uncolonized reaches further supports this hypothesis.

Alternatively, the large number of abandoned reaches misclassified as reaches with active colonies suggests that many of these reaches are not fundamentally different from active colony sites. Further, abandoned reaches misclassified as active had significantly ($P < 0.10$) less aspen, fir, and willow than the correctly classified reaches and significantly less willow than active colony sites; this supports the interpretation that these reaches were physically suitable sites abandoned due to food depletion.

Thus, abandoned colony sites seem to consist of 2 distinct types of reaches. Some of the reaches are similar to active sites with respect to physical variables but have low food availability. It seems likely that these sites will be occupied again when the vegetation recovers. The other abandoned colony sites are similar to uncolonized reaches in that they are characterized by steep gradients and narrow stream widths; these were probably marginal sites occupied for only a year or so and will probably never support persistent colonies.

Howard and Larson (1985) found a significant effect of stream gradient on colony site longevity, supporting our finding that this factor is important in colony abandonment. These findings are also consistent with the pattern of site occupancy and abandonment described by Taylor (1970).

Habitat Saturation

Beavers appear to have saturated suitable habitat during the 40 years since their introduction to the Truckee River Basin. This conclusion is based on the high success rate in clas-

sifying used vs. unused reaches and colonized vs. uncolonized reaches. If there was a substantial amount of suitable habitat awaiting colonization, more of the unused and uncolonized reaches would have been misclassified as suitable habitat.

Impact on Woody Vegetation

The local extinction of aspen and cottonwood on several reaches indicates that beaver use may have a strong negative impact on these species. Seasonal grazing by sheep in much of the Truckee Basin may also be a contributing factor. Loss of aspen and cottonwood was especially severe along the Truckee River, where beaver cutting was high even on reaches far from colonies, apparently because the density of dispersing animals is sufficient to maintain pressure on the depleted species. Without control of beaver populations, aspen and cottonwood may become extinct on much of the Truckee River. In some cases (e.g., private homesites and campgrounds) it may be economically feasible to conserve these species by fencing individual trees.

Although willow suffered vigor decline in many reaches, it generally tolerated heavy harvest by beaver and was present in all 142 reaches used by beaver. Kindschy (1985) also found that prolonged use of willow by beaver did not appear to cause loss of the species. Hall (1960:493) reported that "even severe abuse will discourage [willow] only temporarily."

Management Implications

The finding that beaver habitat use depends mainly on physical variables and not on food abundance variables means that manipulation of forage resources may be of little use in controlling beaver populations. Indeed, the beaver's highly opportunistic food habits, as described by Jenkins (1981) and as observed in the Truckee River Basin (P. Beier and R. H. Barrett, unpubl. data), suggest that removal of favored forage plants is more likely to result in the loss of economically valuable conifers than in the elimination of nuisance beaver.

The classification models developed and tested herein should apply to other 1st–5th-order mountain streams in mixed-conifer habitats. Given that many abandoned colonies are similar to active sites and may be reused, the colonized vs. uncolonized logistic function should be used to estimate total number of potential colony sites.

The total amount of suitable (foraging and colonizable) habitat can be estimated from the used vs. unused logistic function. Both functions can be inexpensively applied using data from maps and aerial photos with a minimum of fieldwork.

These statistical methods can be used to develop classification models for other habitats and species. SLR appears to be a useful and efficient tool for such models because it is relatively robust to violations of the assumptions of normality and homogeneity of variances and because it can be used with interval-level data, which can be obtained quickly over a large area. Unlike discriminant analysis, which can contrast any number of groups simultaneously, SLR can be applied only to 2 groups. However, as illustrated here, several well-chosen pair-wise contrasts are at least as informative. Finally, the validation methodology can be used to help assess whether an introduced population has reached carrying capacity.

Additional study is needed to assess the impact of beaver on aspen and cottonwood because alternative factors, such as disease, were not considered in this study. Nonetheless, the apparent ability of beaver to cause local extinction of these trees may justify management action in areas with high beaver density if the aesthetic or economic value of the trees is high.

LITERATURE CITED

- ANDERSON, J. A. 1972. Separate sample logistic discrimination. *Biometrika* 59:19-35.
- BUMP, G. 1941. Problems of beaver management in a fish and game agency. *Trans. North Am. Wildl. Conf.* 6:300-308.
- COX, D. R. 1970. *The analysis of binary data*. Methuen & Co. Ltd., London, U.K. 142pp.
- ENGLEMAN, L. 1985. Stepwise logistic regression. Pages 330-344 in J. W. Dixon, ed. *BMDP*. Univ. Calif. Press, Los Angeles.
- HALL, J. G. 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. *Ecology* 41:484-494.
- HOWARD, R. J., AND J. S. LARSON. 1985. A stream habitat classification system for beaver. *J. Wildl. Manage.* 49:19-25.
- JENKINS, S. H. 1981. Problems, progress, and prospects in studies of food selection by beavers. Pages 559-579 in J. A. Chapman and D. Pursley, eds. *Worldwide furbearer conference proceedings*. Worldwide Furbearer Conf., Inc., Frostburg, Md.
- KINDSCHY, R. R. 1985. Response of red willow to beaver use in southeastern Oregon. *J. Wildl. Manage.* 49:26-28.
- MUNTER, G. L. 1981. Beaver management in grazed riparian ecosystems. Pages 234-241 in J. M. Peek and P. D. Dalke, eds. *Wildlife-livestock relationships symposium proceedings*. For. Wildl. Exp. Stn., Univ. Idaho, Moscow.
- PRESS, S. J., AND S. WILSON. 1978. Choosing between logistic regression and discriminant analysis. *J. Am. Stat. Assoc.* 73:699-707.
- RETZER, J. L. 1955. Physical environmental effects on beavers in the Colorado Rockies. *Proc. Annu. Conf. Western Assoc. Game and Fish Comm.* 35:279-287.
- SHUGART, H. H., JR. 1981. An overview of multivariate methods and their application to studies of wildlife habitat. Pages 4-10 in D. E. Capen, ed. *The use of multivariate statistics in studies of wildlife habitat*. U.S. For. Serv. Gen. Tech. Rep. RM-87.
- SLOUGH, B. G., AND R. M. F. S. SADLER. 1977. A land capability classification system for beaver (*Castor canadensis* Kuhl). *Can. J. Zool.* 55:1324-1335.
- TAYLOR, D. 1970. Growth, decline, and equilibrium in a beaver population at Sagehen Creek, California. Ph.D. Thesis, Univ. California, Berkeley. 162pp.
- WALKER, S. H., AND D. B. DUNCAN. 1967. Estimation of the probability of an event as a function of several independent variables. *Biometrika* 54:167-179.
- WILLIAMS, B. K. 1983. Some observations on the use of discriminant analysis in ecology. *Ecology* 64:1283-1291.

Received 30 October 1986.

Accepted 21 February 1987.