rel in Grand Canyon National Park. Wildl. Monogr. 75. 54pp.

HOFFMEISTER, D. F., AND V. E. DIERSING. 1978. Review of the tassel-eared squirrels of the subgenus *Otosciurus*. J. Mammal. 59:402–413.

HOVIND, H. J., AND C. E. RIECK. 1961. Basal area and point-sampling: interpretation and application. Wis. State Conserv. Dep. Tech. Wildl. Bull. 23. 52pp.

HUSCH, B., C. I. MILLER, AND T. W. BEERS. 1972. Forest mensuration. 2nd ed. The Ronald Press Co., New York, N.Y. 410pp.

KEITH, J. O. 1965. The Abert squirrel and its dependence on ponderosa pine. Ecology 46:150–163.

MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223–249.

MORRISON, D. F. 1967. Multivariate statistical methods. McGraw-Hill Book Co., New York, N.Y. 338pp.

PATTON, D. R. 1975. Abert squirrel cover requirements in southwestern ponderosa pine. U.S. For. Serv. Res. Pap. RM-145. Rocky Mt. For. Range Exp. Stn., Fort Collins, Colo. 12pp.

———. 1977. Managing southwestern ponderosa pine for the Abert squirrel. J. For. 75:264–267.

———, H. G. HUDAK, AND T. D. RATCLIFF. 1976. Trapping, anesthetizing, and marking the Abert squirrel. U.S. For. Serv. Res. Note RM-307, Rocky Mt. For. Range Exp. Stn., Fort Collins, Colo. 2pp.

PEDERSON, J. C., R. N. HASENYAGER, AND A. W. HEGGEN. 1976. Habitat requirements of the Abert squirrel (*Sciurus aberti navajo*) on the Monticello District, Manti-LaSal National Forest of Utah. Utah Div. Wildl. Resour. Publ. 76-9, Salt Lake City. 108pp.

PIELOU, E. C. 1977. Mathematical ecology. John Wiley & Sons, New York, N.Y. 385pp.

RASMUSSEN, D. I. 1941. Biotic communities of Kaibab Plateau, Arizona. Ecol. Monogr. 11:229–275.

———. 1971. The Kaibab squirrel in the Kaibab National Forest. U.S. For. Serv. Southwest. Reg., Albuquerque, N.M. 91pp.

RATCLIFF, T. D., D. R. PATTON, AND P. F. FFOLLIOTT. 1975. Ponderosa pine basal area and the Kaibab squirrel. J. For. 73:284–286.

SKINNER, T. H., AND J. O. KLEMMEDSON. 1978. Abert squirrels influence nutrient transfer through litterfall in a ponderosa pine forest. U.S. For. Serv. Res. Pap. RM-353, Rocky Mt. For. Range Exp. Stn., Fort Collins, Colo. 8pp.

STEPHENSON, R. L. 1975. Reproductive biology and food habits of Abert's squirrel in central Arizona. M.S. Thesis, Arizona State Univ., Tempe. 66pp.

TROWBRIDGE, A. H., AND L. L. LAWSON. 1942. Abert squirrel-ponderosa pine relationships at the Fort Valley Experimental Forest, Flagstaff, Ariz. Ariz. Coop. Wildl. Res. Unit, Tucson. 38pp.

*Received 14 February 1984.*
*Accepted 22 May 1984.*

# A STREAM HABITAT CLASSIFICATION SYSTEM FOR BEAVER

REBECCA J. HOWARD,[1] Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, MA 01003
JOSEPH S. LARSON, Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, MA 01003

*Abstract:* Documentation over a 28-year period of beaver (*Castor canadensis*) habitat use permitted development and testing of two models to predict maximum density of active beaver colonies on streams. Principal components regression, a technique that reduced the confounding effects of closely correlated ecological variables found in earlier studies of this type, and discriminant analysis were used for model development. In mixed coniferous–deciduous forest habitat, the percentage of hardwood vegetation, watershed size, and stream width had significant positive effects on active colony density. Increasing stream gradient and progressively well-drained soils had negative effects. In field-tests, the models were 80% and 75% reliable in predicting active colony density.

***J. WILDL. MANAGE. 49(1):19–25***

Evaluation and classification of North American beaver habitat have progressed from early qualitative descriptions (Atwater 1940, Packard 1947, Northcott 1964) and systems based solely on woody food requirements (Buckley 1950, MacDonald 1956) to more recent quantitative studies. Retzer et al. (1956) quantified the relationship of habitat variables to habitat suitability in the Rocky Mountain region. Boyce (1974) used linear regression analysis to relate stream distances between colonies to major plant associations and physical properties of streams in Alaska. In British Columbia, Slough and Sadleir (1977) described the relation of colony site

[1] Present address: National Coastal Ecosystems Team, U.S. Fish and Wildlife Service, 1010 Gause Blvd., Slidell, LA 70458.

numbers to various physical and vegetative parameters using backwards stepwise multiple regression analysis. Willis (1978) used stepwise discriminant analysis to evaluate the importance of habitat components in discriminating between trees cut by beaver and those left standing. Allen (1982) designed a mathematical model for use in impact assessment (i.e., comparison of habitat value before and after proposed development).

This paper describes a beaver habitat classification system based on a study of an area used by beaver over a 28-year period. The objectives were to: (1) identify vegetation and physical components of habitat critical to longevity (length of time occupied) of beaver colonies on streams in central Massachusetts; and (2) use the variables critical to site longevity to develop mathematical models to predict the maximum density of active beaver colonies on streams. Land capability classes, defined by colony density, were distinguished.

We thank W. E. Dodge, Mass. Coop. Wildl. Res. Unit, for securing partial funding for this study and providing vehicles for field use. We also thank J. T. Finn and K. A. Converse for statistical advice and A. J. Steiner for computer assistance.

## STUDY AREA

The study was conducted on Prescott Peninsula, New Salem, Massachusetts. Prescott Peninsula is part of the Quabbin Reservation and covers 60 km² in central Massachusetts. The vegetation, dominated by species typical of the eastern mixed coniferous–deciduous forest, and physical features of the peninsula have been described previously (Hodgdon 1978, Brooks et al. 1980).

Hunting and trapping have been prohibited on Quabbin Reservation since 1936. The first evidence of beavers on Prescott Peninsula since their extirpation from the region about 200 years ago was found in 1952, and the population expanded thereafter (Hodgdon 1978). The rate of increase in number of active shore and interior (stream) colony sites has slowed in recent years (Fig. 1). The peninsula was assumed to be near carrying capacity at the time of this study based on historical information and on observation of habitat utilization. In 1980 there were 35 active stream colonies, a density of 0.83 colonies/km of stream. Nordstrom (1972) reported that 1.25 beaver colonies/km represented saturation density in New Brunswick, and Collins (1976) reported that 0.9 colonies/km appeared to be carrying capacity for Wyoming streams.

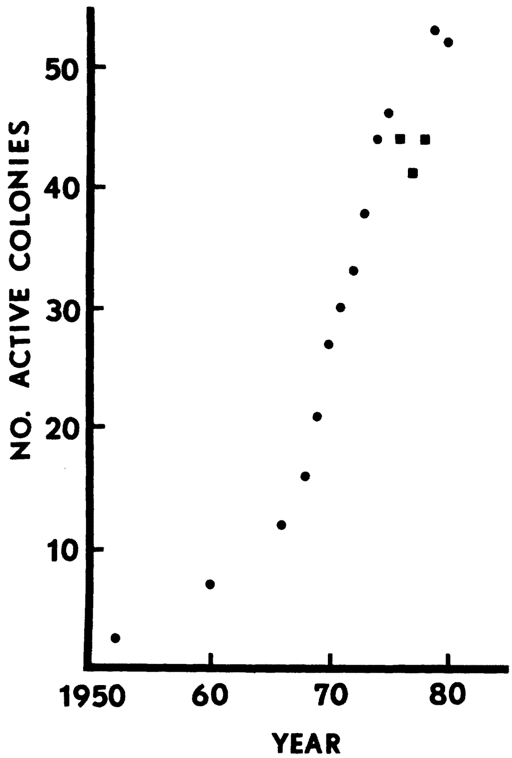

Fig. 1. Number of active beaver colonies on Prescott Peninsula, 1950–80. Surveys conducted during 1976, 1977, and 1978 were not as intensive as those conducted during other years.

## METHODS

### Colony Site Longevity

Potential habitat variables selected for this study define water reliability and food availability. Variables were included based on their importance as indicated in the literature and their ease of measurement on available maps and aerial photographs. The 14 habitat variables selected are described in Table 1. No attempt was made to distinguish tree species composition of hardwood and softwood stands.

A beaver colony was defined as a group of beaver occupying a pond or stretch of stream, using a common food supply, and maintaining a common dam or dams (Bradt 1938). A colony may have used several lodges or bank dens in summer, but only one lodge was occupied in winter and a single food cache was constructed in the autumn (Hay 1958). A colony site, as

Table 1. Abbreviated names and descriptions of habitat variables.

| Variable name | Description |
|---|---|
| WSS | Watershed size (ha) above the colony site |
| SW | Stream width (m) below the final dam |
| GRAD | Stream gradient |
| SOD | Soil drainage class<br>1. Very poorly drained<br>2. Poorly drained<br>3. Moderately well to well drained<br>4. Somewhat excessively to excessively drained |
| H1 | Percentage hardwood vegetation within 100 m of the site center |
| H2 | Percentage hardwood vegetation within 200 m of the site center |
| S1 | Percentage softwood vegetation within 100 m of the site center |
| S2 | Percentage softwood vegetation within 200 m of the site center |
| HS1 | Percentage hardwood/softwood mixed vegetation within 100 m of the site center |
| HS2 | Percentage hardwood/softwood mixed vegetation within 200 m of the site center |
| SS1 | Percentage shrub/wetland vegetation within 100 m of the site center |
| SS2 | Percentage shrub/wetland vegetation within 200 m of the site center |
| AF1 | Percentage abandoned fields within 100 m of the site center |
| AF2 | Percentage abandoned fields within 200 m of the site center |

used in this study, was a pond or series of ponds used by a colony of beaver throughout the year. Individual sites were usually separated by an unaltered section of stream. If no unaltered section of stream remained, separate food caches in the autumn were presumed to distinguish colonies.

The history of beaver establishment and occupancy patterns of 55 colony sites on Prescott Peninsula from 1952 to 1980 was compiled from aerial photographs, forester field notes, and ground survey records. Vegetation characteristics were obtained for pre-beaver occupancy by stereoscopic examination of 1:20,000 black-and-white panchromatic aerial photographs taken in June 1952, before beaver altered the habitat. A dot grid was used to sample the composition of vegetation within 100 m of the site center, a distance reported as the maximum beaver will travel from water to obtain food (Hodgdon and Hunt 1953, MacDonald 1956, Rutherford 1964, Jenkins 1980). To account for vegetation that becomes available to a colony as dams are enlarged and canals are built over time, vegetation within 200 m of the site center was also measured using a dot grid.

Watershed size above each site was determined by delineation of watersheds on 1:25,000-scale U.S. Geological Survey topographic maps. Gradient was calculated by dividing the vertical drop indicated on the topographic map by horizontal distance and converting to percent. Soil types at the site center and associated drainage class were obtained from Soil Conservation Service soil survey maps (Mott and Fuller 1967). Stream width was measured with a meter tape in the field at the point below the final (downstream) dam where the channel appeared to be unaffected by beaver activities. Measurement was taken bank to bank and was the average of three values taken 30 m apart.

Principal components regression (PCR), a restricted type of ordinary least squares (OLS) regression, was used to assess the relation of habitat variables to beaver colony site longevity. A linear relationship between the dependent variable (the length of time a site was occupied) and the independent (explanatory) habitat variables was assumed. Converse and Morzuch (1981) described the utility of PCR in reducing the confounding effects of multicollinearity (lack of independence among explanatory variables) that are frequently associated with regression analyses (Morzuch 1980). Principal components analysis transforms a set of highly correlated variables into a set of uncorrelated, or independent, components that account for all variation in the original variables (Green 1979). The components created from the habitat variables in this study were regressed against the dependent variable to develop the PCR model. Components accounting for insignificant amounts of variation in the data were sequentially deleted. A modified Fisher (1970) equation was used to test for a significant difference between the unrestricted (OLS) and restricted (PCR) models at $P < 0.05$ using noncentral mean square error (MSE) $F$ criteria (Wallace and Toro-Vizcarrando 1969) as component deletion progressed. Component deletion was halted at the step previous to that which caused a significant difference to appear between the two models. Principal components estimators were then transformed to estimators on the original variables. The final PCR model was tested for bias by comparing the classical (central) $F$ value to the noncentral $F$ value.

Linear discriminant analysis (DA) was the second technique used to assess the relation of 14 habitat variables to colony site longevity. DA is analogous to an OLS regression analysis in which the dependent variable assumes a value indicating membership in one of two or more groups (Linderman et al. 1980). Beaver colony sites in this study were assigned to two groups based on length of occupancy. Group I was comprised of 29 sites considered good (occupied 5 years or more). Group II had 26 sites considered poor (occupied less than 5 years). Discriminant functions developed were linear combinations of the variables that maximized separation of the groups. Standardized coefficients indicated the relative contribution of the associated habitat variables to discriminating between the two occupancy groups. Stepwise discriminant analysis using the Wilks method (Nie et al. 1975) was also used to discern relative importance of the variables. Independent variables were selected for entry into analysis in the stepwise procedure on the basis of discriminating power. Classification functions developed by the statistical procedure assigned a probability of an unknown case belonging to each group (Nie et al. 1975). Computer statistical packages SPSS (Nie et al. 1975) and SHAZAM (White 1978) were used for data analysis.

### Maximum Colony Density and Land Capability

Habitat variables significantly affecting colony site longevity, as indicated by data analyses (see Results), were assumed to also affect the potential density of active colonies. These significant variables were measured at 36 1-km stream sections whether or not beaver were present in the stream section. Maximum density of colonies associated with each section was obtained from a ground survey of food caches conducted in October 1980.

PCR and DA were also used to construct models that predicted the maximum density of active beaver colonies on streams. The number of active colonies per km (1, 2, and 3 or more colonies) was used as the dependent variable in PCR and as the group designator in DA. Land capability was assessed by converting the maximum number of active colonies per km of stream habitat into classes.

Table 2. Estimated coefficients for principal components regression model of the effect of habitat variables on beaver colony site longevity.

| Variable | Mean ± SD | Estimated coefficient | $t$ ratio |
|---|---|---|---|
| WSS | 133.52 ± 169.43 ha | −0.009 | −1.535 |
| SW | 2.85 ± 1.34 m | 1.515 | 2.139*[a] |
| GRAD | 2.65 ± 2.06% | −0.976 | −3.236** |
| SOD | 2.73 ± 0.87 | −2.289 | −2.901** |
| H1 | 50.95 ± 38.03% | −0.011 | −2.358* |
| H2 | 49.75 ± 31.97% | −0.021 | −2.688* |
| S1 | 18.67 ± 22.12% | 0.009 | 0.737 |
| S2 | 20.48 ± 20.23% | −0.004 | −0.238 |
| HS1 | 17.47 ± 27.52% | −0.017 | −1.329 |
| HS2 | 19.04 ± 22.39% | 0.004 | 0.356 |
| SS1 | 4.35 ± 13.33% | 0.024 | 0.796 |
| SS2 | 2.03 ± 5.68% | 0.011 | 0.176 |
| AF1 | 6.03 ± 15.27% | 0.042 | 2.197* |
| AF2 | 5.31 ± 11.62% | 0.046 | 1.801 |
| Intercept | 14.170 | | |

[a] Levels of significance are * $P < 0.05$, ** $P < 0.01$.

An independent test of the predictive models was accomplished using streams on the east side of Quabbin Reservation. Habitat on the east side is similar to the study area's and has the same history of hunting and trapping closure.

## RESULTS

### Colony Site Longevity

The PCR model developed to alleviate the problem of multicollinearity retained 8 of 14 components under both the MSE and classical $F$ deletion criteria, indicating an insignificant ($P > 0.05$) amount of bias was introduced through use of the procedure. Final PCR coefficients appear in Table 2. Stream width (SW), stream gradient (GRAD), soil drainage class (SOD), hardwoods within 100 m (H1), hardwoods within 200 m (H2), and abandoned fields within 100 m (AF1) were significantly related to colony site longevity.

All 14 habitat variables significantly ($P < 0.01$) explained variance between the two occupancy length groups in discriminant analysis. The standardized canonical discriminant function coefficients developed, however, could not be interpreted as the relative contribution of the variables to discriminating between the two groups because of correlations among the variables. Stepwise discriminant analysis added the four water reliability variables in the following

Table 3. Estimated coefficients from principal components regression model of maximum colony density on streams in central Massachusetts.

| Variable | Mean ± SD | Estimated coefficient | *t* ratio |
|---|---|---|---|
| WSS | 152.71 ± 166.63 ha | 0.001 | 2.351*[a] |
| SW | 2.81 ± 1.27 m | 0.106 | 2.726* |
| GRAD | 3.69 ± 2.61% | −0.058 | −3.371** |
| SOD | 2.63 ± 0.56 | −0.263 | −3.170** |
| AF1 | 8.23 ± 9.77% | −0.003 | −1.336 |
| H1 | 45.55 ± 29.25% | 0.005 | 2.186* |
| H2 | 48.26 ± 26.31% | 0.005 | 2.236* |
| Intercept 1.034 | | | |

[a] Levels of significance are * $P < 0.05$, ** $P < 0.01$.

order: GRAD, SOD, SW, and watershed size (WSS). The four variables significantly ($P < 0.05$) explained the variation between groups. Although the selection procedure was rendered invalid by multicollinearity among the variables, the relative importance of the water reliability variables was indicated by the classification results. Classification functions derived from the stepwise results correctly classified 78% of the sites, the same results achieved in the initial direct analysis using all 14 variables. Food availability variables alone did not significantly explain variation between the groups and correctly classified only 63% of the cases. Several other combinations of variables were investigated, but no combination discriminated as well as the water reliability variables.

### Maximum Colony Density and Land Capability

Statistical analyses indicated that seven variables—WSS, SW, GRAD, SOD, H1, H2, and AF1—significantly affected beaver colony site longevity. These variables were measured over 1-km sections of stream. Simple pairwise correlations between variables showed high degrees of dependence between WSS and SW ($r = 0.85$) and between H1 and H2 ($r = 0.96$). The final PCR model retained two components under both the MSE and classical *F* deletion criteria, indicating the model did not gain a significant ($P < 0.05$) amount of bias. All variables excluding AF1 were significant when the components were transformed back to the original variables (Table 3). The final PCR model to predict the maximum number of active colonies per km of stream (Y) took the form:

$$Y = 1.034 + 0.001(\mathrm{WSS}) + 0.106(\mathrm{SW}) - 0.058(\mathrm{GRAD}) - 0.263(\mathrm{SOD}) - 0.003(\mathrm{AF1}) + 0.005(\mathrm{H1}) + 0.005(\mathrm{H2}). \quad (1)$$

In the DA model, the seven habitat variables significantly ($P < 0.05$) explained the variance among the three colony density groups. Classification functions correctly classified 78% of the cases. Guidelines for applying both predictive models were provided by Howard (1982).

Three land capability classes for beaver on stream habitat in central Massachusetts were distinguished based on the results of this study. Class I habitat is excellent and can support two or more active colonies per km. Class II habitat is suitable and is capable of supporting one active colony per km. Class III habitat is unsuitable for beaver colonization and supports no colonies.

### Model Tests

An independent test of both predictive models was carried out using information obtained at 20 stream sections on the east side of Quabbin Reservation. A chi-square test compared actual number of colonies to the number predicted by the PCR model (eq. 1). No difference ($P > 0.01$) was found. A goodness-of-fit test comparing true capability class to class predicted by the DA model also indicated no difference ($P > 0.01$). Prediction of capability class was successful at a rate of 75% for the PCR model and 80% for the DA model. The models were 95% (DA) and 90% (PCR) successful in predicting simply the presence or absence of beaver.

## DISCUSSION

### Colony Site Longevity

All 4 water reliability variables significantly affected colony site longevity, whereas only 3 of 10 food availability variables had significant effects. Aside from the obvious conclusion that beaver habitat suitability is governed by sufficiency of a year-round water supply, there is probably a relationship between this physical factor (water reliability) and food availability. The importance of herbaceous and aquatic vegetation in the summer diet of the beaver has been noted in several studies (Bradt 1938, Hall 1971, Svendsen 1980). The beaver is traditionally believed to depend upon the food cache for survival during the winter in northern latitudes. Because the food cache mainly is comprised of woody vegetation, the availability of woody vegetation has received the most attention in habitat classification studies. Availability of herbaceous vegetation, including roots and tubers, is difficult to quantify. If beaver continue to feed on aquatic roots and tubers throughout the winter, sufficient water during the summer for maximum growth of that vegetation could influence food availability. Availability of woody vegetation might therefore be of secondary importance in habitat suitability, with its main contribution occurring early in the occupation of a site when construction materials are required.

Examination of the Prescott Peninsula beaver colony occupation records yielded additional information concerning colony site selection by beaver. Of the 19 sites colonized between 1952 and 1969, 17 were occupied longer than 10 years. The remaining two sites were occupied 8 and 9 years. Of these 19 sites, 12 were still used by beaver in 1980. It was not until 1971 that sites were selected, occupied for 1 or 2 years, and then abandoned. This information indicates that the best sites were chosen first and that variables critical to site longevity may also be critical to site selection.

A potential problem exists in interpreting longevity results of our study when the nature of the site occupancy records is examined. Some error was introduced to the methodology if sites occupied for the first time recently, and therefore classified with the older abandoned sites, are in the future occupied for long periods of time. However, these sites probably represented temporary habitat utilized while a more permanent site was recovering, such as noted by Hall (1971) in central Ontario. Several instances of reoccupation of long-term sites after abandonment of 1 or 2 years were noted.

### Maximum Colony Density

The final PCR model indicated that abandoned fields did not affect the maximum density of beaver colonies. Watershed size had a positive effect on the density of colonies ($P < 0.05$). This effect, combined with the positive effect ($P < 0.05$) of stream width and the negative effects ($P < 0.01$) of gradient and soil drainage class, indicated the best beaver habitat occurred on relatively wide streams with low gradient on soil with poor drainage. The models to predict maximum colony density were developed on streams with relatively narrow widths (<8 m) and small watersheds (<750 ha) and should be applied only in similar habitat.

This study represents an advance beyond the beaver habitat classification of Slough and Sadleir (1977). Our results were based on actual colony sites, as determined by number of occupied lodges (i.e., food cache present in autumn), whereas Slough and Sadleir (1977) used a count of all lodges regardless of whether or not they were currently occupied. This latter procedure results in an inflated estimate of colony site numbers. In addition, statistical methods used in this study avoided the problem of multicollinearity among habitat variables that plagues most habitat analyses. Finally, field evaluation of our stream habitat models provided a robust test that is lacking in earlier studies of beaver habitat.

## MANAGEMENT IMPLICATIONS

The habitat models for beaver were developed and tested on small streams in a mixed coniferous–deciduous forested region of Massachusetts and should be applicable in similar habitat. The statistical methodology described can be applied to develop beaver habitat classification models in dissimilar habitat if the assumption that carrying capacity for active colonies has been attained can be made with a degree of certainty. The models can be used to rank beaver stream habitat quality and thus aid in land use decisions. As an example, they provide justification for management practices to increase populations in high quality habitat where conflict with humans is likely to be minimal.

Additional studies are needed to refine beaver habitat classification systems. Use of below-ice aquatic vegetation during the winter should be investigated to better assess the relative importance of woody vs. herbaceous vegetation as food sources during this critical period. Inclusion of nonwoody food availability in beaver habitat models may be crucial to constructing reliable models in southern latitudes where food caching does not occur.

## LITERATURE CITED

ALLEN, A. W. 1982. Habitat suitability index models: beaver. U.S. Fish Wildl. Serv. FWS/OBS-82/10.30. 20pp.

ATWATER, M. M. 1940. South Fork (Montana) beaver survey: 1939. J. Wildl. Manage. 4:100–103.

BOYCE, M. S. 1974. Beaver population ecology in interior Alaska. M.S. Thesis, Univ. Alaska, Fairbanks. 161pp.

BRADT, G. W. 1938. A study of beaver colonies in Michigan. J. Mammal. 19:139–162.

BROOKS, R. P., M. W. FLEMING, AND J. J. KENNELLY. 1980. Beaver colony response to fertility control: evaluating a concept. J. Wildl. Manage. 44: 568–575.

BUCKLEY, J. L. 1950. The ecology and economics of the beaver (*Castor canadensis* Kuhl) with a plan for its management on the Huntington Wildlife Forest Station. Ph.D. Thesis, State Univ. New York, Syracuse. 251pp.

COLLINS, T. C. 1976. Population characteristics and habitat relationships of beaver, *Castor canadensis*, in northwest Wyoming. Ph.D. Thesis, Univ. Wyoming, Laramie. 188pp.

CONVERSE, K. A., AND B. J. MORZUCH. 1981. A descriptive model of snowshoe hare habitat. Pages 232–241 *in* D. E. Capen, ed. The use of multivariate statistics in studies of wildlife habitat. U.S. For. Serv. Tech. Rep. RM-87.

FISHER, F. M. 1970. Tests of equality between sets of coefficients in two linear regressions: an expository note. Economics 38:361–366.

GREEN, R. H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley & Sons, New York, N.Y. 275pp.

HALL, A. M. 1971. Ecology of beaver and selection of prey by wolves in central Ontario. M.S. Thesis, Univ. Toronto, Ontario. 116pp.

HAY, K. G. 1958. Beaver census methods in the Rocky Mountain region. J. Wildl. Mange. 22: 395–402.

HODGDON, H. E. 1978. Social dynamics and behavior within an unexploited beaver (*Castor canadensis*) population. Ph.D. Thesis, Univ. Massachusetts, Amherst. 292pp.

HODGDON, R.W., AND J. H. HUNT. 1953. Beaver management in Maine. Maine Dep. Inland Fish. Game Bull. 3. 102pp.

HOWARD, R. J. 1982. Beaver habitat classification in Massachusetts. M.S. Thesis, Univ. Massachusetts, Amherst. 67pp.

JENKINS, S. H. 1980. A size-distance relation in food selection by beavers. Ecology 61:740–746.

LINDERMAN, R. H., P. F. MERENDO, AND R. Z. GOLD. 1980. Introduction to bivariate and multivariate analysis. Scott, Foresmen, and Co., New York, N.Y. 444pp.

MACDONALD, D. 1956. Beaver carrying capacity of certain mountain streams in North Park, Colorado. M.S. Thesis, Colorado A&M Coll., Fort Collins. 136pp.

MORZUCH, B. J. 1980. Principal components and the problem of multicollinearity. J. Northeast. Agric. Econ. Counc. 9:81–83.

MOTT, J. R., AND D. C. FULLER. 1967. Soil survey of Franklin County, Massachusetts. U.S. Dep. Agric. Soil Conserv. Serv., Washington, D.C. 204pp.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT, editors. 1975. SPSS. Statistical package for the social sciences. 2nd ed. McGraw-Hill Book Co., New York, N.Y. 675pp.

NORDSTROM, W. R. 1972. Comparison of trapped and untrapped beaver populations in New Brunswick. M.S. Thesis, Univ. New Brunswick, Frederickton. 104pp.

NORTHCOTT, T. H. A. 1964. An investigation of the factors affecting carrying capacity of selected areas in Newfoundland for the beaver, *Castor canadensis caecator* Kuhl (Bangs 1913). M.S. Thesis, Memorial Univ., St. Johns, Newfoundland. 134pp.

PACKARD, F. M. 1947. A survey of the beaver population of Rocky Mountain National Park, Colorado. J. Mammal. 28:219–227.

RETZER, J. L., H. M. SWOPE, J. D. REMINGTON, AND W. H. RUTHERFORD. 1956. Suitability of physical factors for beaver management in the Rocky Mountains of Colorado. Colo. Dep. Game and Fish. Tech. Bull. 2. 33pp.

RUTHERFORD, W.H. 1964. The beaver in Colorado: its biology, ecology, management, and economics. Colo. Game, Fish, and Parks Dep. Tech. Bull. 17. 48pp.

SLOUGH, B. G., AND R. M. F. S. SADLEIR. 1977. A land capability classification system for beaver (*Castor canadensis* Kuhl). Can. J. Zool. 55:1324–1335.

SVENDSEN, G. E. 1980. Seasonal change in feeding patterns of beaver in southeastern Ohio. J. Wildl. Manage. 44:285–290.

WALLACE, T. D., AND C. E. TORO-VIZCARRANDO. 1969. Tables for the mean square error test for exact linear restrictions in regression. J. Am. Stat. Assoc. 64:1644–1693.

WHITE, K. J. 1978. A general computer program for econometric methods—SHAZAM. Econometrica 46:239–240.

WILLIS, R. M. A beaver habitat classification system for the Truckee River. M.S. Thesis, Univ. Nevada, Reno. 69pp.

*Received 6 April 1983.*
*Accepted 3 April 1984.*