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An evaluation of beaver habitat models for Illinois rivers

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An Evaluation of Beaver Habitat Models for Illinois Rivers

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AN EVALUATION OF BEAVER HABITAT MODELS FOR ILLINOIS RIVERS

A Thesis Presented

by

DANIEL R. COX

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Summary

Beavers (*Castor canadensis*) are agents of landscape change, altering the structure and species composition of vegetative communities through herbivory and water impoundment. To better manage beavers in Illinois, improved methods of monitoring riverine populations of this species are needed. The objectives of the study were to (1) locate, map and quantify the spatial distribution of beaver colonies along the Embarras River, (2) test the efficacy of 2 existing beaver habitat models, the U.S. Fish and Wildlife Service's Habitat Suitability Index (HSI) model and Missouri's beaver habitat model, for predicting the relative density of beavers and (3) develop a new multiple regression habitat model for predicting the density of beavers in Illinois' riverine habitats.

The Embarras River, in east-central Illinois, was partitioned along its length into 3 ecological divisions. Each division was divided into 25-km sections, and then each section was subdivided into 10 2.5-km segments. Two segments in each section were randomly selected and surveyed. This resulted in a total of 26 2.5-km segments of the river in which the number of beaver colonies (dependent variable) and the set of habitat variables (independent variables) were quantified during November 2001 to September 2002.

I located and mapped a total of 125 colonies on the Embarras, with a mean of 0.40 colonies/ km for the total river. Based on nearest-neighbor distances, colonies tended to be uniformly distributed along the river, with a disproportionate number occurring approximately 1-km apart (X^2 = 32.6; 8 df; P<0.01). The minimum distances between adjacent colonies were 0.4 km, 0.8

km and 0.6 km in the upper, middle and lower divisions of the river, respectively. HSI scores ranged from 0.00 to 1.00, with a mean = 0.82 (SD = 0.28). Overall, HSI scores did not correlate significantly with density of beaver colonies (r = 0.111, P = 0.588). The Missouri habitat model scores correlated significantly with colony density (r = 0.578; P = 0.002). Scores fell in the 42.9% to 71.4% range (mean = 59.4, SD = 6.7), suggesting that beaver habitat along much of the river was fairly good. The multiple regression model that I developed was a significant predictor of colony density (r^2 = 0.431, P = 0.034, F = 3.033, df = 5, 25). The following equation is the model:

Number of colonies per km = 2.687 + 0.021 (percent canopy cover) – 0.062 (percent of trees >45 cm dbh) + 1.744 (number of tributaries/km) – 0.876 (stream sinuosity) – 0.256 (number of roads within 200 m of stream)

Intraspecific competition and the changing physical environment along the river appeared to be the forces driving the spatial distribution of beavers on the Embarras River. My results suggest that the HSI model fails to incorporate local preferred foods and probably defines the water levels and stream substrates that can support high density beaver populations in the Midwest too narrowly. My results suggest that the Missouri model can serve as a useful predictor of riverine beaver habitat in Illinois and that existing land cover maps and soil surveys can provide most of the data necessary to evaluate the quality of beaver habitat in Illinois.

The multiple regression model that I developed proved to be a significant predictor of density. The model provides wildlife managers with an alternative tool for scoring habitat quality using existing data sets. Both the Missouri model and my regression model provide useful tools for predicting the relative abundance of beavers in the Embarras River. However, further testing of these models in other Illinois watersheds should be conducted to validate their value in other parts of the state.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

AN EVALUATION OF BEAVER HABITAT MODELS FOR ILLINOIS RIVERS

INTRODUCTION

Beavers (*Castor canadensis*) are ecologically and economically important throughout most of North America (Novak 1987). They are agents of landscape change, altering the structure and species composition of plant communities through herbivory and water impoundment (Broshcart et. al. 1989). Ecologically, they are a keystone species capable of creating and maintaining vital wetland communities. Economically, beavers are valued for their fur, castor glands and the recreational opportunities that they provide for trappers. They also can be costly nuisances when their activities bring them into conflict with humans. Beavers are common in Illinois and populations have grown dramatically in some areas during the past 30 years (Hoffmeister 1989). However, they are not uniformly distributed across the state and population trends vary regionally.

For these reasons, the Illinois Department of Natural Resources (IDNR) has monitored beaver populations annually using estimates of harvests and the number of nuisance complaints. However, these methods do not provide the necessary levels of precision and accuracy to develop biologically sound and effective management plans for this species. Consequently, research was initiated by the IDNR, in cooperation with Eastern Illinois University and the Cooperative Wildlife Research Laboratory at Southern Illinois University-

Carbondale, to develop more accurate techniques for censusing beaver populations in Illinois.

One method for determining beaver densities are helicopter surveys. These aerial surveys can provide a cost-effective method of censusing beavers in lakes, ponds and marshes where lodges, dens and feeding activity are observable from the air (Woolf et al. 2002). However, riverine habitats are more difficult to survey because canopy cover and fluctuating water levels can obscure evidence of beaver activity. Furthermore, beavers inhabiting rivers and streams often use bank dens rather than lodges, rarely build dams and secure their food caches near the bank making it very difficult to see these from the air or during ground searches (Swenson et. al. 1983).

Since surveys may not be practical for estimating beaver densities in riverine habitats, I tested the relationships between habitat characteristics and beaver density to determine whether a habitat suitability model could be developed and used to predict the relative density of beavers in Illinois' rivers and streams. The specific objectives of my study were to: (1) locate, map, and quantify the spatial distribution of beaver colonies along the Embarras River, (2) test the efficacy of 2 existing beaver habitat models, the U.S. Fish and Wildlife Service's Habitat Suitability Index (HSI) model and Missouri's beaver habitat model, for predicting the relative density of beavers, and (3) develop a new multiple regression habitat model for predicting the density of beavers in Illinois' riverine habitats.

LITERATURE REVIEW

Natural History of Beavers

Beavers typically live in individual family groups called colonies. Colonies may contain 2-4 age-classes including breeding adults, non-breeding adult offspring and juveniles born during the spring (Novak 1987). The monogamous breeding pair and their offspring defend a territory. Only the dominant female in a territory breeds, producing one litter a year. The pair bond is long-term and the family unit is closed to outsiders. Large colonies may have 1-2 non-breeding ≥2 years olds, 2-3 yearlings and several juveniles living with the breeding pair (Novak 1987). McTaggart and Nelson (2003) reported that the mean colony size in central Illinois was 5.6 beavers. Colonies occupying lakes and ponds tended to be larger (6.3 beavers/colony) than those in rivers (5.6 beavers/colony) or ditches (4.0 beavers/colony).

Beavers are territorial and these distinct, non-overlapping territories are the fundamental units of a beaver population. Territories are marked and defended by members of the colony, typically adults (Novak 1987). During spring and summer, scent mounds are constructed along waterways to delineate and mark territories (Brenner 1964). Both males and females deposit scent from the castor glands on the scent mounds (Long 2000). Each colony may establish and utilize several lodges or bank dens within their territory (Allen 1983).

Sub-adult beavers usually disperse into vacant habitat during the late-winter and early-spring of their second year, a time coinciding with increased stream flow caused by snowmelt and spring rains (Allen 1983). During the summer, sub-adults forage at considerable distances from the colony's den offering opportunities to search for unoccupied habitat. When densities are high and vacant suitable habitat is not available the sub-adults tend to stay with their parents' colony, increasing the numbers of beavers in a colony (Boyce 1981). However, when trapping or natural mortality factors increase adult mortality rates, more vacant territories become available. These vacant territories allow for increased chances of successful dispersal, leading to a decrease in mean colony size. Dispersing subadult beavers may be forced to occupy poor quality sites when all of the best colony sites are occupied. In marginal habitats, more dens are occupied by single adults or a young breeding pair with few or no offspring (Boyce 1981). Therefore, territoriality is an important factor determining the spacing patterns of colonies along streams and territory size may be dependent on habitat quality.

Habitats with abundant and diverse food resources support higher beaver densities, whereas areas dominated by lower quality food have fewer colonies and larger distances between neighboring colonies (Boyce 1981). The density of colonies in favorable habitat ranges from 0.4 to 0.8 colonies/km^2 (Allen 1983). In an Alaskan riverine habitat, Boyce (1981) found the mean nearest neighbor distance between colonies to be 1.59 km and a minimum nearest neighbor distance of 0.48 km. The maximum distance that beavers were observed retrieving food items was 800 m upstream and 300 m downstream from their dens. Robel et al. (1993) found that rivers with good quality habitat had densities of 0.12 to 1.40 colonies/km of stream. Semyonoff (1951 *in* Novak 1987) found mean densities of 1.5 colonies/km for rivers with good habitat, 0.5 colonies/km in moderate habitat, and 0.1-0.2 colonies/km in poor habitat.

Factors Influencing Habitat Quality

Several physical and biological factors influence habitat quality for beavers. However, most research on beaver habitat has been conducted in the northern and western portions of the beaver's geographic range, such as Newfoundland, Maine, Michigan, Wyoming, Montana and Alaska (Allen 1983). Few studies have been conducted in the Midwest where different habitat variables may affect population densities (Robel 1993). For example, Robel et al. (1993) found that the USFWS Habitat Suitability Index (HSI) model was not an adequate predictor of beaver abundance on rivers in Kansas. Major regional differences occur in food availability (including agriculture crops), topography and the physical characteristics of watersheds making it unlikely that a single habitat model can be useful over the broad geographic range of this species.

Physical aspects of streams and watersheds, such as gradient, channel width, substrate, stream sinuosity and water fluctuation, can impact the quality of beaver habitat. Beavers prefer streams with low gradients (<6%) and slow flows, while intermittent streams or streams with major fluctuations in discharge have little year-round value for beavers, because they do not provide year-round travel corridors and access to food (Allen 1983). Streams with major fluctuations in flow make it difficult for beavers to swim and transport food when the flow is high and expose den entrances or strand beavers in isolated pools when the flow is low. Greater stream sinuosity creates more habitat along a stream and makes the riparian zone more prone to flooding which can make additional food available. Similarly, stream braiding and tributaries (stream bifurcations) provide larger areas from which a beaver can forage for food resources (Boyce 1981). Finally, the composition, height and angle of stream banks influence the availability and quality of den sites. Loose bank substrates such as sand and gravel are likely to collapse and rocky substrates are too hard to excavate, while bank height may affect the beavers' ability to access food and also influence the extent of flooding in the riparian zone and adjacent wetlands. Finally, woody vegetation also provides essential structural material for building dams and bank dens.

Several biological factors, including plant composition and riparian width, also influence habitat quality (Allen 1983). Since beavers forage up to 200 m from streams, the extent of the riparian zone and the diversity and composition of plants found there may influence the quantity and quality of food and cover and lead to a positive correlation between colony density and plant diversity. Given that winter food sources are limited, the best habitats contain a high proportion of woody food plants (Boyce 1981).

Beavers are generalist herbivores feeding on a wide variety of plants, including aquatic herbs, grasses, forbs, ferns, shrubs and trees. Furthermore, they consume many parts of these plants, including the flowers, leaves and rhizomes of aquatic plants, as well as the bark, twigs and leaves of woody plants (Jenkins 1975). Robel et al. (1993) found that beavers in Kansas were as likely to forage on corn and sorghum as preferred trees such as cottonwood and willows. Beavers forage primarily on herbaceous vegetation during the summer and this resource is usually not a limiting factor for beaver populations (Boyce 1981). During fall and winter, when food resources can be limiting, the diet shifts to woody vegetation. Therefore, the availability, composition and stem size of woody species are important components of beaver habitat during these seasons. Woody stems typically used as winter food are less than 10 cm dbh and include willows (*Salix* spp.), maples (*Acer saccharinum, A. saccharum, A. negundo*), cottonwoods (*Populus deltoides*), river birch (*Betula nigra*) and dogwoods (*Cornus* spp.) (Hoffmeister 1989). Food caches on the Embarras River were found to include silver maple (26%), green ash (18%), sycamore (13%), black willow (11%) and corn (10%; T. A. Nelson, unpublished data). Beavers cut a smaller range of stem sizes and utilize relatively more small trees and fewer large trees at greater distances from water (Jenkins 1980). This selectivity is a result of increased provision time at a greater distance from the safety of dens. Furthermore, large diameter trees felled farther from shore would result in many trips to transport branches, increasing energy expenditure, whereas a tree of small diameter may result in a reduced number of trips and decreased energy cost.

Beavers will live in close proximity to humans if all of their habitat requirements are met. However, railways, roads and land clearing adjacent to waterways may decrease the quality of beaver habitat (Allen 1983). Intraspecific competition, predators, parasites, disease and trapping pressure also affect habitat, but these can be difficult to quantify and may vary dramatically over small spatial and temporal scales.

Habitat Models

Central to the study of beaver ecology and management is the use that this species makes of its environment; specifically, the kinds of food it consumes and the varieties of habitats it utilizes (Johnson 1980). Animal-habitat interactions can be complex, but understanding these relationships is critical for successful species management. Habitat use usually is studied to infer selection and preference. It is assumed (although seldom tested) that species should prefer those habitats in which they survive and reproduce more successfully. Once habitat preferences have been determined, wildlife managers can manipulate landscapes to alter the amount of high quality habitat available to achieve their management goals (Garshelis 2000).

To better understand animal-habitat interactions, researchers often develop habitat models which have become essential tools for wildlife management. A common practice in developing habitat models is to compare the characteristics of sites used by an animal to those of unused sites to identify those variables that best characterize the used sites. Garshelis (2000) categorized these as "site-attribute design" studies and noted that the dependent variable is whether each site is used or unused and the independent variables can be any habitat characteristics thought to be biologically important to a species. A measure of habitat selection is inferred from the magnitude of the relationship between habitat variables and use.

Both the utility and validity of a habitat model is important if the model is to provide a framework for understanding the animal-habitat relationship. However, from a manager's standpoint utility is the key issue and must reflect both biological accuracy and immediate usefulness (Salwasser 1984). Because a wildlife manager's time and budget are limited, models should incorporate habitat characteristics that are easily quantifiable and produce results that can be clearly interpreted (Hurley 1984).

Several models have been developed to classify and evaluate beaver habitat. Boyce (1981) used multiple regression to investigate the relationship between colony density and both physical and vegetative components of habitat in Alaskan streams. Slough and Sadleir (1977) described the relationship between the number of colonies at different sites in British Columbia to various physical and vegetative parameters of each site, using backwards stepwise multiple regression analysis to develop a habitat model. Howard and Larson (1985) developed 2 models, using principal components regression and discriminant function analysis, to predict the maximum density of active beaver colonies on streams in Massachusetts.

Allen (1983) constructed a simple habitat suitability index (HSI) for use in environmental impact assessments. This model produces a suitability index from 0.0 (unsuitable habitat) to 1.0 (optimal habitat) based on habitat characteristics thought to influence the relative abundance of beavers, which include percent tree canopy cover, average water fluctuations, percent stream gradient, percent shrub crown closure, average height of shrub canopy and species composition of woody vegetation. The HSI model was not developed to predict beaver densities per se, but Robel et al. (1993) noted that HSI values should be positively correlated to beaver densities if the model is composed of key habitat variables. Van Horne (1983) noted that habitat quality and population density might not be correlated because local densities may be confounded by social interactions and seasonal shifts in habitat use. However, Robel et al. (1993) noted that the latter are unlikely to affect beavers because they are colonial and territorial.

Tests of Allen's (1983) HSI model have shown the model to be inadequate for classifying habitat quality across the beaver's geographic range. Robel et al. (1993) and Stromayer (1999) reported poor performance for the HSI model in the midwestern and eastern U.S., respectively. Limitations for the HSI model in these regions included its failure to incorporate local plant species as high quality foods and narrow definitions of suitable water quality and stream substrates. Consequently, these authors recommended that the HSI model should be modified for use in the East and Midwest.

A second model was developed by Hallett and Erickson (1980) to quantify habitat suitability for beavers in upland and bottomland forests in central Missouri. The model is a scoring rubric based on important habitat characteristics, including: the presence of permanent water, bank den characteristics, forest species composition, abundance and diversity of preferred foods, size class of trees and proximity of cropland. Individual scores (1-10; unsuitable to highly suitable) are assigned to each characteristic, then these scores are summed and divided by the maximum possible points to derive a score representing the habitat unit value (HUV). To my knowledge, this is the only model specifically designed for use in the riverine habitats of the Midwest. However, its validity had not been tested prior to my study. Therefore, my goals were to test the validity of 2 existing beaver habitat models, and to develop a habitat suitability model based on my assessment of the beaver-habitat relationships along the Embarras River.

METHODS

Study Area

The study was conducted on the Embarras River in east-central Illinois, one of 9 major watersheds in the state. The river is approximately 315 km in length, extending south and east from Champaign Co. in the north to its confluence with the Wabash River in Lawrence Co., Illinois (Fig. 1). Over this distance, the river channel increases from 5 m in the north to 28 m in the south. The Embarras River was selected because it is a moderate-sized, low gradient stream, typical of many rivers in Illinois in that it drains a large, relatively flat watershed and its riparian zone has been impacted by agriculture and development. Over 50% (190 km) of the Embarras is classified as "biologically significant", a designation reserved for Illinois' highest quality streams (Wiggers 1998).

The 6,800-km^2 Embarras watershed is almost entirely rural, encompassing a mix of farmland and small towns typical of central Illinois, containing only 1.6% of the state's population and one city with at least 20,000 people. Approximately 75% of the watershed is cropland, 11% grassland, 11% forests, and 2% urban. Loss of natural habitats in this area has exceeded rates statewide, where 30% of the pre-settlement forests and 11% of wetlands remain. Non-forested wetlands cover only 0.3% and native prairies <0.01% of the watershed. Corn and soybeans are the predominant crops in the northern half of this area; small grains and hay complement row crops in the southern half of the watershed (Wiggers 1998).

The topography along the river is relatively flat and the river's gradient ranges from 2.1 to 3.4%. Annual precipitation averages 94 cm (range 44-137 cm) with approximately 28% of this water entering the Embarras and its tributaries (Hamilton 1993). The large watershed and seasonal changes in precipitation cause water levels to fluctuate dramatically. Drainage of cropfields and channelization of the lower river have increased the volume and velocity of water in the main channel aggravating bank erosion and sedimentation. In spite of this erosion and siltation, water quality in the river is good: 45% of the river meets all Illinois water standards, 46% is considered degraded to a minor extent, and only 2% is considered severely degraded. Upper stretches may be dry during late-summer droughts, but flooding along all stretches of the river is common during the spring. For 2001 and 2002, the extreme water levels recorded at the Camargo gauging station (Douglas Co.) ranged from 0.6 m to 7.1 m. Downstream at the Ste. Marie station (Jasper Co.) these levels ranged from 0.2 m to 8.3 m, and at Lawrenceville, near its confluence, the extreme river levels were 5.4 m and 13.3 m during this 2-year period (Wiggers 1998).

For this study, the river was partitioned along its length into 3 ecological divisions based on topography, channel width, and land use adjacent to the river

(Fig. 2). Division 1, located between the cities of Champaign and Charleston, was 105 km in length and included the upper reaches of the river where the channel is narrow and shallow. This portion of the watershed is very flat and dominated by row crop agriculture. Division 2 extended from Charleston to Ste. Marie, a stretch approximately 135 km in length. Here the channel is deeper and wider, with steeper banks. The land adjacent to the river is gently rolling and dominated by row-crops and pasture. Division 3, from Ste. Marie to the Wabash River east of Lawrenceville, is 75 km in length. The river is heavily channelized with a deep channel and high, steep bank. The topography in the lower portion of the watershed is rolling and the landscape consists primarily of row crops, pastures, and small grains.

Measuring Habitat Parameters

Biotic and physical variables that may influence the quantity and quality of beaver habitat were selected *a priori* based on natural history and variables used by other researchers in previous beaver habitat models. Habitat measurements were collected from each division of the river using a stratified-random sampling scheme. Each division was divided into 25-km sections, and then each 25 km section was subdivided into 10 2.5-km segments. Two 2.5 km segments in each 25 km section were randomly selected and surveyed. This resulted in a total of 26 2.5-km segments of the river in which the number of beaver colonies (dependent variable) and the set of habitat variables (independent variables) were quantified. Of these 26 segments, 9 were in Division 1, 11 were in Division

2, and 6 were in Division 3 (Fig. 2). Before going to the field, I recorded the UTM coordinates corresponding to the beginning and ending of each segment to be sampled, and then a Garmin IV GPS receiver was used to locate each segment.

In each segment, 5 100-m transects were established for sampling vegetation. All sampling was conducted between mid-June and early-September 2002 when most vegetation was fully developed. Transects were located perpendicular to the river at 500-m intervals on alternating banks. Along each transect, sample points were established at 10, 30, 50, 70 and 90 m from the river. At each point, 4 trees were identified using the point-quarter technique and their diameter at breast height (dbh) measured using a dbh tape (Cox 2002). The percentages of grasses, forbs and bare soil were estimated within 0.5 m^2 circular quadrats at each sample point and a densiometer was used to estimate percent canopy cover. The percent shrub cover and mean height of shrubs were measured using the line intercept method and a height pole along 2 10-m sections (20-30 m and 50-60 m) of each transect (Cox 2002). In addition, I measured the width of the riparian zone, bank height and channel width at each transect. The composition of the bank (silt, sand, or clay) and presence of agriculture fields within 50 and 200 m of the river also were recorded at each transect. In some locations where it was difficult to measure either the width of the river channel or the riparian zone in the field, these were measured on georectified aerial photographs.

The percent stream gradient in each division and the number of tributaries in each 25-km section of the river were collected from the Illinois Stream

Identification System (ISIS) database developed by the IDNR. Stream sinuosity and the number of roads and buildings present within 200 m of the river in each section were measured using digital ortho-photographic quadrangles (DOQs) supplied by the Illinois Geologic Survey. Stream sinuosity was defined similar to Schieler (1995) as a ratio of the actual river distance (km)/straight-line distance (km) (Fig. 3). River bends were taken into account when determining stream sinuosity. A river bend occurred at any point where the river changed its course >60°.

The number and location of beaver colonies were mapped during November 2001-February 2002 when bank dens, food caches and chewed trees were most evident. The entire river was searched once during this time frame and searches were conducted by foot or by boat. I followed the guidelines of Robel et al. (1993) in defining a beaver colony. Most colonies were identifiable based on the presence of a den or set of dens in close proximity and a food cache. However, when dens were not visible, a colony was considered to be present wherever there was an area at least 0.3 km in length with fresh sign. The location of each active colony was determined based on fresh sign including bank dens, food caches, dams and fresh cuttings and recorded on 7.5-minute USGS topographic maps. The UTM coordinates of each bank den and food cache were located using a Garmin IV GPS receiver.

Testing the HSI Model

The HSI was calculated using a mathematical model developed by the U.S. Fish and Wildlife Service (Allen 1983; Appendix A) and can be used to quantify habitat suitability in a variety of cover types. The variables used in the riverine habitat model include: percent stream gradient, average annual water fluctuation (m), percent tree canopy closure, percent trees in the 2.5-15.2 cm dbh class, percent shrub crown cover, average shrub height and the species composition of woody vegetation within 200 m of the stream. I calculated the mean for each variable using transect data for each 2.5 km segment. A suitability index (SI) score was then determined for each habitat variable, based on SI graphs for habitat variables. Finally, an HSI score was calculated from SI values. The average annual water fluctuation, categorized in the model as small, moderate, or extreme, was evaluated based on minimum and maximum flow rates reported by the USEPA at gauging stations in Camargo, Ste. Marie, and Lawrenceville, IL. The HSI scores were compared to the number of colonies/segment to determine the efficacy of the HSI model for measuring the quality of beaver habitat along the Embarras River.

Testing the Missouri Model

To test the Missouri model (Hallett and Erickson 1980; Appendix B), I recorded soil texture (clay, silt, loam, sand) and slope of the bank at each transect. The species composition of the forest in each river segment was based on the dominant trees recorded along transects using the point-quarter method.

The number of important food plants was assessed by recording the presence of these species in the overstory, shrub and ground cover strata along each transect. The predominant size class of trees (sawtimber: >23 cm dbh, pole: 5 – 23 cm dbh, or reproduction: <5 cm dbh) in each segment was derived from dbh measurements of sampled trees. The proximity of cropfields and permanent water sources to each segment was measured in the field or on aerial photographs. Since all of the beaver colonies used in this study occurred on the Embarras River, which provides permanent water year-round, I did not use the "distance to permanent water" variable in the model. Consequently, the maximum possible score was reduced from 45 to 35 points. Scores were then assigned to each characteristic, which were used to determine the habitat value (HUV) of each segment. Finally, the correlation between habitat value and numbers of colonies in each segment were calculated and tested using simple linear regression.

Testing a Multiple Regression Model

Before testing the multiple regression model, I first conducted a Spearman correlation analysis to determine whether pairs of habitat variables were closely related. When 2 variables were highly correlated ($P<0.05$), the variable that was most easily measured or the variable most commonly used in other models was selected for testing in my model. I again checked for highly correlated variables and when no significant correlations were found among the remaining 21 independent variables, I tested these as candidates for inclusion in the model.

Forward regression analyses were used to determine which variables provided the greatest predictive significance. The cutoff for variables to be entered into the model was set at the $P < 0.05$ level. Both the Spearman correlation analysis and regression analyses were performed using SPSS software (SPSS Inc. Chicago, IL: Version 11.0).

RESULTS

Location and spatial distribution of colonies

I located and mapped a total of 125 colonies on the Embarras River, with a mean of 0.40 colonies/ km for the total river (Fig. 4). Colony densities were 0.46, 0.36 and 0.39 colonies/ km for the upper, middle and lower divisions of the river, respectively (Table 1). Based on nearest-neighbor distances, colonies tended to be uniformly distributed along the river, with a disproportionate number occurring approximately 1-km apart ($X^2 = 32.6$; 8 df; $P<0.01$; Fig. 5). This pattern was most evident in the 2 lower divisions of the river, whereas colonies in the upper division were randomly distributed ($X^2 = 1.92$, 5 df, $P=0.83$; Figs. 6). The minimum distances between adjacent colonies were 0.4, 0.8 and 0.6 km in the upper, middle and lower divisions of the river, respectively.

Most of the 26 2.5-km segments of river that I sampled contained active beaver colonies. Six segments (23.1%) contained no beavers. The small number of segments in which beavers were absent precluded the development of a habitat model using logistic regression. Of the segments with beaver colonies, 9 (34.6%) had a single colony and 11 (42.3%) contained 2 colonies. The vast majority (122/125; 97.6%) of the colonies that I located along the river occupied bank dens. It was not uncommon for a colony to have several individual dens in close proximity to each other. Sometimes den entrances were stacked vertically on top of each other, an apparent adaptation to fluctuating water levels. Only 3 colonies occupied lodges instead of bank dens and these were located in Division 1. Similarly, only 2 dams were found on the main channel of the Embarras River, both in Division 1 where the channel was narrow and flow rates were low.

Of the habitat characteristics measured for each division of the river, only 1 was significantly correlated with colony density. Stream gradient was negatively correlated to the number of colonies per segment ($r = -0.440$, $P = 0.024$). Stream gradients were lowest in Divisions 1 and 3 where colony densities were highest. In Division 2, which had the highest gradient, colonies were more sparse. Several other habitat parameters approached statistical significance, including percent shrub cover ($r = 0.351$, $P = 0.079$), mean riparian width ($r = 0.355$, $P = 0.075$), percent of the river with low banks ($r = 0.363$, $P = 0.068$) and percent canopy cover ($r = 0.337$, $P = 0.092$). There also were some habitat characteristics that I expected to correlate with beaver density, but did not. These included: percentage of trees in the small diameter class ($r = 0.196$, $P = 0.337$) and number of tributaries per km ($r = 0.244$, $P = 0.230$).

Testing the Habitat Suitability Index (HSI) model

For the segments surveyed, tree canopy closure ranged from 0-52% (mean = 30.5, SD = 14.2), proportion of trees in the small diameter (2.5–15.2 cm dbh) class ranged from 0 to 92% (mean = 50.8, SD = 18.7), shrub crown cover did not exceed 19% (mean = 7.4, SD = 5.3) and mean shrub height never exceeded 2 m (mean = 1.8, SD = 0.4; Table 2). Twenty-four of the 26 segments were dominated by mixed deciduous forests (maples, elms and ashes). Segment 50 of Division 2 was dominated by willows and Segment 1 of Division 1 was lined entirely with agricultural fields resulting in the highest and lowest suitability indices (SI) for these 2 segments, respectively. The stream gradient was <5% over the entire river. Fluctuating water levels are common on the Embarras River; however, fluctuations were more pronounced in the upper and lower reaches of the watershed.

The SI values for tree canopy closure (V_1) ranged from 0 to 1 (mean = 0.72, SD = 0.30), proportion of trees in the small diameter class (V_2) from 0.20 to 0.94 (mean = 0.61, SD = 0.15), proportion of shrub crown cover (V_3) from 0.00 to 0.47 (mean = 0.20, SD = 0.13) and height of shrub canopy (V_4) from 0 to 1 (mean = 0.89, SD = 0.21; Table 3). Segment 1 from division 1 and Segment 50 from Division 2 had the lowest and highest SI values for species composition of woody plants (V_5), with values of 0.2 and 1.0, respectively. The SI value was 0.60 for this parameter in all other segments of the river, suggesting that beavers generally had suitable forage trees available along the Embarras River. Similarly, the stream gradient (V_7) on the whole river (<5%) was favorable for beavers, resulting in an SI value of 1.0 in all segments. SI scores for stream fluctuation (V_8) ranged from 0.00-1.00 (mean = 0.83, SD = 0.28).

Overall, HSI scores ranged from 0.00 to 1.00, with a mean = 0.82 (SD = 0.28). The only segment with unsuitable habitat (HSI = 0) had no beavers present (Fig. 7). However, overall HSI scores did not correlate significantly with density of beaver colonies (r = 0.111, P = 0.588). Five segments with good habitat (HSI >0.8) had no colonies. On the other hand, 3 segments with only moderate habitat (HSI = 0.5) contained 2 colonies in each segment (Fig. 7).

Testing the Missouri model

Generally, the banks of the Embarras River were suitable for bank dens. Soils are predominantly clay-loams or clay; although 3 segments had sandy-loam banks in which dens were likely to collapse. Consequently, HUV scores for bank texture ranged from 2 to 5 (mean = 3.4, SD = 0.8; Table 4). Bank slopes were relatively steep (>30°) contributing to favorable habitat for dens. HUV scores for bank slope ranged from 1 to 5, but most were >3 (mean = 3.8, SD = 0.9; Table 4).

Riparian zones bordering the river provided woody and herbaceous food plants that are used by beavers, but few segments were dominated by species known to be highly preferred by beavers, such as willows and ashes. Consequently, most segments received intermediate scores for forest composition (range = 1-7; mean = 4.0; SD = 1.6; Table 4). However, this lack of preferred species was offset by the relatively wide diversity of forage plants available. HUV scores for the number of important food plant species comprising more than 1% of total plants ranged from 1 to 5 (mean = 4.3, SD = 1.1).

Riparian forests tended to be dominated by trees of large diameter, whereas beavers prefer small diameter trees. This was particularly true in Division 2, where large, mature trees lined much of the river. Therefore, the HUV scores for the tree size class variable tended to be low to moderate (mean = 2.3; SD = 1.2; Table 4). In addition, riparian zones tended to be wide, particularly in Division 1, so distances from the river to cropland generally exceeded 30 m in Division 1 and averaged 15-30 m in Divisions 2 and 3. Only 2 segments in Division 2, where corn and soybeans were planted adjacent to the river, received the maximum HUV score (5) for distance to cropland (Table 4).

The HUV model scores correlated significantly with colony density ($r = 0.578$; $P = 0.002$; Fig. 8). Overall HUV scores fell in the 42.9% to 71.4% range (mean = 59.4, SD = 6.7), suggesting that beaver habitat along much of the river was good. Segments lacking beavers received habitat scores ranging from 42.9% to 60% (Fig. 8). The segment receiving the lowest score lacked a forested riparian zone and provided little winter food after crops were harvested. The individual habitat variables that were most likely to influence the overall HUV scores were the size class of trees and bank texture. Segments dominated by large, mature trees or with sandy banks unsuitable for dens received relatively low scores.

Developing a multiple regression model

Forward multiple regression was used to depict the relationship between selected habitat parameters. The number of beaver colonies in each of the 26 segments of the river were entered as the dependent variable in the model. Twenty-one habitat measurements were entered and tested as predictor variables (Table 5). Of these 21 variables, 5 were retained in the model resulting in a developed model that was a significant predictor of the mean number of colony density ($r^2 = 0.431$, $P = 0.034$, $F = 3.033$, df = 5, 25; Fig. 9). The following equation defines this model:

Number of colonies per km = 2.687 + 0.021 (percent canopy cover) – 0.062 (percent of trees >45 cm dbh) + 1.744 (number of tributaries/km) – 0.876 (stream sinuosity) – 0.256 (number of roads within 200 m of stream)

The density of beaver colonies was positively correlated with tree canopy cover and the number of tributaries, but negatively correlated with the percentage of trees in the large diameter class, stream sinuosity, and road density.

DISCUSSION

Location and spatial distribution of colonies

My first objective was to locate and map beaver colonies along the Embarras River and quantify their spatial distribution. With a mean of 0.40 colonies per km of stream, the Embarras River provides moderate to good quality habitat for beavers along most of its length. Robel et al. (1993) found that rivers with good beaver habitat had densities of 0.12 to 1.40 colonies/ km in Kansas and Semyonoff (1951 *in* Novak 1987) found mean densities of 1.5 colonies/ km for rivers with good habitat, 0.5 colonies/km in moderate habitat, and 0.1-0.2 colonies/km in poor habitat.

The distribution of colonies on the Embarras varied among the 3 divisions and this variation can be explained by the changing environments along the river from its origin in the flat cornfields near Champaign to its channelized confluence with the Wabash River near Lawrenceville. Colony density was relatively high in Division 1 (0.5 colonies/ km). Slow moving water, a narrow channel and a broad floodplain characterize the upper division of the Embarras River. Low water velocity and a narrow channel provide beavers with the opportunity to build and maintain dams and bank dens. I found two dams in Division 1 and three lodges in adjacent wetlands, the only dams and lodges found on the river. Further, the topography of the watershed is very flat in this region and the river is prone to flooding. Consequently, farmers have generally removed low areas adjacent to the river from crop production and these marshes and ephemeral wetlands provide refuge and additional habitat during periods of flooding and low flows. As water movement and channel width increases beavers are less prone to build dams. As a result, they do not alter their local environment in an effort to create habitat with preferred food items.

The vast majority of the landscape matrix surrounding the upper division is dominated by row crop agriculture – corn and soybeans. Robel et al. (1993) found that beavers in Kansas were as likely to forage on corn and sorghum as preferred trees, such as cottonwood and willows. I observed similar preferences for corn and soybeans when these were available and corn stalks were evident in many of the food caches stored by beavers during the fall. However, during winter, when food resources are most limiting, the diet of beavers shifts to woody vegetation. Consequently, the availability, species composition and stem size of woody plants become important factors influencing the quality of beaver habitat during this period (Boyce 1981). Generally, forests in the riparian zones in Division 1 were younger (early- and mid-successional stages) and provided an abundance of small diameter trees within 20 m of the water. These small diameter trees (< 10 cm dbh) provide the preferred woody forage used by beavers in the winter (Hoffmeister 1989).

The upper division was the only portion of the river in which beaver colonies were not distributed uniformly. Beavers are highly territorial and interactions between territorial individuals should lead to maximal spacing and result in a uniform dispersion throughout areas of suitable habitat (Davies 1978). However, this prediction of uniform dispersion in territorial species assumes that resources are evenly distributed. This assumption often is violated in nature because resources are usually spatially and temporally heterogeneous (Wiens 1976). For beavers in the Embarras River, this heterogeneity may be particularly true in the upper portion of the river where low flow rates and shallow water can effectively fragment beaver habitat into isolated patches of food and cover.

The middle division was found to have the lowest density of colonies and the greatest nearest-neighbor distances compared to the other divisions. In some respects, this portion of the river might be expected to provide the best beaver habitat. It is the least disturbed portion of the river with a wider and deeper channel, high water quality and relatively wide forested riparian zones. However, colonies were distributed uniformly here and relatively far apart. This appears to be due in part to the maturity of riparian forests, species composition and the large size of trees in this division. Vegetation transect data showed that the mean diameter of trees was large (26.8 cm). But, the woody stems typically used as winter food by beavers are generally less than 10 cm dbh (Hoffmeister 1989). Also, 47% of the survey points within these segments occurred in agricultural fields, typically starting 30 m from the river.

This combination of large diameter trees and agriculture appears to reduce beaver density. The felling of large trees is labor-intensive and time-consuming. In addition, agricultural fields are far enough from the river that beavers using them must increase their foraging distance and expose themselves to predation. As well, these agricultural fields are typically harvested in September and do not provide a sustainable food source throughout the winter months when food resources are most limiting. Thus, food limitations and lower habitat quality in this portion of the river effectively increase territory size and nearest-neighbor distances. Individuals are less likely to populate low quality areas, preferring to move up or down stream. This displacement effectively decreases colony density.

When I initiated this study, I expected that the lower division of the river might have the lowest beaver density because of stream characteristics caused by channelization, particularly high banks, a deep channel and high fluctuations in water level. Streams with major fluctuations in flow make it difficult for beavers to swim and transport food when the flow is high and expose den entrances when the flow is low (Allen 1983). Beavers can usually control water depth and stability on small streams, ponds and lakes; but, larger rivers and lakes where water depth and/or fluctuation cannot be controlled are often partially or wholly unsuitable for the species. Also, steep topography inhibits food transportation (Slough and Sadleir 1977). However, I found that Division 3 had densities comparable to the middle portion of the river. It is evident that beavers inhabiting the lower portion of the Embarras River have adapted to the fluctuating water level. For example, haul-outs into cornfields and foraging areas often extended up steep, high banks and den openings often were vertically stacked, one on top of the next, allowing beavers to use different den openings depending on water levels.

The uniform dispersion pattern of beaver colonies in the middle and lower divisions of the river suggest that territoriality is an important contributor to the spatial distribution of beavers in these areas (Davies 1978). A far greater proportion of colonies occurred approximately 1-km apart than would be expected by chance. Although the size of beaver home ranges and territories has not been well defined (Novak 1987), Nordstrom (1972) reviewed field studies and reported that home ranges on streams were approximately 0.8 km and Busher (1983) calculated the nearest distance between colonies as 0.84-1.55 km in California streams. Therefore, intraspecific competition, rather than resource limitations, may limit the number of colonies on most of the river.

Testing the HSI model

My second objective was to test the efficacy of 2 existing beaver habitat models for predicting the relative density of beavers, the USFWS HSI model and the Missouri beaver habitat model for bottomland hardwood habitats. The HSI model considers the quality of life requisites for the species in multiple cover types, including riverine habitat. Water and winter food are the only life requisites considered because the cover and reproductive needs of the species are assumed to be identical with water requirements. The model was designed to ease field application and was developed to produce an index value between 0.0 (unsuitable habitat) and 1.0 (optimum habitat) (Allen 1983).

The HSI model did not produce useful estimates of beaver density on the Embarras River and probably is not useful for estimating the abundance of beavers in Illinois rivers. Correlations between HSI scores and colony densities were low ($r = 0.111$; $P = 0.588$). The poor fit may be attributable to the model being developed based on data collected in the northern and western portions of the beaver's geographic range, placing emphasis on winter foods and stream characteristics that are absent or atypical in Midwestern watersheds. My results illustrate that the HSI model fails to incorporate local preferred foods such as ash, maple and corn that can support high density beaver populations in the Midwest. In addition, the model defines suitable stream characteristics too narrowly, particularly fluctuating water levels and stream substrates (Robel et al 1993, Stromayer 1999). It appears that beavers have adapted to fluctuating water levels by using multiple den sites with entrances occurring at staggered heights along the bank. Also, stream gradient is not a density limiting habitat characteristic on the Embarras River. Midwestern streams are not known for steep gradients and most likely this is not a habitat characteristic of concern. My observations suggest that beavers in Illinois have adapted well to fluctuating water levels and high, steep banks, as long as the water in the main channel is deep enough for travel and protection.

Testing the Missouri model

In contrast to the poor performance of the HSI model, the Missouri habitat model proved to be well-suited for predicting habitat quality in Illinois. The model is based on habitat characteristics such as soil texture, slope of banks, tree species composition, abundance and diversity of important food plants, tree size class and distance to cropland. These characteristics are derived from Missouri's bottomland hardwood habitats and fit well with riverine beaver habitats in Illinois. The HUV model provides the user with the option of removing habitat characteristics not applicable to a site. For my purpose, I tested the model excluding the "distance to permanent water" variable since all of my colonies were on the river.

The model captured the apparent importance of age and species composition of riparian forests to beavers on my study area. The combination of large, mature trees of species that are avoided by beavers appears to account for the lower model scores, lower density and greater nearest-neighbor distances observed in Division 2. The model also captured differences in the availability of important food plants and distance to cropland for beavers in the Embarras River.

Overall, the HUV model provided more reliable estimates of colony density when compared to the HSI model. An additional advantage provided by this model is that most of the input variables can be estimated based on existing data sets, eliminating the need to measure these in the field. For example, soil texture and bank slopes can be estimated from county soil maps and computerized digital elevation models (DEMs). Similarly, regional forest cover and land cover maps can be used to estimate the species composition and diameter classes of riparian forests. Estimating the presence and relative abundance of understory and herbaceous food plants is more problematic, but could be inferred from land cover types. As noted earlier, both the validity and utility of a habitat model are important if the model is to be useful for understanding and estimating animal-habitat relationships (Garshelis 2000). But, from the wildlife manager's standpoint, utility is the key issue. My results suggest that the Missouri model can serve as a useful predictor of riverine beaver habitat in Illinois and that existing land cover maps and soil surveys can provide most of the data necessary to evaluate the quality of beaver habitat in Illinois. Furthermore, advances in remote sensing and GIS systems could allow refinement of statewide habitat maps in the future, leading to models that would better estimate beaver abundance.

Developing a multiple regression model

The final objective of the study was to develop a multiple regression habitat model for predicting the density of beaver colonies in riverine habitat. First, I tested whether 22 individual physical and biological habitat characteristics correlated with the density of beaver colonies. Of these characteristics, only stream gradient correlated with colony density. Beavers prefer streams with low gradients and slow flows, but streams with gradients up to 6% may provide high quality habitat (Allen 1983). Typically, increases in stream gradient result in increased stream flow which could make travel and the transportation of food more difficult for beavers. Also, high flows can destroy dams, bank dens and food caches. Midwestern streams typically have low gradients and the Embarras River and its tributaries are no exceptions. The river has a mean gradient of 2.4%. The steepest gradient (4.4%) was in Division 2 where stream segments lacking beavers were most prevalent and nearest-neighbor distances were greatest. No other single habitat characteristic proved to be a significant predictor of beaver density, suggesting that the quality of beaver habitat probably is influenced by a suite of variables and that multivariate habitat models may better predict habitat quality. However, as stated earlier stream gradient is neither a density limiting factor on the Embarras River, nor a habitat characteristic of concern in Midwestern streams. For this reason, stream gradient was not entered in the multiple regression model.

The multiple regression model that I developed proved to be a significant predictor of density. Twenty-one habitat characteristics were entered into the regression, of which 5 were retained in the final model. Two parameters were positively associated with colony density: percent canopy cover and tributary density. The remaining 3 characteristics were negatively related to colony density: percentage of large diameter trees, stream sinuosity and number of roads within 200 m of the stream.

The model retained both biotic and abiotic variables that represent key components of beaver habitat. Riparian forests provide important foods for beavers, particularly during the winter when herbaceous vegetation is dead or dormant and crops have been harvested from agricultural fields. In addition, beavers use woody vegetation to construct dens and dams and bank dens are frequently situated under the exposed root balls of trees lining the river. Percent canopy cover provides a measure of the availability of trees for these purposes, so it is not surprising that the variable proved to be an important element in the regression model. Stream tributaries effectively enlarge the area of habitat and amount of resources available to a colony, providing more den sites, greater food supply and travel corridors.

The characteristics that negatively influence beaver habitat in the model include both natural and anthropogenic factors. Road density within 200 m of the river provides an indirect measurement of human access and activity along the river. Beavers can live in close proximity to humans if all of their habitat requirements are met (Rue 1964 *in* Allen 1983). However, other researchers have noted that roads, railways and land clearing near waterways may be important factors limiting the suitability of sites for beavers (Slough and Sadleir 1977).

A high percentage of large diameter trees in the riparian zone may negatively impact beavers in at least 3 ways. First, these trees are generally avoided for foraging, presumably because of the high energetic cost of cutting them. As noted earlier, beavers prefer to forage on small diameter trees. Second, large canopy trees shade the ground reducing the germination and growth of shade-intolerant trees preferred by beavers, such as willows, silver maple, green ash and cottonwood. Finally, the presence of large trees probably indicates infrequent disturbance (e.g. flooding, scouring, forest fires) needed to create the conditions for early-successional trees, shrubs and herbaceous plants.

It is not clear why colony density was negatively correlated with stream sinuosity. All else being equal, winding streams would provide more extensive banks and access to food. In addition, my observations suggest that sinuous stretches of the river often had more log jams and exposed root balls used as den sites by beavers. A possible explanation is that Division 2 had the lowest number of colonies as well as the highest stream sinuosity. Other, coincidental environmental factors appear to limit beaver densities in these areas and I think that stream sinuosity was pulled into the model by these confounding independent variables. A second explanation is that water velocity increases at stream bends, negatively affecting beaver movements and their ability to transport food.

This multiple regression model provides wildlife managers with an alternative tool for scoring habitat quality using existing data sets. Percent canopy cover and tree diameter could be estimated from forest cover maps. Road densities can be measured using GIS to create 200 m buffering along streams, then overlaying these buffers on county road maps. Similarly, the density of tributaries and stream sinuosity could be measured directly from digital orthoquadrangle (DOQ) aerial photographs in a GIS. One advantage provided by the multiple regression model is that it does not include soil type as an independent variable. Currently, digital soil maps are not available for most counties in Illinois.

As stated, the Embarras River provides high quality beaver habitat and is a suitable Midwestern stream for both the testing of existing habitat models and the production of new techniques. Both the Missouri model and the regression model provide useful tools for predicting the relative abundance of beavers in the Embarras River. Because this watershed is typical of many riverine habitats in Illinois, these models are likely to be useful throughout most of the state. However, further testing of these models in other Illinois watersheds should be conducted to validate their value in other parts of the state.

LITERATURE CITED

Allen, A. W. 1983. Habitat suitability index models: beaver. U. S. Fish and Wildlife Service, FWS/OBS-82/10.30. 20 pp.

Bender, Louis C., Gary J. Roloff, and Jonathan B. Haufler. 1996. Evaluating confidence intervals for habitat suitability models. Wildlife Society Bulletin 24:347-352.

Boyce, Mark S. 1981. Habitat ecology of an unexploited population of beavers in interior Alaska. M.S. Thesis. University of Alaska, Fairbanks.

Brenner, F. J. 1964. Reproduction of the beaver in Crawford County, Pennsylvania. Journal of Wildlife Management 28:743-747.

Broschart, Michael R., Carol A. Johnston, and Robert J. Naiman. 1989. Predicting beaver colony density in boreal landscapes. Journal of Wildlife Management 53:929-934.

Busher, P. E. 1983. Interactions between beavers in a montane population in California. Acta Zoologica. Fennica. 174:109-110.

Cox, G. W. 2002. General ecology laboratory manual. 8th ed. McGraw-Hill Co. Inc. New York, NY. 312 pp.

Davies, N. B. 1978. Ecological questions about territorial behaviour. Pages 317–350 *in* J. R. Krebs and N. B. Davies (eds.). Behavioural ecology: an evolutionary approach. Sinauer, Sunderland, Mass. 494 p.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111-164 *in* L. Boitani and T. K. Fuller (eds.). Research techniques in animal ecology. Columbia University Press, New York, N.Y.

Hallett, D. L. and D. W. Erickson. 1980. Beaver (Castor canadensis). Pages 99-105 *in* T. S. Baskett, D. A. Darrow, D. L. Hallett, M. J. Armbruster, J. A. Ellis, B. F. Sparrowe, and P. A. Korte (eds.) A handbook for terrestrial habitat evaluation in central Missouri. U. S. Department of Interior, Fish and Wildlife Service Resource Publication 133. Washington, D. C.

Hamilton, G. 1993. Soil survey of Coles County, Illinois. U.S. Department of Agriculture, Soil Conservation Service. Washington, D. C. 145 pp.

Hoffmeister, D. 1989. Mammals of Illinois. University of Illinois Press, Urbana and Chicago, IL. 348 pp.

Howard, Rebecca J. and Joseph S. Larson. 1985. A stream habitat classification system for beaver. Journal of Wildlife Management 49:19-25.

Hurley, Janet F. 1986. Development, testing, and application of wildlife-habitat models-the manager's viewpoint. Pages 151-153 *in* J. Verner, M. L. Morrison, and C. John Ralph (eds.). Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. The University of Wisconsin Press, Madison, WI.

Jenkins, Stephen H. 1980. A size-distance relation in food selection by beavers. Ecology 61:740-746.

Jenkins, Stephen H. 1975. Food selection by beavers: a multidimensional contingency table analysis. Oecologia 21:157-173.

Johnson, Douglas H. 1980. The comparison of usage and availability measurements for evaluating measurements for evaluating resource preference. Ecology 61:65-71.

Long, Kim. 2000. Beavers: a wildlife handbook. Johnson Books, Boulder, CO. 128 pp.

McTaggert, Stanley T. and Thomas A. Nelson. 2003. Composition and demographics of beaver (*Castor canadensis*) colonies in central Illinois. American Midland Naturalist 150:139-150.

Nordstrom, W. R. 1972. Comparison of trapped and untrapped beaver populations in New Brunswick. M.S. thesis, University of New Brunswick, Fredricton. 104 pp.

Novak, M. 1987. Beaver. Pages 283-312 *in* Wild furbearer management and conservation in North America. M. Novak, J. A. Baker, M. E. Obbard and B. Malloch, (eds.). Ontario Trappers Association, North Bay, Ontario, Canada.

O'Neil, Jean L., Thomas H. Roberts, James S. Wakeley, James W. Teaford. 1988. A procedure to modify Habitat Suitability Index models. Wildlife Society Bulletin 16:33-36.

Robel, Robert J., Lloyd B. Fox, and Kenneth E. Kemp. 1993. Relationship between habitat suitability index values and ground counts of beaver colonies in Kansas. Wildlife Society Bulletin 21:415-421.

Salwasser, Hal. 1986. Modeling habitat relationships of terrestrial vertebrates- The manager's viewpoint. Pages 419-424 *in* J. Verner, M. L. Morrison, and C. John Ralph (eds.). Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. The University of Wisconsin Press, Madison, WI.

Schieler, Chad T. 1995. Habitat characterization of an otter release area in southcentral Illinois. M.S. Thesis. Southern Illinois University, Carbondale, IL. 23 pp.

Slough, B. G., and R. M. F. S. Sadlier. 1977. A land capability classification system for beaver (*Castor canadensis* Kuhl). Canadian Journal of Zoology 55:324-335.

Stromayer, Karl A. K. 1999. Developing management alternative to promote beaver occupancy. Abstract of paper presented at the Virginia Wildlife Society Meeting, Virginia Tech University, Blackburg, VA.

Swenson, Jon E., Stephen J. Knapp, Peter R. Martin, and Thomas C. Hinz. 1983. Reliability of aerial cache surveys to monitor beaver population trends on prairie rivers in Montana. Journal of Wildlife Management 47:697-703.

Van Horne. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7:81–120.

Wiggers, R. 1998. The Embarras River Basin: an inventory of the region's resources. A project of the critical trends assessment program, Illinois Department of Natural Resources, Springfield, IL.

Woolf, A. and T. Nelson. 2002. Relative abundance of beavers in Illinois. Final Report, Illinois Federal Aid Project W-135-R-3. IL Department of Natural Resources, Springfield, USA.

Table 1. Physical and biological parameters for each of the 3 divisions of the Embarras River used in this study of determining beaver distribution. Divisions 1, 2, and 3 span from the cities of Champaign to Charleston, from Charleston to Ste. Marie, and from Ste. Marie to the Wabash River east of Lawrenceville, respectively.

Parameter	Division 1	Division 2	Division 3	Total
Total length (km)	105	135	75	315
Number of beaver colonies	48	48	29	125
Beaver colonies/ km	0.5	0.4	0.4	0.4
% Stream gradient	2.7	3.4	2.1	2.9
Mean channel width (m)	23	32	33	29
Meander index	1.3	1.3	1.0	1.2
Tributaries/ km	0.35	0.13	0.17	0.22
Mean riparian width (m)	111	68	72	84
Mean bank height (m)	1.2	4.5	5.4	3.6
Adjacent wetlands/ km	0.21	0.07	0.29	0.17
Bridges/ km	0.26	0.10	0.15	0.17

Table 2. Mean values for habitat characteristics for 26 segments in 3 divisions of the Embarras River during 2003.

	% Canopy Closure (V_1)	Small tree class (V_2)	% Shrub cover (V_3)	Shrub height (V_4)	Tree species (V_5)	Stream gradient (V_7)	Water fluctuation (V_8)
Division 1							
Segment 1	0.0	0.0	0.0	0.0	C	4.40	C
Segment 5	0.8	92.0	0.6	2.0	B	3.60	B
Segment 17	45.0	58.0	19.0	2.0	B	2.90	B
Segment 19	44.0	54.0	9.0	2.0	B	2.30	B
Segment 24	52.0	42.0	7.0	1.5	B	1.60	A
Segment 27	22.0	54.0	6.0	2.0	B	1.20	A
Segment 36	42.0	45.0	9.0	1.5	B	2.60	A
Segment 40	34.0	40.0	6.0	2.0	B	0.10	A
Segment 41	43.0	80.0	17.0	2.0	B	0.10	A
Division 2							
Segment 5	27.0	57.0	9.0	2.0	B	2.20	A

Table 2. continued.

	% Canopy Closure (V_1)	Small tree class (V_2)	% Shrub cover (V_3)	Shrub height (V_4)	Tree species (V_5)	Stream gradient (V_7)	Water fluctuation (V_8)
Segment 8	50.0	70.0	18.0	2.0	B	2.30	A
Segment 12	26.0	66.0	8.0	1.5	B	2.30	A
Segment 19	28.0	37.0	4.0	1.5	B	4.20	A
Segment 23	42.0	28.0	1.0	2.0	B	3.80	A
Segment 30	13.0	32.0	2.0	2.0	B	4.40	A
Segment 33	36.0	43.0	8.0	2.0	B	2.40	A
Segment 40	24.0	43.0	4.0	2.0	B	2.40	A
Segment 44	16.0	75.0	2.0	2.0	B	4.20	A
Segment 50	24.0	63.0	13.0	1.5	A	3.10	A
Segment 51	23.0	61.0	4.0	2.0	B	3.30	A
Division 3							
Segment 3	45.0	46.0	9.0	1.5	B	2.90	A

Table 2. continued.

	% Canopy Closure (V_1)	Small tree class (V_2)	% Shrub cover (V_3)	Shrub height (V_4)	Tree species (V_5)	Stream gradient (V_7)	Water fluctuation (V_8)
Segment 5	16.0	29.0	2.0	1.5	B	2.90	B
Segment 20	22.0	58.0	8.0	2.0	B	2.00	B
Segment 22	32.0	48.0	4.0	2.0	B	2.10	B
Segment 27	45.0	55.0	14.0	2.0	B	0.01	A
Segment 29	40.0	44.0	10.0	2.0	B	0.01	B

V_1 = percent tree canopy closure; V_2 = percent of trees in 2.5 to 15.2 cm dbh size class; V_3 = percent shrub crown cover; V_4 = average height of shrub canopy (m); V_5 = species composition of woody vegetation (where A, B, and C correspond to woody vegetation dominated (≥ 50%) by one or more of the following species: aspen, willow, cottonwood, or alder, woody vegetation dominated by other deciduous species, and woody vegetation dominated by coniferous species, respectively); V_7 = percent stream gradient; V_8 = average water fluctuation on annual basis (where A, B, and C correspond to small fluctuations that have no effect on burrow or lodge entrances, moderate fluctuations that affect burrow or lodge entrances, and extreme fluctuations or water absent during part of the year, respectively)

Table 3. Suitability Indices (SI), Water SI, Winter Food SI, and HSI scores for each of the 26 segments of the Embarras River measured during 2003.

	V_1	V_2	V_3	V_4	V_5	V_7	V_8	Water SI	Winter food SI	HSI score
Division 1										
Segment 1	0.00	0.20	0.00	0.00	0.2	1	0.0	0.0	0.00	0.00
Segment 5	0.02	0.94	0.01	1.00	0.6	1	0.5	0.5	0.56	0.50
Segment 17	1.00	0.66	0.47	1.00	0.6	1	0.5	0.5	1.00	0.50
Segment 19	1.00	0.63	0.23	1.00	0.6	1	0.5	0.5	1.00	0.50
Segment 24	1.00	0.54	0.17	0.75	0.6	1	1.0	1.0	1.00	1.00
Segment 27	0.56	0.63	0.15	1.00	0.6	1	1.0	1.0	1.00	1.00
Segment 36	1.00	0.56	0.23	0.75	0.6	1	1.0	1.0	1.00	1.00
Segment 40	0.86	0.52	0.15	1.00	0.6	1	1.0	1.0	1.00	1.00
Segment 41	1.00	0.84	0.42	1.00	0.6	1	1.0	1.0	1.00	1.00
Division 2										
Segment 5	0.69	0.66	0.23	1.00	0.6	1	1.0	1.0	1.00	1.00

Table 3. continued

	V_1	V_2	V_3	V_4	V_5	V_7	V_8	Water SI	Winter food SI	HSI score
Segment 8	1.00	0.76	0.45	1.00	0.6	1	1.0	1.0	1.00	1.00
Segment 12	0.66	0.73	0.20	0.75	0.6	1	1.0	1.0	1.00	1.00
Segment 19	0.71	0.50	0.10	0.75	0.6	1	1.0	1.0	1.00	1.00
Segment 23	1.00	0.42	0.30	1.00	0.6	1	1.0	1.0	0.93	0.93
Segment 30	0.33	0.46	0.05	1.00	0.6	1	1.0	1.0	0.85	0.85
Segment 33	0.90	0.54	0.20	1.00	0.6	1	1.0	1.0	1.00	1.00
Segment 40	0.61	0.54	0.10	1.00	0.6	1	1.0	1.0	1.00	1.00
Segment 44	0.41	0.80	0.05	1.00	0.6	1	1.0	1.0	0.95	0.95
Segment 50	0.61	0.70	0.33	0.75	1.0	1	1.0	1.0	1.00	1.00
Segment 51	0.59	0.69	0.10	1.00	0.6	1	1.0	1.0	1.00	1.00
Division 3										
Segment 3	1.00	0.57	0.23	0.75	0.6	1	1.0	1.0	1.00	1.00

Table 3. continued

	V_1	V_2	V_3	V_4	V_5	V_7	V_8	Water SI	Winter food SI	HSI score
Segment 5	0.41	0.43	0.05	0.75	0.6	1	1.0	0.5	0.84	0.50
Segment 20	0.56	0.66	0.20	1.00	0.6	1	1.0	0.5	1.00	0.5
Segment 22	0.81	0.58	0.10	1.00	0.6	1	0.5	0.5	1.00	0.5
Segment 27	1.00	0.64	0.35	1.00	0.6	1	1.0	1.0	1.00	1.00
Segment 29	1.00	0.55	0.25	1.00	0.6	1	0.5	0.5	1.00	0.50

V_1 = percent tree canopy closure; V_2 = percent of trees in 2.5 to 15.2 cm dbh size class; V_3 = percent shrub crown cover; V_4 = average height of shrub canopy; V_5 = species composition of woody vegetation; V_7 = percent stream gradient; V_8 = average water fluctuation on annual basis

Table 4. Habitat unit scores and HUV's for each of the 26 segments of the Embarras River measured during 2003, using the Missouri habitat model for beavers in bottomland hardwoods.

	Soil text.	Bank slope	Spp. comp.	No. of food	Tree class	Dis. to crops	HUV
Division 1							
Segment 1	4	5	1	1	0	4	42.9
Segment 5	3	4	3	3	5	2	57.1
Segment 17	3	3	7	4	2	1	57.1
Segment 19	3	3	5	4	3	2	55.6
Segment 24	3	4	5	5	2	1	64.4
Segment 27	3	3	4	5	3	3	48.9
Segment 36	2	4	5	5	3	2	57.8
Segment 40	5	4	4	5	3	3	62.2
Segment 41	3	1	4	4	4	1	48.9
Division 2							
Segment 5	4	5	4	4	1	3	55.6
Segment 8	3	4	4	5	2	3	57.8
Segment 12	4	5	3	4	1	3	46.7
Segment 19	2	4	3	5	2	3	46.7
Segment 23	2	4	4	5	2	3	57.8
Segment 30	4	4	2	2	1	4	40.0
Segment 33	4	4	4	5	1	3	51.1

Table 4. continued

	Soil text.	Bank slope	Spp. comp.	No. of food	Tree class	Dis. to crops	HUV
Segment 40	4	4	2	5	1	5	48.9
Segment 44	5	3	2	5	3	5	53.3
Segment 50	3	3	7	5	3	4	57.8
Segment 51	3	3	7	5	2	3	55.6
Division 3							
Segment 3	4	4	5	5	3	3	64.4
Segment 5	4	5	2	3	1	4	44.4
Segment 20	4	3	4	5	2	3	48.9
Segment 22	3	5	3	4	2	4	48.9
Segment 27	4	4	5	5	4	2	57.8
Segment 29	3	4	4	5	3	4	64.4

Soil text. = soil texture; Bank slope = slope of bank; Spp. comp. = species composition of 40% or more of the forest; No. of food = number of important food plant species comprising more than 1% of total plants present; Tree class = tree size class; Dis. to crops = distance to cropland; HUV = habitat unit value calculated at sum of scores/ maximum score possible (35).

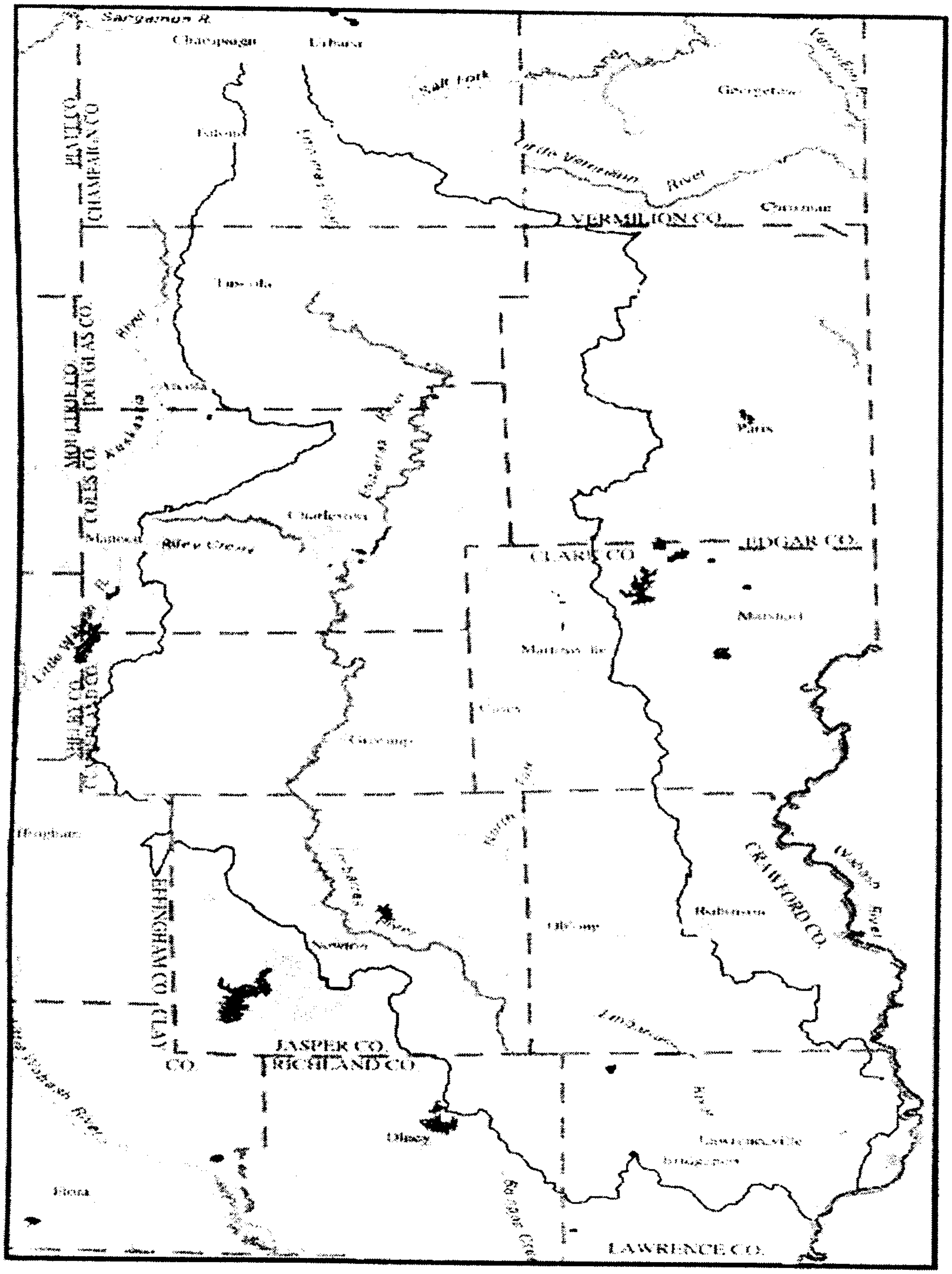

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Figure 1. The Embarras River watershed in southeastern Illinois extends from Champaign County in the north to Lawrence County in the south.

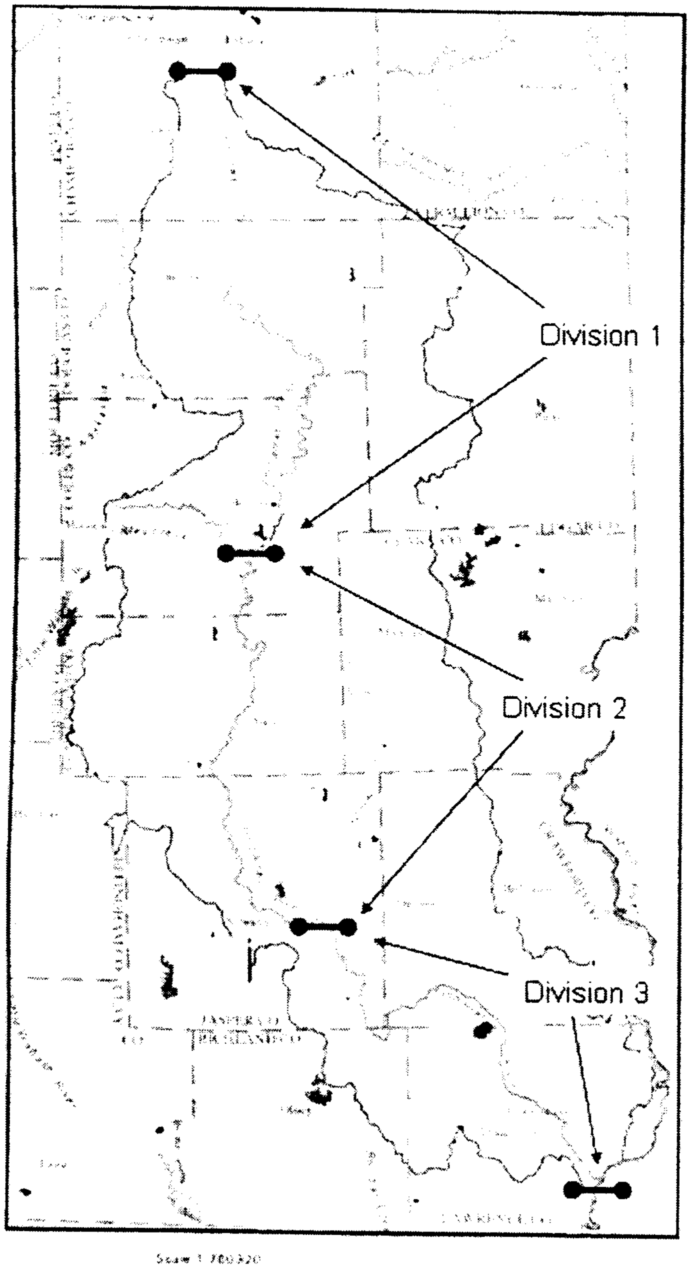
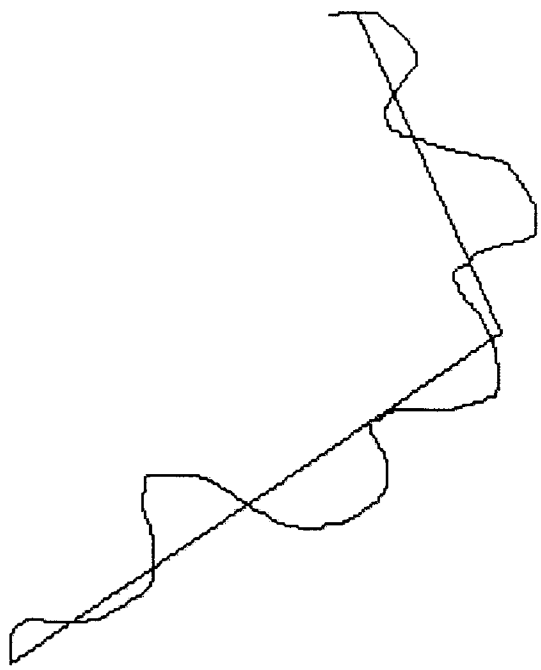


Fig. 2. The Embarras River was divided into 3 divisions for sampling based on channel characteristics and adjacent land use. Division 1 was the upper river from Champaign to Charleston, Division 2 included the middle river from Charleston to Ste. Marie, and Division 3 was the lower river from Ste. Marie to the Wabash River.



$$\text{Stream Sinuosity} = \frac{\text{actual distance}}{\text{straight distance}}$$

Figure 3. Technique for estimating stream sinuosity.

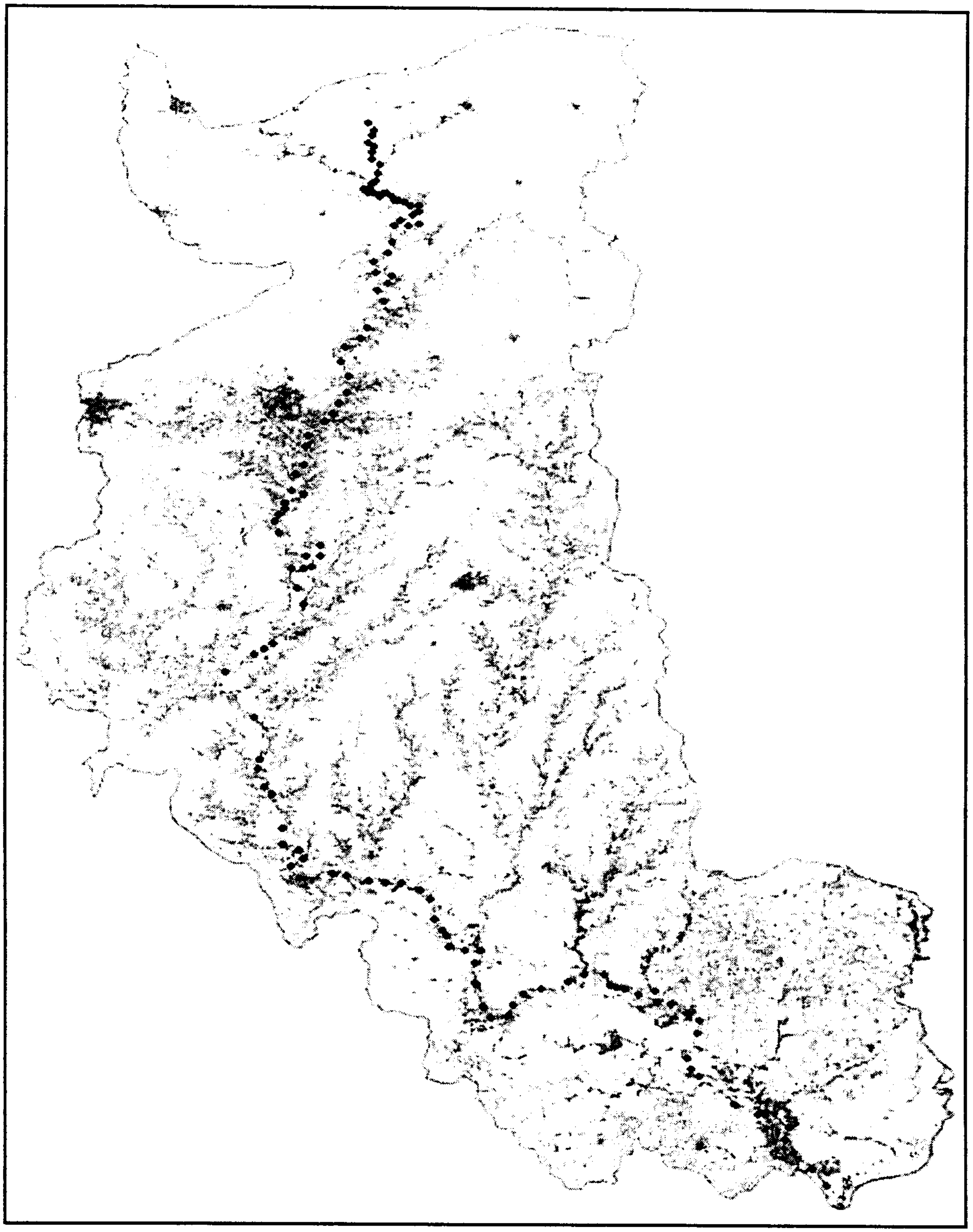


Figure 4. Distribution of 125 beaver colonies observed along a 315-km stretch of the Embarras River in southeastern Illinois during November 2001– February 2002. Each dot represents one colony.

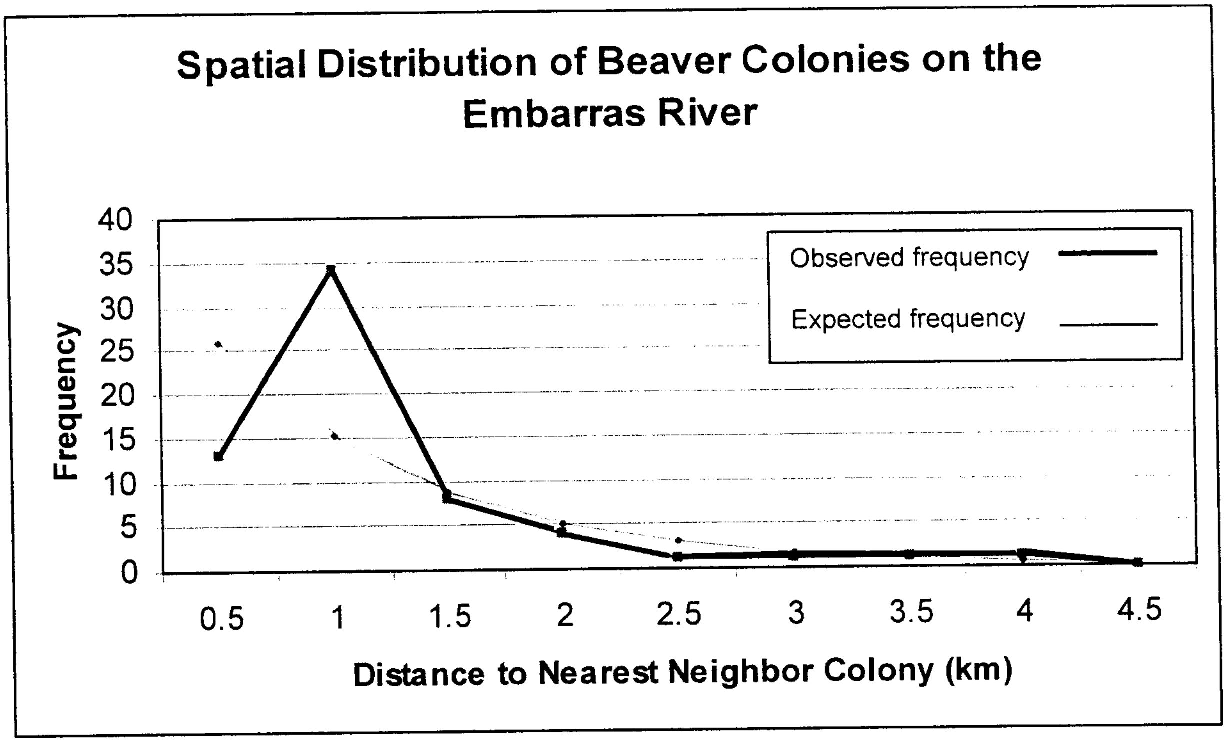


Figure 5. Observed and expected distributions of nearest neighbor distances between beaver colonies on the Embarras River. Values are plotted at the upper end of each distance interval (e.g. 13 colonies had nearest neighbors that were 0.00 to 0.50 km away and 34 colonies had nearest neighbors 0.51 to 1.00 km away). The expected distribution is an exponential distribution that would occur if colonies were distributed randomly along a linear feature such as a river. The spatial distribution of colonies was more uniform than would be expected by chance ($X^2 = 32.6$; 8 df; $P<0.01$).

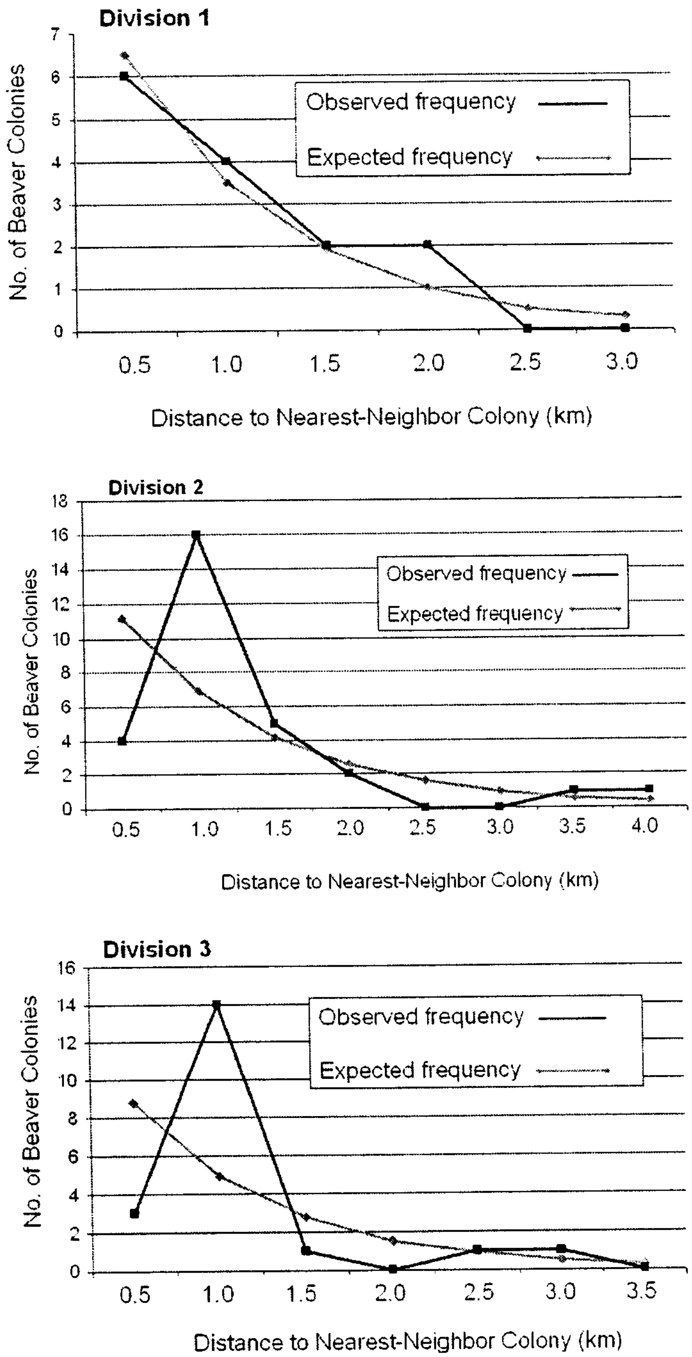


Figure 6. Observed and expected frequencies of nearest-neighbor distances between beaver colonies in each division of the Embarras River. Colonies were randomly distributed in Division 1 (X^2=1.92, 5 df, P=0.83), but uniformly distributed in Divisions 2 (X^2= 20.69, 7 df, P<0.01) and 3 (X^2= 24.19, 6 df, P<0.001).

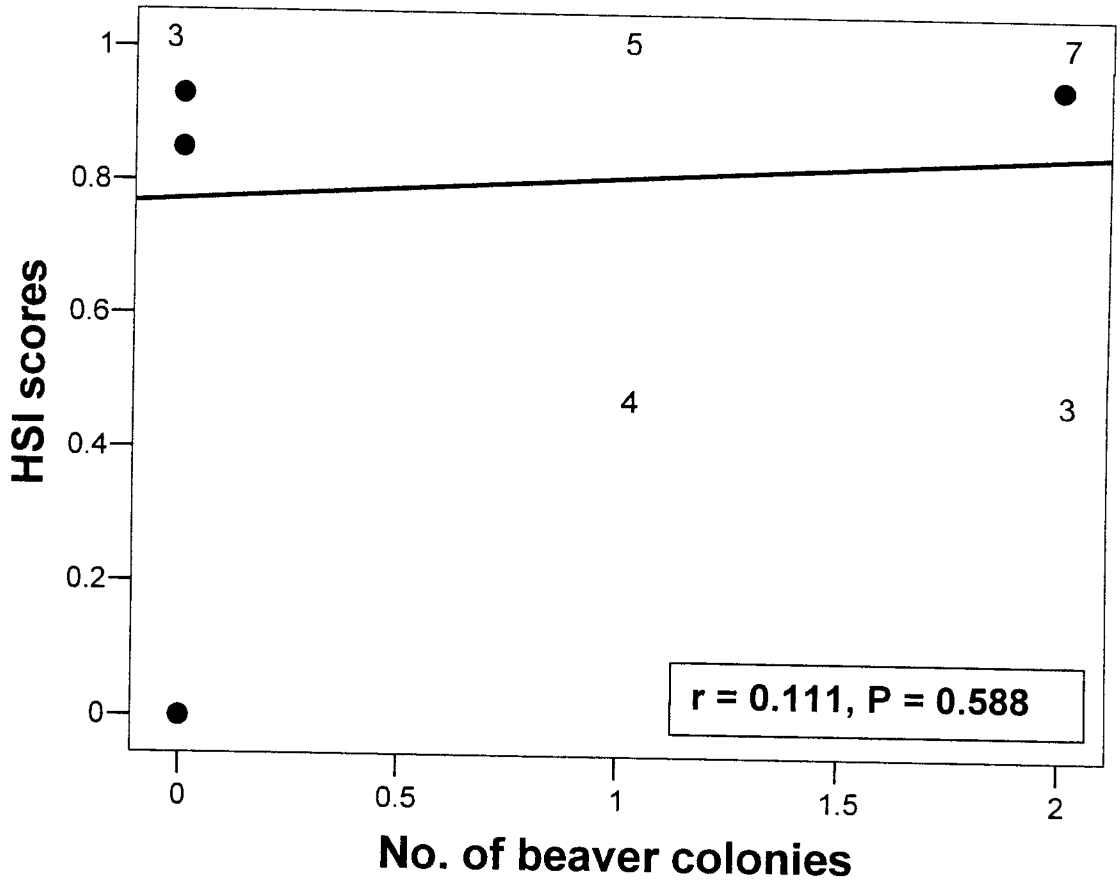


Figure 7. Relationship between Habitat Suitability Index (HSI) and abundance of beaver colonies in 26 2.5-km segments of the Embarras River in central Illinois. Numbers on graph indicate the number of segments with each score. Colony density did not correlate significantly with habitat suitability as scored by the HSI model (r = 0.111, P = 0.588).

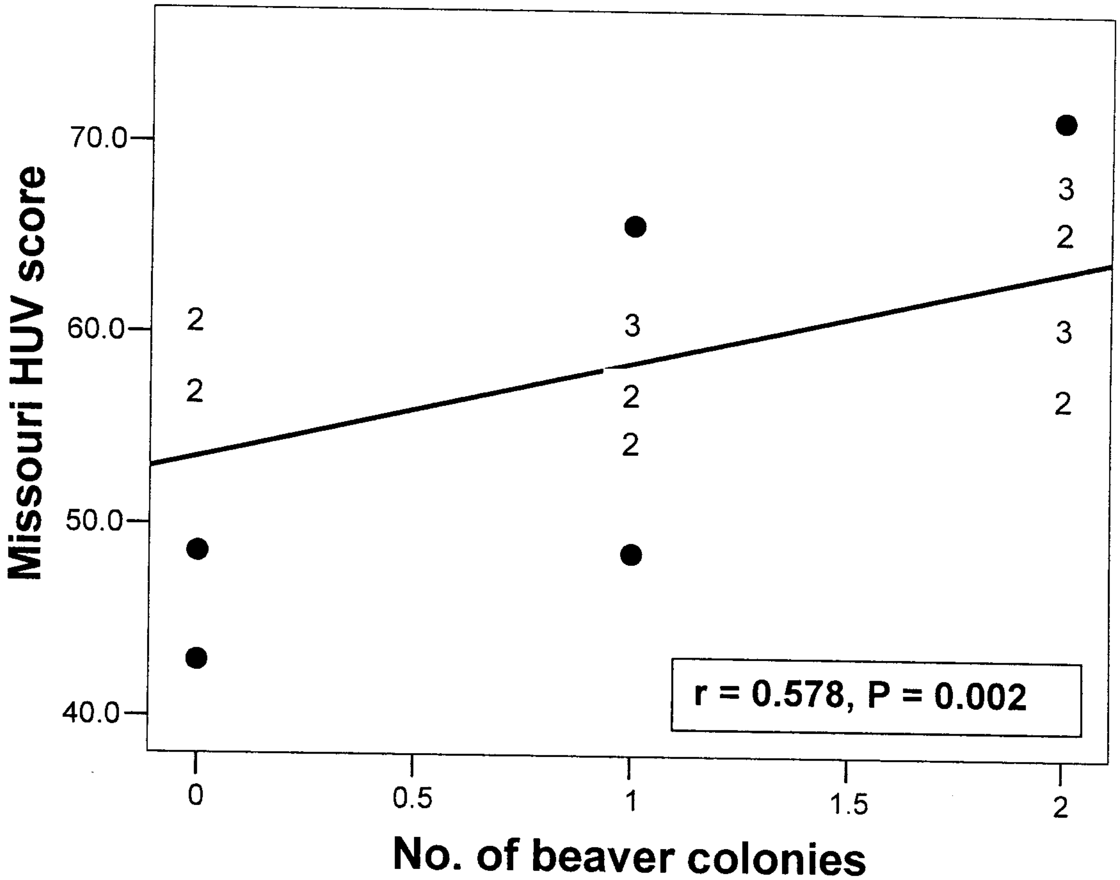


Fig. 8. Relationship between Missouri model Habitat Unit Values (HUV) and abundance of beaver colonies in 26 2.5-km segments of the Embarras River in central Illinois. Numbers on graph indicate the number of segments with each score. Colony density correlated significantly with habitat suitability as scored by the Missouri model (r = 0.578, P = 0.002).

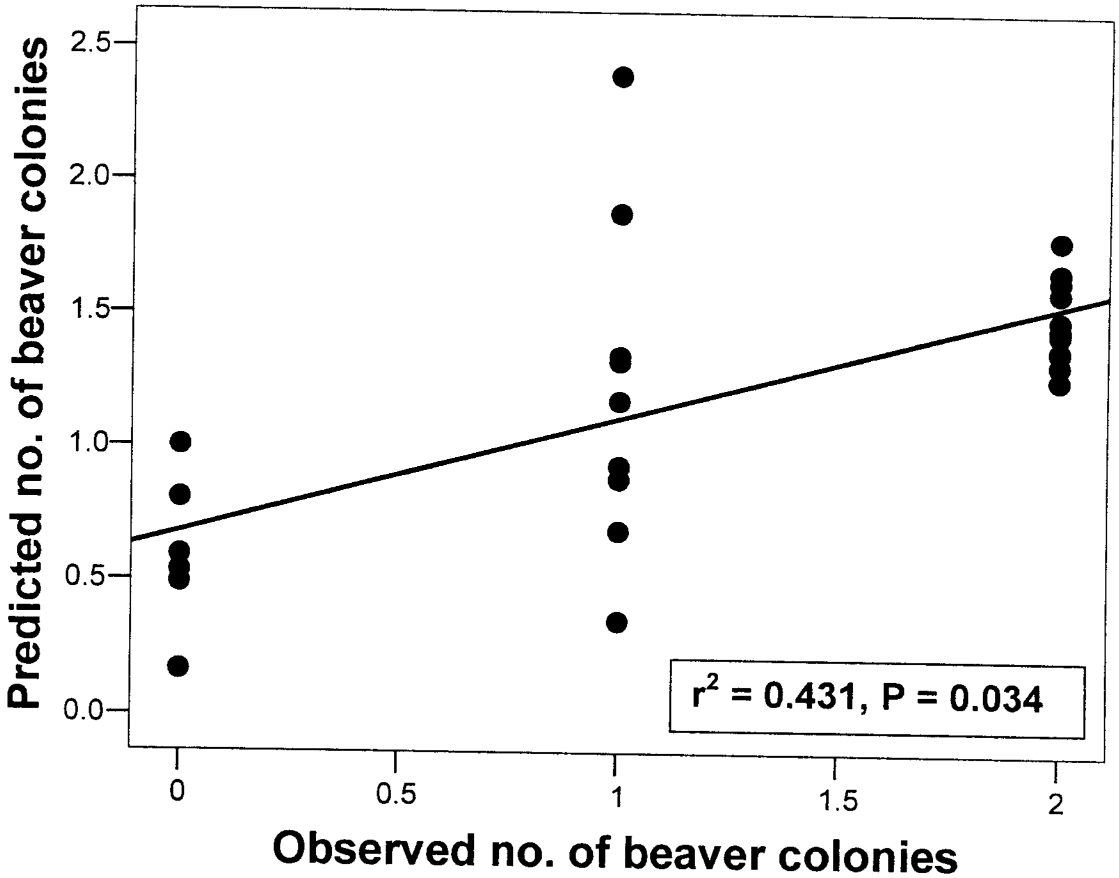


Fig. 9. Relationship between multiple regression model and abundance of beaver colonies in 26 2.5-km segments of the Embarras River in central Illinois. Colony density correlated significantly with habitat suitability as scored by the Missouri model (r^2 = 0.431, P = 0.034, F = 3.033, df = 5, 25).

Appendix A. Habitat Suitability Index (HSI) model for beavers (Allen 1983).

HABITAT SUITABILITY INDEX (HSI) MODEL

Model Applicability

Geographic area. This HSI model was developed for application throughout the range of the beaver. However, preferred foods may vary throughout the range of the species, depending on local availability. The food component of this model assumes that woody vegetation potentially may limit the ability of an area to support beavers. Herbaceous vegetation is an important component of the summer diet of beavers and is believed to be preferred over woody vegetation during all seasons, if available. Because herbaceous vegetation is generally available throughout the year in the southern portion of the beaver's range, it may have a more important influence on the annual diet than is indicated in this model.

Season. This model has been developed to evaluate the quality of year-round habitat for the beaver.

cover types. This model has been developed to evaluate habitat quality in the following cover types (terminology follows that of U.S. Fish and Wildlife Service 1981): Evergreen Forested Wetland (EFW); Deciduous Forested Wetland (DFW); Evergreen Scrub-Shrub Wetland (ESW); Deciduous Scrub-Shrub Wetland (DSW); Herbaceous Wetland (HW); Riverine (R); and Lacustrine (L).

Due to the foraging behavior of the beaver, the application of this model and determination of habitat units will vary by cover type. When evaluating beaver habitat in riverine, lacustrine, and wetland cover types, the model considers the area of the cover type plus a 200 m (656 ft) band of habitat on each side of the riverine channel or surrounding the water body or wetland. Figure 1 illustrates the relationship of cover types to the suggested evaluation area.

Minimum habitat area.. Minimum habitat area is defined as the minimum amount of contiguous habitat that is required before an area will be occupied by a species. Information on minimum habitat area for beavers was not found in the literature. However, it is assumed that a minimum of 0.8 km (0.5 mi) of stream channel and 1.3 km^2 (0.5 mi^2) of lake or marshland habitat must be available before these areas are suitable for colonization by beaver. If this minimum amount of habitat is not present, the HSI is assumed to be 0.0.

<u>Cover type</u> | <u>Area for evaluation</u>

Lacustrine [> 8 ha (20 acres)]

HSI determined only for area contained within 200 m (656ft) band around lake.

Lacustrine [≤ 8 ha (20 acres)]

HSI determined for area contained within 200 m band plus area of lake.

Riverine

HSI determined for area within 200 m band on both sides of river plus area of river.

Palustrine (herbaceous wetland, forested wetlands, or shrub wetlands)

HSI determined for area contained within cover type plus area within 200 m band around wetland cover type.

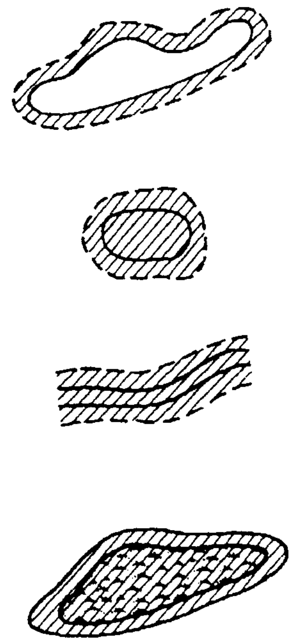


Figure 1. Guidelines for determining the area to be evaluated for beaver habitat suitability under various cover type conditions.

<u>Special model considerations</u>. Potential beaver habitat must contain a permanent source of surface water. Lakes and reservoirs that have extreme annual or seasonal fluctuations in the water level will be unsuitable habitat for beaver. Similarly, intermittent streams, or streams that have major fluctuations in discharge (e.g., high spring runoff) or a stream channel gradient of 15% or more, will have little year-round value as beaver habitat.

Assuming that there is an adequate food source available, small lakes [< 8 ha (20 acres) in surface area] are assumed to provide suitable habitat. Large lakes and reservoirs [> 8 ha (20 acres) in surface area] must have irregular shorelines (e.g., bays, coves, and inlets) in order to provide optimum habitat for the species.

Evaluation of potential beaver habitat must be centered in and around a suitable aquatic habitat. Therefore, the following factors must be taken into consideration in order to determine if this model is applicable to the habitat being evaluated:

If aquatic component of the cover type typically has extreme changes in water level or flow rate or has a channel gradient exceeding 15% -	Do not continue with model; HSI for beaver is assumed to be 0.0.
If aquatic component of the cover type has moderate or no fluctuation in water level or flow rate and channel gradient does not exceed 15% -	Continue with model to determine HSI values for water and food.

Verification level. This model was reviewed by Stephen H. Jenkins, Ph.D., Department of Biology, University of Nevada, and Rebecca J. Howard, Research Assistant, Department of Forestry and Wildlife Management, University of Massachusetts, Amherst. Improvements suggested by these reviewers were incorporated into this model.

Model Description

Overview. The HSI model for the beaver considers the quality of life requisites for the species in each cover type. Water and winter food are the only life requisites considered because the cover and reproductive needs of the species are assumed to be identical with water requirements. It also is assumed that all of the habitat requirements of the beaver can be provided within each cover type in which it occurs. Figure 2 illustrates how the HSI is related to cover types, life requisites, and specific habitat variables.

The following sections provide a written documentation of the logic and assumptions used to translate habitat information for the beaver to the variables and equations used in the HSI model. Specifically, these sections cover: (1) identification of the variables used in the model; (2) definition and justification of the suitability levels of each variable; and (3) description of the assumed relationships between variables.

Food component. Woody and herbaceous vegetation comprise the diet of the beaver. Herbaceous vegetation is a highly preferred food source throughout the year, if it is available. Woody vegetation may be consumed during any season, although its highest utilization occurs from late fall through early spring. It is assumed that woody vegetation (trees and/or shrubs) is more limiting than herbaceous vegetation in providing an adequate food source. Therefore, this model evaluates the potential of an area to provide an adequate winter food source.

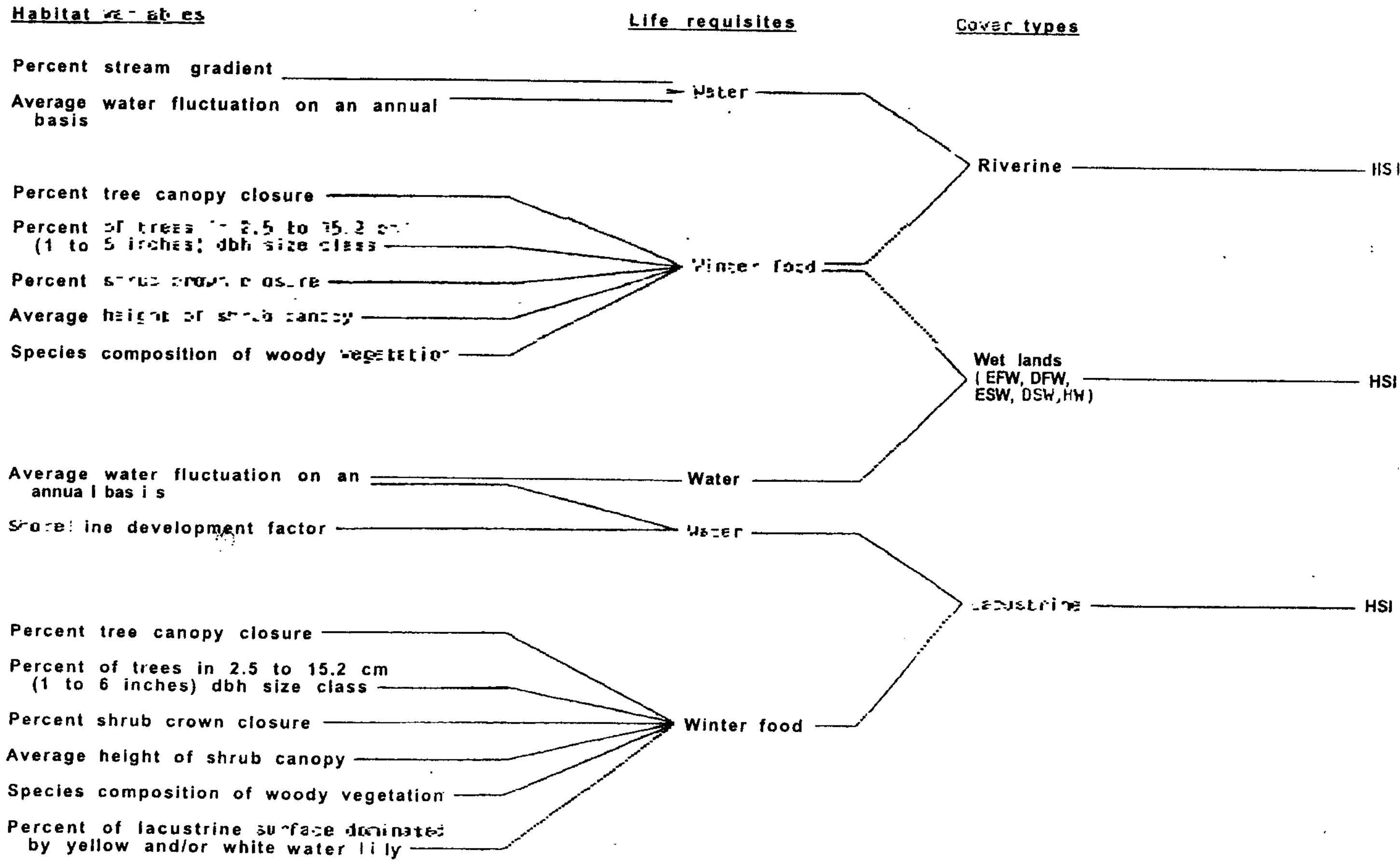


Figure 2. Tree diagram illustrating the relationships of habitat variables, life requisites, and cover types to the HSI for the beaver.

Several tree and shrub species (willow, aspen, cottonwood, and alder) have often been reported to be preferred foods; however, highly preferred species may vary in different geographic regions., Although coniferous trees and shrubs may be consumed, they are a less desirable food source for beavers than are deciduous tree species. Local variations in food preference and availability should be taken into consideration when evaluating the food component of this model.

Although beavers forage at distances up to 200 m (656 ft) from water, the majority of foraging occurs within 100 m (328 ft) of the water's edge. Even though woody vegetation may be within the optimum density and size classes, it is assumed that potential food sources farther than 100 m (328 ft) from water will be of less value than woody vegetation within 100 m (328 ft). Woody vegetation in excess of 200 m (656 ft) is assumed to have no value as a potential food source.

It is assumed that a tree and/or shrub canopy closure between 40 and 60% is an indication of optimum food availability. Tree or shrub crown closures exceeding 60% are assumed to be less suitable due to the decreased accessibility of food. Extremely dense stands result in decreased mobility and the increased likelihood of cut trees hanging up in adjacent trees. To be assigned a maximum suitability value, the dbh of trees should range from 2.5 to 15.2 cm (1 to 6 inches), and shrubs should be at least 2 m (6.6 ft) tall.

The food value in a cover type is a function of the density, size class, and species composition of woody vegetation. Optimum conditions are a stand of preferred tree and/or shrub species, of medium density, less than 15.2 cm (6 inches) dbh. An adequate food source includes some trees, or shrubs, or both. The species composition of the vegetation present influences the value obtained for density and size class. Stands of highly preferred species enhance the habitat value of the site, while foods of low preference will lower the overall food value of the site. White or yellow water lilies in lacustrine cover types may be used to supplement the winter food supply. Lakes or ponds supporting these aquatic species have a higher value as winter habitat than lacustrine cover types lacking this additional food source.

Water component. Water provides cover for the feeding and reproductive activities of the beaver. A permanent and relatively stable source of water is mandatory for suitable beaver habitat.

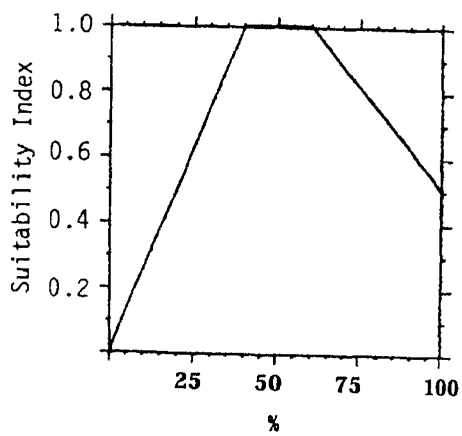
In riverine cover types, a major change in the rate of flow or a channel gradient exceeding 15% indicate poor or unsuitable habitat. Stream channel gradients of 6% or less have optimum value as beaver habitat. Stable water levels are of optimum value as beaver habitat, while major fluctuations in the water level or flow rate decrease the value of the site. Rivers or streams that are dry during some parts of the year are assumed to be unsuitable beaver habitat.

Lacustrine habitat types less than 8 ha (20 acres) in surface area are assumed to provide suitable habitat, if an adequate food source is present. Lacustrine cover types larger than 8 ha (20 acres) in surface area must provide physical diversity (e.g., bays, coves, and inlets) in the shoreline configuration in order to provide suitable beaver habitat. It is assumed that large reservoirs or lakes that are roughly circular in shape or are comprised of extensive stretches of straight shoreline provide little shelter from wind and wave action and, therefore, have little value as beaver habitat. Variation in the water level in lacustrine cover types results in less suitable habitat quality for beavers. Lakes or ponds that are dry during portions of the year are assumed to be unsuitable beaver habitat.

All wetland cover types (e.g., herbaceous wetland and deciduous forested wetland) must have a permanent source of surface water with little or no fluctuation in order to provide suitable beaver habitat.

Model Relationships

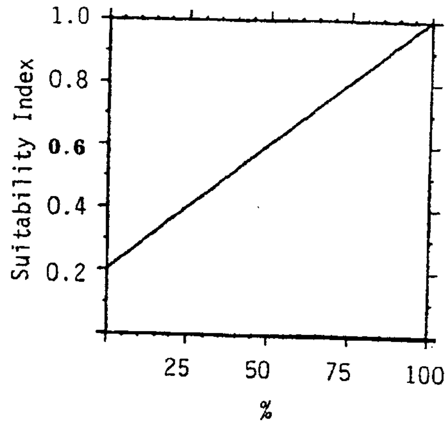
Suitability Index (SI) graphs for habitat variables. The relationships between various conditions of habitat variables and habitat suitability for the beaver are graphically represented in this section.

Cover type	Variable		
EFW, DFW, ESW, DSW, HW, R, L	V_1	Percent tree canopy closure.	

EFW,DFW,
ESW,DWS,
HW,R,L

V_2

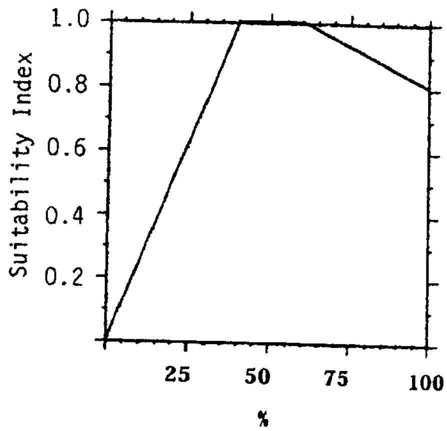
Percent of trees in 2.5 to 15.2 cm (1 to 6 inches) dbh size class.



EFW,DFW,
ESW,DSW,
HW,R,L

V_3

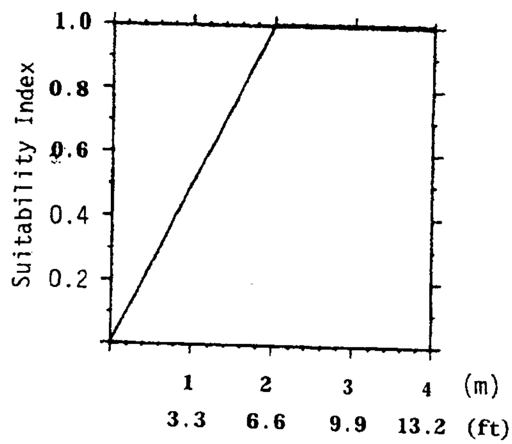
Percent shrub crown cover.



EFW,DFW,
ESW,DSW,
HW,R,L

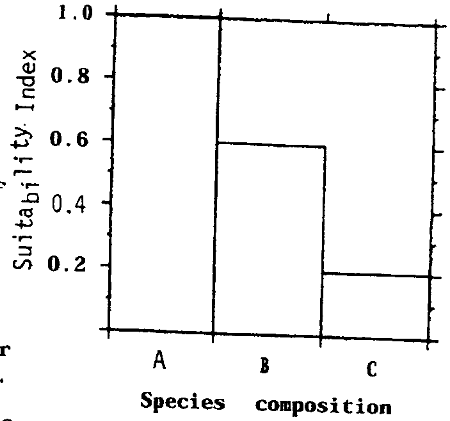
V_4

Average height of shrub canopy.

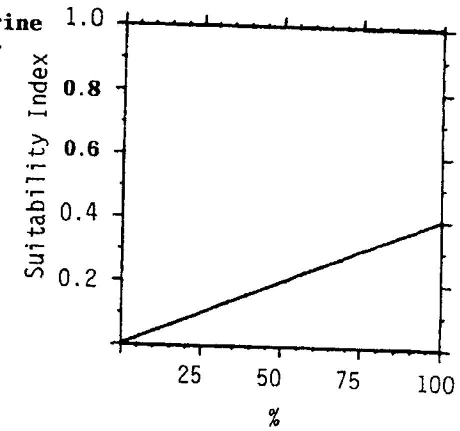


EFW, DFW, ESW, DSW, HW, R, L — V_5 — Species composition of woody vegetation (trees and/or shrubs)

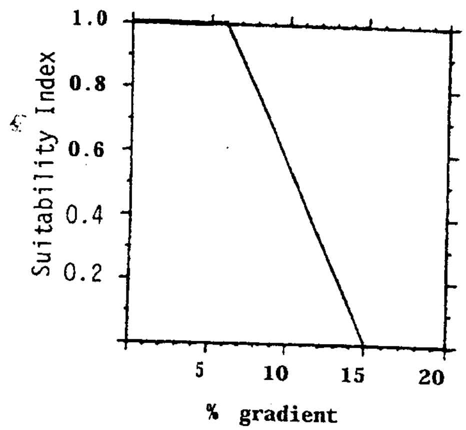
A) Woody vegetation dominated (≥ 50%) by one or more of the following species: aspen; willow; cottonwood; or alder.
B) Woody vegetation dominated by other deciduous species.
C) Woody vegetation dominated by coniferous species (e.g., fir and pine).

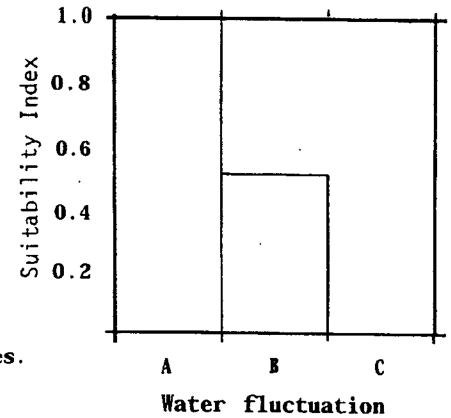
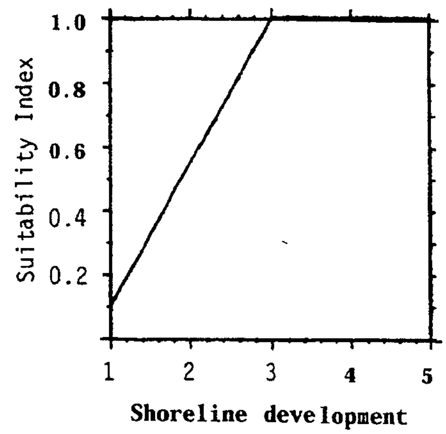


L — V_6 — Percent of lacustrine surface dominated by yellow and/or white water lily.



R — V_7 — Percent stream gradient.



EFW,DFW, ESW,DSW, HW,R,L	V_8	Average water fluctuation on annual basis. A) Small fluctuations that have no effect on burrow or lodge entrances. B) Moderate fluctuations that affect burrow or lodge entrances. C) Extreme fluctuations or water absent during part of year.	
L	V_9	Shoreline development factor (see variable definition in Figure 4).	

Equations. In order to obtain life requisite values for the beaver, the suitability index values for appropriate variables must be combined with the use of equations. A discussion and explanation of the assumed relationships between variables was included under Model Description. The suggested equations for obtaining food and water values for the beaver are presented by cover type in Figure 3.

Life requisite	Cover type	Equation
Winter food	DFW, EFW, DSW, ESW, HW	$\frac{a+b+c}{2.5}$
Winter food	R	$\frac{b+c}{1.5}$
Winter food	L	$\frac{b+c}{1.5} + V_6$

where: a = woody vegetation value within actual wetland boundary. The suggested equation is:

$$[(V_1 \times V_2)^{1/2} \times V_5]^{1/2} + [(V_3 \times V_4)^{1/2} \times V_5]^{1/2}$$

b = woody vegetation value within 100 m (328 ft) from the water's edge. The suggested equation is:

$$[(V_1 \times V_2)^{1/2} \times V_5]^{1/2} + [(V_3 \times V_4)^{1/2} \times V_5]^{1/2}$$

c = woody vegetation value within 100 m (328 ft) to 200 m (656 ft) from the water's edge. The suggested equation is:

$$0.5\ [(V_1 \times V_2)^{1/2} \times V_5]^{1/2} + [(V_3 \times V_4)^{1/2} \times V_5]^{1/2}$$

Life requisite	Cover type	Equation
Water	R	V_7 or V_8, whichever is lowest.
Water	L	V_8 or V_9, whichever is lowest, if lacustrine area ≥ 8 ha (20 acres) in surface area. V_8, if lacustrine area is < 8 ha (20 acres) in surface area.
Water	DFW, EFW, DSW, ESW, HW	V_8

Figure 3. Equations for determining life requisite values by cover type for the beaver. If equation products exceed 1.0, they should be considered equal to 1.0.

HSI determination. Based on the limiting factor concept, the HSI is equal to the lowest life requisite value obtained for either food or water.

Application of the Model

Definitions of variables and suggested field measurment techniques (Hays et al. 1981) are provided in Figure 4.

SOURCES OF OTHER MODELS

Slough and Sadleir (1977) developed a land capability classification system for beaver that related habitat variables to beaver colony site density through multiple regression analysis. The model can be used for beaver population inventory because it predicts beaver colony site density.

Howard (1982) developed a land capability classification system for the identification and ranking of potential, beaver habitat. Discriminant and principle components regression analysis models are used to relate habitat variables that quantify food availability and water reliability to beaver colony site selection and longevity. The models are applicable to stream habitats in typical mixed coniferous-deciduous forests of the Northeast.

Variable (definition)		Cover types	Suggested technique
V_1	Percent tree canopy closure [the percent of the ground surface shaded by a vertical projection of the canopies of woody vegetation ≥ 5.0 m (16.5 ft) in height].	R,L,DFW EFW,DSW, ESW,HW	Transect, line intercept, remote sensing
V_2	Percent of trees in 2.5 to 15.2 cm (1 to 6 inches) dbh size class [the percent of trees with a dbh of 2.5 to 15.2 cm (1 to 6 inches)].	R,L,DFW, EFW,DSW, ESW,HW	Transect, quadrat, diameter tape
V_3	Percent shrub crown cover [the percent of the ground surface shaded by a vertical projection of the canopies of woody vegetation < 5 m (16.5 ft) in height].	R,L,DFW, EFW,DSW, ESW,HW	Line intercept, quadrat, remote sensing
V_4	Average height of shrub canopy (the average height from the ground surface to the top of those shrubs that comprise the uppermost shrub canopy).	R,L,DFW, EFW,DSW, ESW,HW	Line intercept, quadrat, graduated rod
V_5	Species composition of woody vegetation (trees and/or shrubs) (refer to model page 12).	R,L,DFW, EFW,DSW, ESW,HW	Transect, line intercept
V_6	Percent of lacustrine surface dominated by yellow and/or white water lily [the percent of the surface dominated by yellow water lily (<u>Nymphaea variegatum</u>) and/or white water lily (<u>N</u>. <u>odorata</u>)].	L	Line intercept, remote sensing

Figure 4. Definitions and suggested measurement techniques of habitat variables.

Variable (definition)	Cover types	Suggested technique
V_7 Percent stream gradient (the vertical drop in meters or feet per kilometer or mile of stream or river channel). % stream gradient = $(\frac{A}{B})$ 100 where A = difference in elevation between sample points. B = distance between sample points.	R	Topographic map
V_8 Average water fluctuation on an annual basis (refer to model page 13).	R,L,HW, DFW,EFW, DSW,ESW	Local data
V_9 Shoreline development factor (a ratio relating the relative edge of a water body to its area. To obtain a value for shoreline development factor (SDF), divide the length of the shoreline by the length of the circumference of a circle with the same area as the water body. The following formula may be used: $SDF = \frac{\ell}{2\sqrt{A\pi}}$ where SDF = shoreline development factor; ℓ = length of shoreline; A = area of water body A circle would have a SDF equal to 1.0. The greater the deviation from a circular shape, the greater the SDF value will be. Values of 3 or more are assumed to be optimum for beavers).	L [≥ 8 ha (20 acres)]	Remote sensing, topographic map, dot grid, map wheel

Figure 4. (concluded).

ıppendix B. Missouri habitat model for beavers in Missouri's bottomland ıardwood habitats (Hallett and Erickson 1980).

Evaluation Element: BEAVER

Habitat Type: BOTTOMLAND HARDWOOD

CHARACTERISTIC	POSSIBLE SCORE	ACTUAL SCORE
I. Distance to permanent water (m)		I.______
1. Less than 75	7-10	
2. 75-200	2- 6	
3. More than 200	1	
(NOTE: If characteristic I is scored as 1, disregard other criteria, and enter 1 on line (8) as Habitat Unit Value for Bottomland Hardwood.)		
II. Bank den characteristics		II.______
A. Soil texture (see "Definition of Terms")		A.______
1. Clay or silty clay	5	
2. Loam, clay loam, or silty clay loam	3- 4	
3. Sand or sandy loam	1- 2	
(NOTE: If soil is more than 80% sand or stone, enter 1 for characteristic II and go directly to characteristic III.)		
B. Slope of bank		B.______
1. More than 60°	5	
2. 30-60°	3- 4	
3. Less than 30°	1- 2	
(NOTE: Add A and B to obtain value for characteristic II.)		
III. Species composition of 40% or more of the forest		III.______
1. Willows, cottonwood, ashes	7-10	
2. River birch, elms, red maple, silver maple	4- 6	
3. Black cherry, dogwoods, hackberry, white oak, and others	1- 3	
IV. Number of important food plant species comprising more than 1% of total plants present (See NOTE on "Food List")		IV.______
1. More than 7	5	
2. 5-7	2- 4	
3. Less than 5	1	

Evaluation Element: BEAVER

Habitat Type: BOTTOMLAND HARDWOOD

CHARACTERISTIC	POSSIBLE SCORE	ACTUAL SCORE
V. Tree size class		V.______

Code

Size Class (dbh) of Trees Composing Predominant Foliage Layer (Overstory)

S=sawtimber (more than 23 cm)
P=poles/small trees (5-23 cm dbh)
R=reproduction (less than 5 cm dbh)

No Size Class Predominant in Overstory

M=mixed (must include sawtimber component)

1. R	5	
2. P	3- 4	
3. M, S	1- 2	

VI. Distance to cropland (m)		VI.______
1. Less than 15	5	
2. 15-30	3- 4	
3. More than 30	1- 2	

NOTES: (A) IF CHARACTERISTIC NOT APPLICABLE, ENTER NA AND DO NOT COUNT IT AS A CHARACTERISTIC USED.

(B) IF ALL CHARACTERISTICS ARE SCORED AS 1, DISREGARD COMPUTATIONS BELOW, AND ENTER 1 ON LINE (5) AS HABITAT UNIT VALUE.

---

(1) Maximum possible score for form .... (1) 45

(2) Total maximum possible score(s) for characteristic(s) tallied as NA .... (2) ______

(3) Corrected maximum possible score: (1) - (2) .... (3) ______

(4) Total actual scores .... (4) ______

(5) (4) ÷ (3) x 10 .... (5) ______ HABITAT UNIT VALUE

Reproduction

The young are born between April and June. They remain dependent on the female until weaning at about 6 weeks of age. After they are weaned, their diet is similar to that of the adults (Schwartz and Schwartz 1959:168).

Important Foods of Beaver

(Listings generally reflect relative order of importance.)

NOTE: In tallying species of food plants for field form, use lists from all seasons.

Fall & Winter & Spring	Summer
Willows	Willows
Cottonwood	Cat-tails
Ashes	Blackberries
River birch	Yellow pond lily
Elms	Arrowheads
Silver maple	Goldenrods
Black cherry	Eelgrass
Hackberry	Bur-reeds
Dogwoods	Waterweed
White oak	Watercress
Corn	Duckweeds