Forage utilization habitat selection and population indices of beaver in northwestern Montana

Andrea L. Easter-Pilcher

The University of Montana

1987

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FORAGE UTILIZATION, HABITAT SELECTION AND
POPULATION INDICES OF
BEAVER IN NORTHWESTERN MONTANA

By

Andrea L. Easter-Pilcher
B.A., Bowdoin College, 1977

Presented in partial fulfillment of the requirements for the degree of
Master of Science
UNIVERSITY OF MONTANA
1987

Approved by:

[Signatures]
Chairman, Board of Examiners
Dean, Graduate School

Date: Dec. 7, 1987
ABSTRACT

Easter-Pilcher, Andrea L., M.S., August 1987 Wildlife Biology
Forage Utilization, Population Indices, and Habitat Selection of Beaver in Northwestern Montana. (88 pp.)

Directors: Dr. Daniel Pletscher and Dr. Lee Metzgar

Field investigations were conducted for beaver (Castor canadensis) in northwestern Montana from June 1985 through December 1986. General habitat and population sampling of 550 km of waterway was initiated on 1 July 1985 and completed on 31 August 1986.

Intensive habitat and population sampling at 10 randomly selected colony sites (occupied) and 10 stratified random sites (unoccupied) in each of the Swan, Clearwater, and Fish Creek drainages was initiated in September 1986 and completed in December 1986. Synopses of the 3 papers resulting from the intensive surveys are presented below in the order they appear in the thesis.

Forage utilization plots (n=360) were run on these occupied and unoccupied sites. The Chi-square goodness of fit test and Bonferroni Z confidence intervals showed a general preference for small stems (less than 5.0 cm in diameter) with willow (Salix spp.), cottonwood (Populus trichocarpa), alder (Alnus spp.), and red osier dogwood (Cornus stolonifera) as the preferred species. Beaver cuttings also showed preference of medium size stems (2.5-5.0 cm) over smaller stems (less than 2.5 cm) farther from the water, suggesting more selectivity farther from the waterway.

Beaver colony size was assessed through nocturnal observation with infrared night vision goggles. Colony size was regressed with various population indices which included number of dams, tracks, stems cut, and cache volume. Cache volume accounted for the only source of variation in colony size ($R^2 = 0.68$).

A discriminant function model for winter colony site selection by beaver was developed from measured stream and vegetation characteristics at the occupied and random sites. Water depth, slope distance between low and high water marks, and availability of understory willow correctly classified 96% of the occupied sites and 92% of the random sites, suggesting that these variables are critical for successful winter colony sites.

Beaver colony size was regressed with principal components of the habitat variables. Water depth, stream width, availability of willow, slope distance, vertical water fluctuation (vertical distance between low and high water marks), and the presence of a confluence were positively correlated with colony size.
PREFACE

The western Montana beaver (Castor canadensis) project set initial objectives of determining population status, distribution, and ecology of the beaver throughout northwestern Montana. Funding is being provided by Montana Department of Fish, Wildlife and Parks through the Montana Cooperative Wildlife Research Unit at the University of Montana in Missoula, Montana. The current plan is for 3 graduate students to conduct consecutive research over a period of 6 years, July 1985 - July 1991. This study was the first of the three.
ACKNOWLEDGEMENTS

I would like to thank Montana Department of Fish, Wildlife and Parks for providing the funding for this project. Special thanks are extended to Dr. Lee Metzgar and Dr. Daniel Pletscher who guided me through "the Masters process" offering continual support, enthusiasm and advice on a generous scale. Thanks also to Mr. Howard Hash who passed along to me his knowledge of Montana furbearers and offered pertinent advice on study design. His exuberance and support meant a great deal to this project. I would also like to thank Dr. Bart O'Gara for thoughtful reviews of my thesis drafts and Dr. Andrew Sheldon for guidance with the multivariate statistical techniques.

Lisa Jerez and Kit Hershey made valuable contributions to the project by gamely taking on the horrors of riparian vegetation work. Thanks go to both of them for their unselfish contribution to the research.

The cooperation and insight of trappers Butch Harmon, Bud and Vicki Moore, Bruce Graham and Will Katz were greatly appreciated.

I would also like to thank the people of Fish Creek, especially Ellen Basque, Clyde Trego, and the Fords as well as Jack and Anne Taylor in the Swan Valley for their hospitality, conversation and hot coffee.
Thanks also to my family and friends who supported me from across the miles and to Jessie who lent her own unique perspective to the project—"critical" applied only to a blue, 2 inch diameter rubber ball with a bell in it. All else was trivial.

Finally, but especially to my husband Brian, who endured it all, I extend my abiding respect, appreciation, and thanks for invaluable support and critical comments as the project unfolded.

This thesis is dedicated to Cady, Peter, and Stephen; Michael, Brian, and Megan; Jane-Kate and Jonah; Mario and Renato; Britt and Annika; Alex; and Caitlyn, all young faces in the next generation for whom proper management and conservation of wildlife will make a difference.
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THESIS INTRODUCTION

General surveys on 550 km of waterway were conducted June - October 1985 and June - August 1986 to assess relative densities, general distribution, and habitat of beaver in northwestern Montana (Appendix A) and to select 3 waterways for further intensive research.

Winter colony sites on the Swan and Clearwater rivers and Fish Creek were selected for intensive study. Stream and vegetation characteristics surrounding winter colony sites may have the greatest potential influence on survival and reproductive success of beaver in northern climates. Knowledge of the abundance and availability of preferred woody taxa at winter colony sites is an important criteria for intensive management of beaver. Knowledge of stream characteristics important for winter colony sites and probably influencing beaver abundance are also criteria for managers to consider.

Finally, the key to proper, intensive beaver management is the determination of an accurate and precise index to beaver populations. Attempts to quantify the relationship between qualitatively different riparian habitats and beaver numbers necessitates this information.
Objectives

1) Determine population status and relative densities of beaver populations within diverse habitats on selected rivers and creeks in northwestern Montana;

2) Develop a general habitat classification scheme for riverine beaver habitat in northwestern Montana;

3) Quantify beaver sign indices and determine their utility in predicting colony size and population density;

4) Discriminate use/non-use areas using habitat variables and evaluate the importance of those variables;

5) Correlate selected habitat variables with colony size; and

6) Assess utilization-availability data to determine preference of woody plant species.

Thesis format

Three separate papers addressing the issues of forage preference, population indices, and winter colony site selection are presented as separate chapters in this thesis. Each paper is complete and needs no supportive information outside its respective chapter.

Information collected during this project that was not used in the three papers has been included in the appendices. These data may be used to complement future research on beaver in northwestern Montana.
CHAPTER I

UTILIZATION OF WOODY TAXA BY BEAVER IN NORTHWESTERN MONTANA

Andrea L. Easter-Pilcher, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana 59812

Abstract: Preference of woody species by beaver (Castor canadensis) was investigated during the fall of 1986 on the Swan and Clearwater rivers and Fish Creek in northwestern Montana. Three-hundred sixty plots were examined for utilization of woody stems. Taxon, stem diameter and distance from the waterway were assessed. Application of the chi-square goodness of fit test and Bonferroni Z confidence intervals showed a general preference for stem diameter less than 5.0 cm. Small willow (Salix spp.) stems were generally preferred on the Clearwater River and Fish Creek while small cottonwood (Populus trichocarpa) was preferred on the Swan River. Cottonwood was available in significant quantities only on the Swan River. The data also revealed a trend towards preference of medium size stems (2.5 - 5.0 cm in diameter) over smaller stems (less than 2.5 cm) farther from the waterway.
The need for determining an animal's preference for or avoidance of a given plant species relative to that plant's availability has long been acknowledged (Neu et al. 1974). The abundance and availability of preferred woody species at winter colony sites for beaver may contribute greatly to the fitness of individuals at those sites. Knowledge of forage preference at this level of habitat selection is critical for developing proper management strategies for beaver.

Denney (1952) listed aspen (*Populus tremuloides*), willow, cottonwood, and alder (*Alnus* spp.), in that order, as the preferred woody species for North American beaver. It is generally agreed that aspen is the preferred food item for beaver (Aldous 1938, Bradt 1938, Brenner 1962) if it is available. In areas where aspen is less, or not, available, willow and sometimes cottonwood seem to replace aspen as the preferred species (Bailey 1927, Hammond 1943, Townsend 1953, Hall 1960, Rutherford 1964, Swenson and Knapp 1980).

Jenkins (1980) pointed out that most beaver food use studies seldom shed light on optimal foraging strategies because they lack measurements of at least one of three critical parameters: stem diameter, species, and distance from water. Forage preference of beaver in northwestern Montana is examined in this paper taking into account these parameters.
A problem inherent in many forage preference studies is the arbitrary selection by the researcher of the plant species to measure for availability. Conclusions about whether individual species are used in proportion to their availability depend on the array of species the investigator regards as available to the animal (Johnson 1980). Plants selected for analysis were those found to be utilized by beaver in a previous survey (Easter-Pilcher 1987) of 550 km of waterway in northwestern Montana.

"Availability" is defined by prior use of, and access to, a specific plant species by beaver. "Utilization" is the measured use of a given plant species by beaver during a fixed time interval. "Preference" of a plant species is utilization measured in proportion to that plant's relative availability.

STUDY AREAS AND METHODS

Data were collected at 10 stratified random sites and 10 randomly selected occupied sites in each of the Swan, Clearwater and Fish Creek (South Fork) drainages in northwestern Montana (Fig. 1). These drainages were selected for their generally different characteristics representing a broad spectrum of northwestern Montana riparian areas. The inclusion of random sites as well as randomly selected occupied sites ensured a more accurate representation of shrub availability on the entire river.
Fig. 1. Map of northwestern Montana rivers showing the location (*) of the Swan and Clearwater Rivers and Fish Creek study areas.

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The Swan Valley, located 80 km northeast of Missoula, Montana, lies between the Swan Range to the East and the Mission Range to the West. The Swan River drops 1142 m during the course of its northward run from Grey Wolf Lake (at 2024 m) to Flathead Lake at (882 m). The straight-line distance from source to mouth is 90 km. Dominant woody vegetation along the banks of the Swan River is willow with secondary vegetation consisting of red osier dogwood (*Cornus stolonifera*), alder and hawthorne (*Crataegus douglasii*). The surrounding area is dominated by montane forest, a mosaic of larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and cottonwood. The Swan is generally characterized by variable but steep banks, substrate that ranges from mud to medium rock, moderate to steep gradient, slow to swift velocity, low turbidity, dense shrub cover, log jams, and channeling.

The head of the Clearwater Valley, located 8 km southeast of the Swan Valley, also lies between the Swan and Mission ranges. The Clearwater drops 378 m in its southern flow, from the source at Clearwater Lake (1460 m) to its convergence with the Blackfoot River (1082 m). Straight-line distance is 50 km. Dominant woody vegetation along the Clearwater River is willow with
secondary vegetation consisting of twinberry (*Lonicera involucrata*), dogwood, and alder. The surrounding area is dominated by a montane forest mosaic similar to the Swan with substantially less cottonwood. The meandering river generally is characterized by low banks, mud and gravel substrate, mild gradient, and velocity, low turbidity, and dense shrub cover.

Fish Creek is 50 km west of Missoula. The creek drops 396 m from its source above Sullivan Creek (1341 m) to the confluence with the West Fork (945 m). Straight-line distance from source to mouth is 22 km. Dominant vegetation on Fish Creek is also willow, although abundance is about 0.3 that of the Swan or Clearwater. Alder, the second most abundant species, is more abundant on Fish Creek than on the Swan or the Clearwater. Dogwood ranks third, with abundance being only about 0.5 that of the Clearwater and 0.3 that of the Swan. The area surrounding Fish Creek is dominated by montane forest with overstory similar to that of the Swan River. The creek itself is generally characterized by a variable bank height, small to medium rock substrate, moderate gradient with moderate to swift velocity, low turbidity, and low to moderate shrub cover.

Occupied sites, on or just off, main stream channels were located by aerial and ground reconnaissance. The first 10 occupied stick-and-mud lodges
encountered, in a general search of the entire stream, were selected for measurements of availability and use. A stratified sampling scheme was employed for the selection of 10 random sites for measurements of availability and use on each stream. Total stream length divided by 9 determined the distance between random sites on the Clearwater and Fish Creek, with the first site falling at the mouth of each waterway. Difficult access on the Swan River limited the study area to the distance between Lindbergh and Swan lakes.

Six sampling plots were flagged at each site (Fig. 2). Three of these plots were laid out along the high water mark. Each plot was 7 m in length (running parallel to the bank) and 3 m in width (1 m below the high water mark and 2 m above that mark) and were 4.5 m apart. These plots were collectively labelled the bank transect. The remaining 3 sampling plots ran inland (inland transect) from the high water mark. Each plot was 7 m in length (running perpendicular to the bank) and 2 m in width (1 m on either side of the mid-point on the bank transect) and 4.5 m apart. These plots were analyzed separately to investigate the relationship between species, stem diameter, and distance from the waterway.

Rooted stems in each plot were classified by taxon and diameter at stump height (dsh estimated at 15 cm above ground) and counted as available if dsh was greater than
Fig. 2. Diagram of the bank (parallel) and inland (perpendicular) utilization-availability plots for occupied and random sites.

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0.625 cm in diameter. Branches were included as available if they were greater than 0.625 cm in diameter and branched off the rooted stem within 60 cm above ground. Available stems and branches were placed in the following diameter class sizes:

<table>
<thead>
<tr>
<th>Class</th>
<th>Diameter (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.625 - 2.5</td>
</tr>
<tr>
<td>2</td>
<td>2.6 - 5.0</td>
</tr>
<tr>
<td>3</td>
<td>5.1 - 7.5</td>
</tr>
<tr>
<td>4</td>
<td>&gt; 7.6</td>
</tr>
</tbody>
</table>

Data collection took place during October and November 1986. Cache construction was underway at all occupied sites. Sixty sites (360 plots) were flagged and surveyed in October to establish shrub availability and prepare for stem utilization counts in November. Previously cut stumps were painted with Aervoe Pacific tree and log marking paint to prevent including them in the later utilization count. Paint was applied conservatively with small sponge brushes to minimize possible avoidance by beaver. Stumps were color-coded to aid in species identification after leaf fall. Fifty-seven sites were resurveyed an average of 39 days later to determine utilization.

The Chi-square goodness-of-fit test (Neu et al. 1974, Byers and Steinhorst 1984) evaluated the hypothesis that beaver utilize forage species in proportion to availability. Upon rejection of the null hypothesis, Bonferroni confidence intervals were applied to the data to
determine preference or avoidance of a forage type. To ensure adequate sample sizes, no more than 20% of all categories used in the analysis had an expected frequency of less than 5 and no categories were included that had an expected frequency of 1 or 2.

RESULTS

The observed number of cuts on both the bank transect and the inland transect differed significantly from the expected number of cuts based on availability (on the bank transect $X^2 = 693.4$, $df = 17$, $P < 0.01$ and on the inland transect $X^2 = 460$, $df = 22$, $P < 0.01$). Bonferroni Z confidence intervals applied to the bank data (Table 1) showed that small willow along the bank were utilized more than expected by chance, while large alder, medium dogwood, and small hawthorne, twinberry, and rose (*Rosa woodsii*) were utilized less than would be expected by chance. The inland transect (Table 2) showed small willow close to a stream, and small, and medium sized willow at an intermediate distance from the stream to be utilized more than expected by chance. Small willow farthest from a stream, rose close to a stream, and small dogwood close to, and an intermediate distance from, a stream were utilized less than expected by chance.

A general preference for small stems along the bank (Table 1) could be seen, with the first five preference ranks being Class 1 and 2 willow, Class 1 alder, Class 1
Table 1. Utilization - availability data for woody taxa on the bank transects of the Swan and Clearwater rivers and Fish Creek in northwestern Montana. Diameter class 1 = 0.5-7.5 cm, class 2 = 7.5-10 cm, class 3 = 10-12.5 cm, class 4 = 12.5-15 cm. Pio represents the expected proportion of cuttings if beaver cut each species in exact proportion to availability. E is calculated by multiplying Pio x n, where n = total cuts. * utilized greater than would be expected by chance. ** utilized less than would be expected by chance.

<table>
<thead>
<tr>
<th>Species</th>
<th>Diameter class</th>
<th>Total stems</th>
<th>Proportion of total stems (Pio)</th>
<th>Expected stems cut (E = Pio x n)</th>
<th>Observed stems cut (O)</th>
<th>Preference index (O/E)</th>
<th>Preference index rank</th>
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<tr>
<td><strong>Salix spp.</strong></td>
<td>1</td>
<td>9809</td>
<td>0.489</td>
<td>1082</td>
<td>1610*</td>
<td>1.488</td>
<td>1</td>
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<tr>
<td></td>
<td>2</td>
<td>767</td>
<td>0.038</td>
<td>84</td>
<td>111</td>
<td>1.321</td>
<td>2</td>
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<tr>
<td></td>
<td>3</td>
<td>87</td>
<td>0.004</td>
<td>9</td>
<td>5</td>
<td>0.555</td>
<td>6</td>
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<tr>
<td><strong>Alnus spp.</strong></td>
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<td>1543</td>
<td>0.077</td>
<td>170</td>
<td>183</td>
<td>1.076</td>
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<tr>
<td></td>
<td>2</td>
<td>469</td>
<td>0.023</td>
<td>51</td>
<td>41</td>
<td>0.804</td>
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<tr>
<td></td>
<td>3</td>
<td>276</td>
<td>0.014</td>
<td>31</td>
<td>16**</td>
<td>0.516</td>
<td>8</td>
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<tr>
<td></td>
<td>4</td>
<td>189</td>
<td>0.009</td>
<td>20</td>
<td>4**</td>
<td>0.200</td>
<td>11</td>
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<td><strong>Cornus stolonifera</strong></td>
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<td>3160</td>
<td>0.157</td>
<td>347</td>
<td>192**</td>
<td>0.553</td>
<td>7</td>
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<tr>
<td></td>
<td>2</td>
<td>157</td>
<td>0.008</td>
<td>18</td>
<td>8</td>
<td>0.444</td>
<td>10</td>
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<td><strong>Lonicera involucrata</strong></td>
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<td>1979</td>
<td>0.099</td>
<td>219</td>
<td>14**</td>
<td>0.064</td>
<td>13</td>
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<td><strong>Rosa woodsii</strong></td>
<td>1</td>
<td>321</td>
<td>0.016</td>
<td>35</td>
<td>4**</td>
<td>0.114</td>
<td>12</td>
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<td><strong>Rubus parviflorus</strong></td>
<td>1</td>
<td>149</td>
<td>0.007</td>
<td>15</td>
<td>0</td>
<td>0.000</td>
<td>—</td>
</tr>
<tr>
<td><strong>Amelanchier alnifolia</strong></td>
<td>1</td>
<td>218</td>
<td>0.011</td>
<td>24</td>
<td>0</td>
<td>0.000</td>
<td>—</td>
</tr>
<tr>
<td><strong>Crataegus douglasii</strong></td>
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<td>358</td>
<td>0.018</td>
<td>40</td>
<td>1**</td>
<td>0.025</td>
<td>14</td>
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<td>0.004</td>
<td>9</td>
<td>0</td>
<td>0.000</td>
<td>—</td>
</tr>
<tr>
<td><strong>Ribes lacustre</strong></td>
<td>1</td>
<td>184</td>
<td>0.009</td>
<td>20</td>
<td>0</td>
<td>0.000</td>
<td>—</td>
</tr>
<tr>
<td><strong>Picea engelmannii</strong></td>
<td>1</td>
<td>118</td>
<td>0.006</td>
<td>13</td>
<td>6</td>
<td>0.461</td>
<td>9</td>
</tr>
<tr>
<td><strong>Populus trichocarpa</strong></td>
<td>1</td>
<td>192</td>
<td>0.009</td>
<td>20</td>
<td>18</td>
<td>0.900</td>
<td>4</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>20,369</td>
<td></td>
<td>2207</td>
<td>2213</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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Table 2. Utilization - availability data for woody taxa on the inland transects of the Swan and Clearwater rivers and Fish Creek in northwestern Montana. Diameter class 1 < 2.5 cm, class 2 = 2.5 - 5.0 cm, class 3 = 5.1 - 7.5 cm. P. represents the expected proportion of cuttings if beaver cut each species in exact proportion to availability. E is calculated by multiplying P. x n, where n = total cuts. * utilized greater than would be expected by chance. ** utilized less than would be expected by chance.

<table>
<thead>
<tr>
<th>Species</th>
<th>Diameter class</th>
<th>Total stems</th>
<th>Proportion of total stems</th>
<th>Expected stems cut (E = nPio)</th>
<th>Observed stems cut (O)</th>
<th>Preference index (O/E)</th>
<th>Preference rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salix spp. 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot 1</td>
<td>1886</td>
<td>0.218</td>
<td>120</td>
<td>241*</td>
<td>1.30</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Plot 2</td>
<td>1590</td>
<td>0.184</td>
<td>101</td>
<td>139*</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot 3</td>
<td>940</td>
<td>0.109</td>
<td>60</td>
<td>5**</td>
<td>0.00</td>
<td>19</td>
<td></td>
</tr>
<tr>
<td>Salix spp. 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot 1</td>
<td>112</td>
<td>0.013</td>
<td>7</td>
<td>8</td>
<td>1.10</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Plot 2</td>
<td>121</td>
<td>0.014</td>
<td>8</td>
<td>39*</td>
<td>4.80</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Plot 3</td>
<td>106</td>
<td>0.012</td>
<td>7</td>
<td>6</td>
<td>0.86</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Alnus spp. 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot 1</td>
<td>271</td>
<td>0.031</td>
<td>17</td>
<td>33</td>
<td>1.90</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Plot 2</td>
<td>148</td>
<td>0.017</td>
<td>9</td>
<td>5</td>
<td>0.55</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>Plot 3</td>
<td>193</td>
<td>0.022</td>
<td>12</td>
<td>12</td>
<td>1.00</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Alnus spp. 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Plot 1</td>
<td>67</td>
<td>0.008</td>
<td>4</td>
<td>1</td>
<td>0.25</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Plot 2</td>
<td>71</td>
<td>0.008</td>
<td>5</td>
<td>6</td>
<td>1.20</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Plot 3</td>
<td>61</td>
<td>0.007</td>
<td>4</td>
<td>6</td>
<td>1.50</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Alnus spp. 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot 1</td>
<td>66</td>
<td>0.008</td>
<td>4</td>
<td>3</td>
<td>0.75</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Cornus stolonifera 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot 1</td>
<td>616</td>
<td>0.071</td>
<td>39</td>
<td>16**</td>
<td>0.41</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>Plot 2</td>
<td>472</td>
<td>0.055</td>
<td>30</td>
<td>9**</td>
<td>0.30</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>Plot 3</td>
<td>335</td>
<td>0.039</td>
<td>21</td>
<td>0</td>
<td>0.00</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Cornus stolonifera 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot 3</td>
<td>43</td>
<td>0.005</td>
<td>3</td>
<td>7</td>
<td>2.30</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Lonicera involucrata 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot 1</td>
<td>800</td>
<td>0.092</td>
<td>51</td>
<td>0</td>
<td>0.00</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Plot 2</td>
<td>244</td>
<td>0.028</td>
<td>15</td>
<td>10</td>
<td>0.67</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Plot 3</td>
<td>221</td>
<td>0.025</td>
<td>14</td>
<td>0</td>
<td>0.00</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Rosa woodsii 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot 1</td>
<td>99</td>
<td>0.011</td>
<td>6</td>
<td>1**</td>
<td>0.17</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>Crataegus douglasii 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot 1</td>
<td>100</td>
<td>0.011</td>
<td>6</td>
<td>0</td>
<td>0.00</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Plot 2</td>
<td>87</td>
<td>0.010</td>
<td>5</td>
<td>2</td>
<td>0.40</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>8,649</td>
<td>549</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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cottonwood, and Class 2 alder. Class 1 cottonwood, spruce, and hawthorne were available in significant amounts only on the Swan River and ranked one, five and ten in order of preference (Table 3). The inland plots (Table 2) showed similar preference ranks as the bank transect, with class 2 willow, class 2 dogwood, class 1 willow, and class 1 and 2 alder as the top five preferred species. Cottonwood was not available in significant quantities on the inland plots.

Willow, alder, and dogwood were further examined to elucidate any trends between size and distance from the waterway (Table 4). The data showed a trend of larger size preference farther from the water. Plots 2 and 3 were lumped to provide an adequate sample size for this analysis.

DISCUSSION

Beaver forage preferences for woody species on the Clearwater and Swan rivers and on Fish Creek generally agreed with earlier studies done in Montana (Townsend 1953, Swenson and Knapp 1980). In the absence of aspen, willow less than 5 cm in diameter was the most preferred item on Fish Creek and the second most preferred item on the Swan and Clearwater rivers. Small cottonwood was the most preferred food item for beaver on the Swan River. This was the only area in which cottonwood was available in significant quantities for analysis (Table 3). This
Table 3. Preference indices (PI) and ranks for woody taxa on each of the Swan and Clearwater rivers and Fish Creek in northwestern Montana. Diameter class 1 = 2.5 cm, class 2 = 2.5 - 5.0 cm, class 3 = 5.1 - 7.5 cm, class 4 > 7.5 cm.

<table>
<thead>
<tr>
<th>Species</th>
<th>Diameter class</th>
<th>Fish Creek</th>
<th>Swan</th>
<th>Clearwater</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>PI Rank</td>
<td>PI Rank</td>
<td>PI Rank</td>
</tr>
<tr>
<td>Salix spp.</td>
<td>1 0.87 3</td>
<td>1.80 2 1.58 2</td>
<td>1.38 3</td>
<td>1.52 2</td>
</tr>
<tr>
<td></td>
<td>2 0.62 4</td>
<td>3.40 1 0.93 3</td>
<td>1.52 2</td>
<td>0.93 3</td>
</tr>
<tr>
<td>Alnus spp.</td>
<td>1 0.32 6</td>
<td>0.87 3 0.19 7</td>
<td>1.75 1</td>
<td>0.87 6</td>
</tr>
<tr>
<td></td>
<td>2 0.21 7</td>
<td>0.62 4 0.18 8</td>
<td>0.87 6</td>
<td>0.18 8</td>
</tr>
<tr>
<td>Cornus stolonifera</td>
<td>1 0.43 5</td>
<td>0.10 8 --</td>
<td>0.12 5</td>
<td>0.03 9</td>
</tr>
<tr>
<td></td>
<td>2 0.63 4</td>
<td>0.43 5 0.37 6</td>
<td>1.12 5</td>
<td>-- 10</td>
</tr>
<tr>
<td>Lonicera involucrata</td>
<td>1 0.10 8</td>
<td>0.10 9 0.10 9</td>
<td>0.21 7</td>
<td>0.03 9</td>
</tr>
<tr>
<td>Rosa woodsii</td>
<td>1 --</td>
<td>0.10 9 0.10 9</td>
<td>0.21 7</td>
<td>0.03 9</td>
</tr>
<tr>
<td>Populus trichocarpa</td>
<td>1 --</td>
<td>1.80 1 1.80 1</td>
<td>1.12 5</td>
<td>0.60 9</td>
</tr>
<tr>
<td>Picea engelmannii</td>
<td>1 --</td>
<td>0.60 5 0.60 5</td>
<td>-- 9</td>
<td>0.05 10</td>
</tr>
<tr>
<td>Crataegus douglasii</td>
<td>1 --</td>
<td>0.05 10 0.05 10</td>
<td>-- 9</td>
<td>-- 10</td>
</tr>
</tbody>
</table>
Table 4. Preference indices for woody taxa by diameter size and distance from the waterway on the Swan and Clearwater rivers and Fish Creek in northwestern Montana. Plot 1 is 0-7 m inland from the high water mark (hwm), plot 2 is 11.5-18.5 m inland from hwm, plot 3 is 23-30 m inland from hwm.

<table>
<thead>
<tr>
<th>Species</th>
<th>Stem diameter</th>
<th>Preference indices</th>
<th>Plot 1</th>
<th>Plots (2 &amp; 3) / 2</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Salix</em> spp.</td>
<td>&lt; 2.5 cm</td>
<td>1.83</td>
<td>0.66</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt; 2.5 cm</td>
<td>0.89</td>
<td>2.54</td>
<td></td>
</tr>
<tr>
<td><em>Alnus</em> spp.</td>
<td>&lt; 2.5 cm</td>
<td>1.70</td>
<td>0.68</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt; 2.5 cm</td>
<td>0.36</td>
<td>0.67</td>
<td></td>
</tr>
<tr>
<td><em>Cornus stolonifera</em></td>
<td>&lt; 2.5 cm</td>
<td>0.37</td>
<td>0.13</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt; 2.5 cm</td>
<td>0.67</td>
<td>1.16</td>
<td></td>
</tr>
</tbody>
</table>

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evidence, as well as evidence from Bailey (1927) and Rutherford (1964), suggests that cottonwood may be preferred to willow in areas where it is available.

Edwards and Guynn (1984) reported a preference for stem sizes that were less than 2.5 cm in diameter. In this study, willow stems between 2.5 and 5.0 cm were preferred on Fish Creek and the Clearwater River over stems that were less than 2.5 cm. This size preference was also seen for red osier dogwood stems on the Swan River. On the other hand, alder stems that were less than 2.5 cm were preferred in all cases over alder stems of greater size (Table 3). Preference for small alder during the late fall (when energy is directed towards caching food for the winter), may indicate greater palatability of small alder stems over larger alder stems. Larger alder stems may be used almost entirely for dam and lodge construction during the late spring and summer months. Thus, size preferences for different shrub taxa may vary by seasons.

The overall preference for smaller stems (less than 5.0 cm) for all taxa supported earlier observations (Shadle et al. 1943, Bradt 1947, Nixon and Ely 1969, Edwards and Guynn 1984).

Several authors have suggested that beaver are more selective farther from the water (Tevis 1950, Northcott 1971, Jenkins 1980). Jenkins (1980) reported that the mean size of cut stems decreased with increasing distance from
the waterway. This study supports the theory that beaver are generally more selective farther from the water. However, the trend is towards beaver cutting larger stems, up to a certain size, as they move farther from the waterway.

I hypothesize that each individual beaver has a stem size threshold over which they cannot carry a stem to the water in one piece. The stems that are larger than an animal's threshold limit will have to be cut into smaller pieces for transport back to the water. Beavers that are vulnerable to predators when out of the water will likely minimize feeding time and maximize potential energy intake by cutting larger preferred stems that are below their threshold limit. Jenkins felt that his beaver were not especially vulnerable to predation. Beaver in northwestern Montana, however, are susceptible to predation by coyotes (*Canis latrans*) and in some areas wolves (*Canis lupus*). I suggest that this difference may account for the discrepancy in our findings.

For beaver in northwestern Montana, willow and/or cottonwood less than 5.0 cm in diameter are preferred forage items (in the absence of aspen). The abundance of these items and their availability (relative distance from the waterway) are important factors for managers to consider when assessing the quality of diverse beaver habitats.
LITERATURE CITED


CHAPTER II
CACHE SIZE AS AN INDEX TO BEAVER COLONY SIZE IN NORTH-WESTERN MONTANA

Andrea L. Easter-Pilcher, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana 59812

Abstract: Population indices for beaver (Castor canadensis) were measured during the fall of 1986 at 24 randomly selected colony sites on the Swan and Clearwater rivers and Fish Creek in northwestern Montana. Colony size was assessed through nocturnal observations with the use of infrared night vision goggles. Number of tracks, number of dams, number of stems cut and cache volume were regressed with beaver numbers counted during nocturnal observations. Cache volume accounted for the only significant source of variation in colony size ($R^2 = 0.68$). Replication results at two colony sites demonstrated minimal observer bias (using experienced observers) and indicated the potential of classifying and enumerating colony members by nocturnal observations during late fall. The numbers of animals observed at a single site on different evenings were in close agreement and indicated precision of the method. Cache volume was shown to have potential as an economical and useful index to beaver colony size.
Precise indices of population abundance are critical to the setting of fish and game harvest regulations. Aerial food cache surveys have proven a reliable index, 1 cache per active colony, to the number of active beaver colonies present in a waterway (Hay 1958, Bergerud and Miller 1977, Payne 1981, Swenson et al. 1983). However, this index (cache presence or absence) is not sensitive to annual changes in colony size and corresponding population fluctuations (Townsend 1953, Bergerud and Miller 1977, Swenson et al. 1983). Intensive beaver management demands an index sensitive to impacts that alter colony size and affect population fluctuations.

This paper investigates direct and indirect indices of colony size that could be useful for monitoring population fluctuations over time. Direct sampling by visual counts of beaver at each colony and indirect sampling by measurement of sign indices (dams, scent mounds, tracks, cuttings, and cache size) are examined. Careful, direct counts of animals on randomly selected sampling units may offer the most accurate method of population estimation (Eberhardt 1978). However, a reasonably precise, indirect index may be a more economical and logistically feasible tool for managers.

STUDY AREAS AND METHODS

Data were collected at 9, 6, and 8 colonies in the Swan, Clearwater, and Fish Creek drainages respectively, in
northwestern Montana (Fig. 1). These drainages were selected for their generally different characteristics representing a broad spectrum of northwestern Montana riparian areas.

The Swan Valley, located 80 km northeast of Missoula, Montana, lies between the Swan Range to the East and the Mission Range to the West. The Swan River drops 1142 m over the course of its northward run from Grey Wolf Lake (2024 m) to Flathead Lake (882 m). The straight-line distance from source to mouth is 90 km. Dominant woody vegetation along the banks of the Swan River is willow (Salix spp.) with secondary vegetation consisting of dogwood (Cornus stolonifera), alder (Alnus spp.), and hawthorne (Crataegus douglasii). The surrounding area is dominated by montane forest, a mosaic of larch (Larix occidentalis), lodgepole pine (Pinus contorta), ponderosa pine (Pinus ponderosa), Douglas fir (Pseudotsuga menziesii), Engelmann spruce (Picea engelmannii), subalpine fir (Abies lasiocarpa), and cottonwood (Populus trichocarpa). The Swan is generally characterized by variable but steep banks, substrate that ranges from mud to medium rock, moderate to steep gradient, slow to swift velocity, low turbidity, dense shrub cover, log jams, gravel bars, and channeling.

The head of the Clearwater Valley, located 8 km southeast of the Swan Valley, also lies between the Swan
Fig. 1. Map of northwestern Montana rivers showing the location (•) of the Swan and Clearwater Rivers and Fish Creek study areas.
Range and the Mission Range. The Clearwater River drops 378 m in its southern flow, from the source at Clearwater Lake (1460 m) to its convergence with the Blackfoot River (1082 m). Straight-line distance is 50 km. Dominant woody vegetation along the Clearwater River is willow with secondary vegetation consisting of twinberry (Lonicera involucrata), dogwood, and alder. The surrounding area is dominated by a montane forest mosaic similar to the Swan but with substantially less cottonwood. The meandering river is generally characterized by low banks, mud and gravel substrate, mild gradient and velocity, low turbidity, and dense shrub cover.

The South Fork of Fish Creek is 50 km west of Missoula. The creek drops 396 m, from the source above Sullivan Creek (1341 m) to the confluence with the West Fork (945 m). Straight-line distance from source to mouth is 22 km. Dominant vegetation on the South Fork of Fish Creek is willow, although abundance is about 0.3 that of the Swan or the Clearwater. Alder, the second most abundant species, is more common on Fish Creek than on the Swan or the Clearwater rivers. Dogwood ranks third, with abundance being only about 0.5 that of the Clearwater and 0.3 that of the Swan. The area surrounding the South Fork of Fish Creek is dominated by montane forest with overstory similar to that of the Swan River. The creek
itself is generally characterized by a variable bank height, small to medium rock substrate, moderate gradient with moderate to swift velocity, low turbidity, and low to moderate shrub cover.

Active colony sites were located by aerial and ground reconnaissance. Two sign survey transects were established at each site (Fig. 2). The first transect (bank transect) was 30 m in length (running parallel to the bank) and 3 m in width (2 m below the high water mark and 1 m above that mark). The remaining transect extended inland (inland transect) from the high water mark. This transect was 30 m in length (running perpendicular to the bank) and 3 m in width (1.5 m on either side of the midpoint on the bank transect). Individual tracks, (weighted by trackability: percent of transect area with appropriate substrate for tracks), scent mounds and dams were counted on both transects at each site and pooled for analysis. Number of stems cut by beaver on both transects were also pooled for analysis. Counting methods were summarized in Easter-Pilcher (1987). Cache length and width (used to estimate cache area) were measured at all sites during a 2 week period in late November and early December.

Beaver were counted at each colony site by age class (kits, subadults, and adults) from late November through early December when cache construction was nearing completion and beaver were active and readily observed.
Fig. 2. Diagram of the bank (parallel) and inland (perpendicular) sign survey transects for occupied sites.
around the cache. A kit was defined as an animal in its first year of life, a subadult in its second or third year of life, and an adult was at least 36 months old. Weight (Townsend 1953) and tail dimensions (length x width) are useful criteria for placing live beaver into 4 distinct age-classes (Patric and Webb 1960). With experience, observers could classify beaver into 3 age categories, combining yearlings and 2-year olds into 1 class.

Infrared night vision goggles were used for the nocturnal observations of beaver. Unit of effort was 150 minutes (from 1630-1900 hours) with 1 observer per site. In the few cases where 2 observers were necessary for complete visual coverage, time of sighting and age-class of each beaver were noted for later comparison. Observers, partially or completely hidden and wearing camouflage face netting and dark clothes, sat within 10 m of the cache. Animals were counted as they emerged from the lodge or as they swam around the cache. Only those animals that could be identified with certainty as different beaver were tallied. Therefore, the final counts were minimum estimates.

The 4 independent variables used in the analyses were weighted tracks, dams, total stems cut, and cache volume (cache area^{1.5}). Scent mounds were dropped from the
analysis because they were not found on the Swan River or Fish Creek colony sites.

Field experience indicated that extremely low temperatures may have adversely affected counting results. Consequently, an analysis of all sites was compared with an analysis of all sites excluding 3 sites observed on nights with temperatures below 20 degrees Fahrenheit. A river otter (*Lutra canadensis*) at another colony site (large cache) potentially affected that count (0 beaver). For comparison with the above analyses, an analysis of all sites excluding the 3 low temperature evenings and the otter site was run and an analysis of all sites excluding only the otter site was run.

Replication of colony counts were conducted at 2 sites. Two experienced observers sat at 1 site for 3 consecutive nights and the second site for 1 night. Each observer counted and classified the beaver she saw. Data were not compared until the end of the replication period.

Stepwise multiple regression was used to evaluate the null hypothesis that no linear relationship existed between the visual census of beaver numbers at a winter colony site and measured sign indices. Linear regression was used to evaluate the null hypothesis that no linear relationship existed between estimated beaver numbers at a winter colony site and cache volume. Linear regression
allowed for the inclusion of 2 extra colonies where only the number of beaver and cache volume had been ascertained.

RESULTS

Stepwise multiple regression showed no significant relationships between weighted tracks, number of dams, or total stems cut at each colony site and the number of animals at those sites. $R^2$ values were 0.005, 0.007, and 0.215 respectively.

Cache volume accounted for significant variation in colony size for all 4 analyses (Table 1). Comparison of the coefficient of determination ($R^2$) for the 4 separate analyses showed that cache volume increased in predictive value as the analyses become more exclusive.

The proportion of variation in the dependent variable explained by each of the linear regression models indicates that cache volume is a useful indirect index for estimating winter colony size.

Results of replicated counts of beaver at 2 colony sites indicated the potential of classifying and enumerating colony members by nocturnal observation in late Fall as a direct index of colony size. Classifications and counts by 2 experienced observers showed close agreement of age-classes and numbers of beaver (Table 2). The numbers of animals observed at a single site on different evenings were also in relatively close agreement.
Table 1. Coefficients of determination showing predictive power of cache volume for different data subsets.

<table>
<thead>
<tr>
<th></th>
<th>( R^2 ) for cache volume and animal numbers</th>
<th>Number of observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>All sites</td>
<td>0.3949</td>
<td>22</td>
</tr>
<tr>
<td>(stepwise multiple regression)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All sites excluding 3 low temperature sites</td>
<td>0.4880</td>
<td>19</td>
</tr>
<tr>
<td>(stepwise multiple regression)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All sites excluding the otter site</td>
<td>0.4955</td>
<td>21</td>
</tr>
<tr>
<td>(stepwise multiple regression)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All sites excluding 3 low temperature sites and otter site</td>
<td>0.6692</td>
<td>18</td>
</tr>
<tr>
<td>(stepwise multiple regression)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All sites</td>
<td>0.4120</td>
<td>24</td>
</tr>
<tr>
<td>(linear regression)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All sites excluding 3 low temperature sites</td>
<td>0.5006</td>
<td>21</td>
</tr>
<tr>
<td>(linear regression)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All sites excluding the otter site</td>
<td>0.5103</td>
<td>23</td>
</tr>
<tr>
<td>(linear regression)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All sites excluding 3 low temperature sites and otter site</td>
<td>0.6762</td>
<td>20</td>
</tr>
<tr>
<td>(linear regression)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Replication and observer bias results for nocturnal observations with infrared night vision goggles of beaver colonies in northwestern Montana.

<table>
<thead>
<tr>
<th></th>
<th>Colony site 1</th>
<th></th>
<th>Colony site 2</th>
<th>Observation night</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observation night</td>
<td></td>
<td></td>
<td>Observation night</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Observer 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beaver seen</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>adult</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>subadult</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>kit</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>6</td>
<td>5</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Observer 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beaver seen</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>adult</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>subadult</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>kit</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>7</td>
<td>5</td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>
DISCUSSION

Green (1979) suggests several criteria for selecting variables for research that are also appropriate to consider when evaluating indices to animal populations. Indices need to be easily measurable, cost-effective, precise, sensitive to population fluctuations, and dependable over time and in different settings.

Tracks, dams, number of stems cut, and scent mounds were not significantly related to beaver numbers and would be poor and unreliable indices in any case. Because of their dependence on topographical conditions (Hay 1958) dams are unreliable as indices for different riparian areas. Track counts depend on available tracking substrate and no precipitation and so are not reliable over time or in different habitats. Assessing stems cut is not cost-effective and precision is questionable. Scent mounds appear to be related to territoriality (Hay 1958, Aleksiuk 1968, Wilsson 1971). Muller-Schwarze and Heckman (1980) found that beaver colonies in close proximity to each other built more scent mounds than did isolated colonies. Scent mounds were numerous on the Clearwater River where colonies were quite close together, while there were no scent mounds on the isolated Fish Creek colony sites and only one on the Swan River colony sites. Scent mounds were unreliable as an index to colony size.
Cache volume represents a relatively precise, easily measured, cost-effective, and non-intrusive index to beaver colony size in northwestern Montana. It is also an index that would be reliable over time and in different areas (recalibration would be necessary) with each winter colony of beaver building a cache which can be measured under most inclement conditions. The utility of cache volume for assessing annual changes in colony size and corresponding population fluctuations exceeds the current index (1 cache/colony) which can be used only to assess gross population changes. Cache volume for estimating colony size needs to be examined further to confirm precision of the method and to determine the sensitivity of the index to impacts on colony size.

Population indices such as cache size must be verified with actual estimates of population size. Live trapping of beaver is ineffective as a reliable estimate of population size (Hay 1958). Smith and Brisbin (1984) demonstrated that total captures on a trapline are not good indices of furbearer populations. Population estimates of unmarked animals can be obtained with nocturnal viewing equipment alone, provided detailed information such as age and sex is not necessary (Brooks 1985). Nocturnal observations of beaver colonies in the fall offers a means of assessing colony size that is more cost-effective, less
intrusive and perhaps just as accurate as the current method of removal trapping to establish colony size.

Assessing the accuracy of colony counts and determining the sensitivity of cache volume to colony size may best be examined through a removal study. Baseline colony counts in September, before cache construction is begun, followed by removal of a known number of individuals (Eberhardt 1982) from experimental colony sites (no removal from control colony sites) followed by colony counts and cache measurements in late November and early December could establish accuracy of colony counts and determine the sensitivity of cache volume to impacts (removals) affecting colony size.

The precision of nocturnal colony counts needs to be further examined in terms of observer bias, climatic conditions (rain, snow, and moonlight affect visibility and low temperatures affect activity), and habitat conditions. Observer bias could be further examined using the techniques described in this study. Additional replications of colony counts within a minimal time period and under similar climatic conditions should be done to confirm the precision of the method. Length of observation and observer distance from the cache are variables that could be manipulated to determine the most effective combination.
Assessing the accuracy and precision of aerial measurement of cache size is a critical research need. The focus should be on cache measurements from both a helicopter and a fixed wing aircraft. Use of a helicopter may produce the more accurate and repeatable cache measurements (when compared with measurements taken on the ground) because of the ability of the helicopter to fly in close proximity to the ground. But, fixed wing reconnaissance may yield adequate measurements with a larger sample size for similar or less cost.

This initial research shows that cache volume, and nocturnal colony size counts are precise, easily measured, cost-effective, and more definitive indices than traditional indices of colony size. Measuring cache volume is less costly than beaver counts and promises to be an effective tool for more intensive management of beaver populations.
LITERATURE CITED


CHAPTER III

WINTER COLONY SITE SELECTION BY BEAVER IN NORTHWESTERN MONTANA

Andrea L. Easter-Pilcher, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana 59812

Abstract: Stream and vegetation characteristics were measured at 25 randomly selected beaver (*Castor canadensis*) winter colony sites (occupied) and 25 stratified random sites on the Swan and Clearwater rivers and Fish Creek in northwestern Montana in the fall of 1986. A discriminant function model was developed for winter colony site selection from these variables. Water depth, slope distance (horizontal distance between high and low water marks) and availability of understory willow (*Salix* spp.) correctly classified 96% of the occupied sites and 92% of the random sites. Colony counts obtained from nocturnal observations with infrared night vision goggles were regressed with principal components of the habitat variables. Water depth, stream width, availability of understory willow, slope distance between low and high water marks, vertical water fluctuation (vertical distance between high and low water marks), and the presence of a confluence were positively correlated to colony size.
Researchers have attempted, during recent years, to establish the relationship between riparian habitat quality and beaver colony density. Boyce (1974) quantified physical and vegetative characteristics of interior Alaskan streams and related those to colony density. Slough and Sadleir (1977) developed a land capability classification system for beaver in northern British Columbia by measuring habitat factors and regressing those factors against colony density. Howard and Larson (1985) measured physical and vegetative components critical to beaver colony site longevity and used those components to predict maximum density of active colonies on a stream.

A primary assumption implicit in most habitat assessment and ensuing management plans for wildlife is that density tends to increase with higher habitat quality. Van Horne (1983) suggests that this assumption often disintegrates under intense scrutiny, particularly in northern climates where fieldwork is frequently done during the milder seasons. Research designed to assess the relationship between species densities and habitat quality should include a focus upon the most critical seasonal habitat.

Stream and vegetation characteristics surrounding winter colony sites may have the greatest potential influence on survival and reproductive success of beaver. In northern climates, the availability of woody plants for
a winter food cache may limit the capacity of an area to support a colony through the winter (Boyce 1981, Allen 1982). Hydrologic and physiographic habitat components may also limit the potential for winter colony sites (Jenkins 1981).

A second, often invalid, assumption in habitat studies is that the animal responds to those individual habitat components selected by the researcher as significant. Animals probably respond to a shifting combination of habitat components, potentially meeting similar requirements in different habitats by substituting among available components (Lyon 1985).

The first hypothesis of this paper is that for winter colony sites in northern climates, there may be critical structural stream components and/or vegetation characteristics that are required for winter survival of beaver. These components may limit the number of potential winter colony sites available on a waterway.

The second hypothesis is that the abundance and availability of preferred woody species at winter colony sites may contribute greatly to the fitness and number of beaver at those sites. Shortages or complete absence of preferred species at winter colony sites, leading to substitutions of less preferred species, lowers "habitat quality" and may effectively lower reproductive fitness and colony size.
To examine the first hypothesis, this paper investigates stream and vegetation characteristics that may allow discrimination between winter colony sites and unoccupied, random sites in northwestern Montana. To explore the second hypothesis, the relationship between beaver numbers and habitat components at individual sites is examined.

STUDY AREAS and METHODS

Data were collected at 25 randomly selected winter colony sites (occupied) and 25 stratified random sites (unoccupied) on the Swan, Clearwater, and Fish Creek (South Fork) drainages in northwestern Montana (Fig. 1). These drainages were selected for their generally different characteristics representing a broad spectrum of northwestern Montana riparian areas.

The Swan Valley, located 80 km northeast of Missoula, Montana, lies between the Swan Range to the East and the Mission Range to the West. The Swan River drops 1142 m during the course of its northward run from Grey Wolf Lake (2024 m) to Flathead Lake (882 m). The straight-line distance from source to mouth is 90 km. Dominant vegetation along the banks of the Swan River is willow with secondary vegetation consisting of red osier dogwood (Cornus stolonifera), alder (Alnus spp.), and hawthorne (Crataegus douglasii). The surrounding area is dominated by montane forest, a mosaic of larch (Larix occidentalis),
Fig. 1. Map of northwestern Montana rivers showing the location (*) of the Swan and Clearwater Rivers and Fish Creek study areas.
lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and cottonwood (*Populus trichocarpa*). The Swan is generally characterized by variable but steep banks, substrate that ranges from mud to medium rock, moderate to steep gradient, slow to swift velocity, low turbidity, dense shrub cover, log jams, gravel bars, and extensive channeling.

The head of the Clearwater Valley, located 8 km southeast of the Swan Valley, also lies between the Swan Range and the Mission Range. The Clearwater River drops 378 m in its southern flow, from the source at Clearwater Lake (1460 m) to its convergence with the Blackfoot River (1082 m). Straight-line distance is 50 km. Dominant woody vegetation along the Clearwater river is willow with secondary vegetation consisting of twinberry (*Lonicera involucrata*), red osier dogwood, and alder. The surrounding area is dominated by a montane forest mosaic similar to that of the Swan but with substantially less cottonwood. The meandering river is generally characterized by low banks, mud and gravel substrate, mild gradient and velocity, low turbidity, and dense shrub cover.

The South Fork of Fish Creek is 50 km west of Missoula. This branch descends 396 m from the source above
Sullivan Creek (1341 m) to the confluence with the West Fork (945 m). Straight-line distance from source to mouth is 22 km. Dominant vegetation on Fish Creek is also willow, although abundance is about 0.3 that of the Swan or the Clearwater. Alder, the second most abundant species, is more common on Fish Creek than on the Swan or the Clearwater. Red osier dogwood ranks third, with abundance being only about 0.5 that of the Clearwater and 0.3 that of the Swan. The area surrounding Fish Creek is dominated by montane forest with overstory similar to that of the Swan. The creek itself is generally characterized by a variable bank height, small to medium rock substrate, moderate gradient with moderate to swift velocity, low turbidity, and low to moderate shrub cover.

Active colony sites on each stream were located by aerial and ground reconnaissance. The first 10 occupied stick-and-mud lodges encountered, in a general search of the entire stream, were selected for measurements of habitat characteristics. A stratified sampling scheme was employed for the selection of 10 unoccupied, random sites for identical habitat measurements. Distance between the 10 random sites on the Clearwater River and Fish Creek, was determined by dividing total stream length by 9 with the first site located at the mouth of each waterway. Difficult access on the Swan River limited that study area to the portion between Lindbergh and Swan lakes.
Two habitat survey transects were established at each site (Fig. 2). The first transect (bank transect) was 30 m in length (running parallel to the bank) and 3 m in width (2 m above the high water mark and 1 m below that mark). The remaining transect extended inland (inland transect) from the high water mark. This transect was 30 m in length (running perpendicular to the bank) and 3 m in width (1.5 m on either side of the mid-point on the bank transect). Number of stems of each species available to beaver were counted on these transects and pooled for analysis. Counting methods were summarized by Easter-Pilcher (1987). Stream characteristics were measured adjacent to the mid-point on the bank transect. All measurements (Table 1) were taken in October and November of 1986.

Colony population counts by age class (kits, subadults, and adults) were obtained from late November through early December 1986. Cache construction was nearing completion and beaver were active and readily observed around the cache. Only those animals that could be identified with certainty as different beaver were tallied. Therefore, the final counts were minimum estimates (Easter-Pilcher 1987).

Linear discriminant analysis (Norusis 1985) was used to evaluate the null hypothesis that no differences existed between habitat factors at winter colony sites and
Fig. 2. Diagram of the bank (parallel) and inland (perpendicular) habitat transects for occupied and random sites.
<table>
<thead>
<tr>
<th>Variable name</th>
<th>Measurement description</th>
</tr>
</thead>
<tbody>
<tr>
<td>SITEGR</td>
<td>Site gradient: vertical drop divided by horizontal distance and converted to percent (topographic map)</td>
</tr>
<tr>
<td>VELOC</td>
<td>Site velocity: speed (cm per second) measured with bobber and stopwatch</td>
</tr>
<tr>
<td>WIDTH</td>
<td>Site width measured from mid-point on the bank transect across channel to opposite side with meter tape</td>
</tr>
<tr>
<td>DEPTH</td>
<td>Site depth: deepest point between banks measured from mid-point on the bank transect with meter tape</td>
</tr>
<tr>
<td>VERTFL</td>
<td>Vertical fluctuation: vertical distance between low and high water marks measured with meter tape</td>
</tr>
<tr>
<td>MEANDR</td>
<td>Meander measured 1.0 (straight stretch of waterway) to 1.5 (waterway makes “S” configuration) by visual estimation</td>
</tr>
<tr>
<td>HIGHLO</td>
<td>Slope distance measured between low and high water marks from mid-point on bank transect with meter tape</td>
</tr>
<tr>
<td>BANKHT</td>
<td>Bank height measured from mid-point on bank transect with meter tape</td>
</tr>
<tr>
<td>BANKSL</td>
<td>Bank slope measured from high water mark at the mid-point on the bank transect with clinometer and recorded in percent</td>
</tr>
<tr>
<td>BKSUBS</td>
<td>Bank substrate classes - visual estimation</td>
</tr>
<tr>
<td></td>
<td>1. Sand</td>
</tr>
<tr>
<td></td>
<td>2. Mud</td>
</tr>
<tr>
<td></td>
<td>3. Dirt</td>
</tr>
<tr>
<td></td>
<td>4. Gravel</td>
</tr>
<tr>
<td></td>
<td>5. Small rock &gt; 2&quot; by 2&quot;</td>
</tr>
<tr>
<td></td>
<td>6. Medium rock &gt; 2&quot; by 10&quot;</td>
</tr>
<tr>
<td></td>
<td>7. Large rock &gt; 10&quot; by 10&quot;</td>
</tr>
<tr>
<td></td>
<td>8. Boulders &gt; 18&quot; by 18&quot;</td>
</tr>
<tr>
<td>ASPECT</td>
<td>Aspect of bank slope from compass reading</td>
</tr>
<tr>
<td>CONFL</td>
<td>Confluence with another waterway or a lake measured as present or absent</td>
</tr>
<tr>
<td>LOGJAM</td>
<td>Logjam measured as present or absent</td>
</tr>
<tr>
<td>WILLOW</td>
<td>Understory willow = # stems available &lt; 5.1 cm</td>
</tr>
<tr>
<td>ALDER</td>
<td>Understory alder = # stems available &lt; 5.1 cm</td>
</tr>
<tr>
<td>DOGWD</td>
<td>Understory dogwood = # stems available &lt; 5.1 cm</td>
</tr>
<tr>
<td>HAWTH</td>
<td>Understory hawthorne = # stems available &lt; 5.1 cm</td>
</tr>
<tr>
<td>TWIN</td>
<td>Understory twinberry = # stems available &lt; 5.1 cm</td>
</tr>
<tr>
<td>ROSE</td>
<td>Understory rose = # stems available &lt; 5.1 cm</td>
</tr>
</tbody>
</table>
those at random sites. Discriminant analysis produces linear combinations of the predictor variables which serve to classify observations into distinct groups. Stepwise discriminant analysis was used to initially prioritize (Wilks' lambda) and select a subset of independent variables by their ability to separate winter colony sites from random sites. The subsequent linear discriminant analysis, using variables retained by the stepwise analysis, allowed for inclusion of two sites which had been excluded from the stepwise analysis due to missing values.

Principal components regression (PCR) (Converse and Morzuch 1981, Joliffe 1986) was used to evaluate the null hypothesis that no relationship existed between numbers of animals at different colony sites and the habitat factors at those sites.

Stream and vegetation characteristics are strongly intercorrelated and therefore unsuitable to standard multiple regression techniques that assume independence of the predictor variables. Principal components analysis changes a set of strongly correlated variables to a set of uncorrelated variables that retain all of the information from the original set for subsequent statistical analysis (Green 1979). Each new variable, or principal component (PC), is a linear additive function of the original predictor (habitat) variables. The first component
accounts for the largest variation in the data set. Each ensuing component is obtained by rotating an axis orthogonally to the previous component's axis until it lines up with the largest remaining amount of variation in the data.

Using subsets of the principal components for the regression analyses, particularly those with large eigenvalues (portion of the total variance in the predictor variables accounted for by that PC) will give a more stable estimate of the regression coefficients (Jolliffe 1986). Methods of determining which principal components to use in a regression analysis have included: selecting components with eigenvalues greater than 1; selecting enough components to explain a certain percentage of the variance; selecting components that exhibit high correlations with the dependent variable; or a combination of the above (Mardia et al. 1979). Selecting only those components with large eigenvalues is the simplest method. However, a component accounting for only a small portion of the total amount of variation in the predictor variables may nonetheless be an important predictor of the dependent variable (Green 1979).

Principal habitat components were selected for these analyses by examining both the size of the eigenvalues and the correlation coefficients of each component with the dependent variable (beaver numbers).
All components with eigenvalues greater than 1 were retained for analysis. In addition, any components that had exhibited low eigenvalues but with a high correlation to the dependent variable would have been retained in the analysis. No components were retained for this reason. The first through the sixth principal components met the "eigenvalue greater than 1" criterion for the regression on all sites (Table 2). Principal components 1 through 7 were retained under the eigenvalue criterion for the regression on occupied sites (Table 2).

Principal component scores for each site are the regressors in PCR. Each habitat variable included in the principal components is multiplied by it's corresponding eigenvector value (Table 3) and these products are summed to give a PC score for each site (Sczerzenie 1981). The relationship between PC scores and the number of beaver at a site may then be examined to ascertain habitat factors that potentially affect colony size.

RESULTS

Stepwise discriminant analysis retained site depth, slope distance, willow availability, and meander factor, in that order, as the habitat components with the most power to discriminate between occupied winter colony sites and random sites in northwestern Montana (Table 4). Discriminant analysis of site depth, slope distance and willow correctly classified 96% of the occupied sites and
Table 2. Principal component analysis for all sites and for occupied sites. Table includes eigenvalues, the Pearson coefficient for the correlation of each component with the dependent variable (beaver numbers), the portion of the variation explained by each component and cumulative variation explained by the components.

<table>
<thead>
<tr>
<th>Component</th>
<th>Eigenvalue</th>
<th>Pearson correlation coefficient</th>
<th>Proportion of variation explained (%)</th>
<th>Cumulative variation explained (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALL SITES</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>4.37</td>
<td>0.65</td>
<td>0.23</td>
<td>0.23</td>
</tr>
<tr>
<td>2</td>
<td>3.51</td>
<td>0.05</td>
<td>0.18</td>
<td>0.41</td>
</tr>
<tr>
<td>3</td>
<td>1.99</td>
<td>0.05</td>
<td>0.10</td>
<td>0.51</td>
</tr>
<tr>
<td>4</td>
<td>1.46</td>
<td>0.31</td>
<td>0.08</td>
<td>0.59</td>
</tr>
<tr>
<td>5</td>
<td>1.19</td>
<td>0.08</td>
<td>0.06</td>
<td>0.65</td>
</tr>
<tr>
<td>6</td>
<td>1.05</td>
<td>0.05</td>
<td>0.06</td>
<td>0.71</td>
</tr>
<tr>
<td>7</td>
<td>0.99</td>
<td>0.04</td>
<td>0.05</td>
<td>0.76</td>
</tr>
<tr>
<td>8</td>
<td>0.79</td>
<td>0.10</td>
<td>0.04</td>
<td>0.80</td>
</tr>
<tr>
<td>9</td>
<td>0.67</td>
<td>0.10</td>
<td>0.04</td>
<td>0.84</td>
</tr>
<tr>
<td>10</td>
<td>0.63</td>
<td>0.02</td>
<td>0.03</td>
<td>0.87</td>
</tr>
<tr>
<td>11</td>
<td>0.53</td>
<td>0.18</td>
<td>0.03</td>
<td>0.90</td>
</tr>
<tr>
<td>12</td>
<td>0.43</td>
<td>0.17</td>
<td>0.02</td>
<td>0.92</td>
</tr>
<tr>
<td>13</td>
<td>0.36</td>
<td>0.12</td>
<td>0.02</td>
<td>0.94</td>
</tr>
<tr>
<td>14</td>
<td>0.31</td>
<td>0.20</td>
<td>0.02</td>
<td>0.96</td>
</tr>
<tr>
<td>15</td>
<td>0.26</td>
<td>0.08</td>
<td>0.01</td>
<td>0.97</td>
</tr>
<tr>
<td>16</td>
<td>0.18</td>
<td>0.20</td>
<td>0.01</td>
<td>0.98</td>
</tr>
<tr>
<td>17</td>
<td>0.14</td>
<td>0.03</td>
<td>0.01</td>
<td>0.99</td>
</tr>
<tr>
<td>18</td>
<td>0.12</td>
<td>0.04</td>
<td>0.01</td>
<td>0.99</td>
</tr>
<tr>
<td>19</td>
<td>0.02</td>
<td>0.12</td>
<td>0.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

| OCCUPIED SITES |            |                               |                                      |                                  |
| 1         | 5.37       | 0.51                          | 0.28                                 | 0.28                             |
| 2         | 2.95       | 0.50                          | 0.15                                 | 0.43                             |
| 3         | 2.39       | 0.02                          | 0.13                                 | 0.56                             |
| 4         | 1.91       | 0.32                          | 0.10                                 | 0.66                             |
| 5         | 1.45       | 0.00                          | 0.08                                 | 0.74                             |
| 6         | 1.31       | 0.11                          | 0.07                                 | 0.81                             |
| 7         | 1.18       | 0.49                          | 0.06                                 | 0.87                             |
| 8         | 0.77       | 0.01                          | 0.04                                 | 0.91                             |
| 9         | 0.54       | 0.02                          | 0.03                                 | 0.94                             |
| 10        | 0.48       | 0.05                          | 0.03                                 | 0.97                             |
| 11        | 0.21       | 0.01                          | 0.01                                 | 0.98                             |
| 12        | 0.16       | 0.08                          | 0.01                                 | 0.99                             |
| 13        | 0.12       | 0.01                          | tr                                   | 0.99                             |
| 14        | 0.08       | 0.25                          | tr                                   | 0.99                             |
| 15        | 0.04       | 0.16                          | tr                                   | 0.99                             |
| 16        | 0.02       | 0.00                          | tr                                   | 0.99                             |
| 17        | 0.01       | 0.05                          | tr                                   | 0.99                             |
| 18        | tr         | 0.19                          | tr                                   | 0.99                             |
| 19        | 0.00       | 0.00                          | 0.00                                 | 1.00                             |
Table 3. Principal components selected for use in the regression analysis of all sites and the regression analysis of occupied sites and their variable loadings.

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Table 4. Results of stepwise discriminant analysis of occupied and unoccupied sites. Significance level to enter and significance level to stay = 0.1500

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<tr>
<th>Variable name</th>
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<th>Partial R**2</th>
<th>F statistic</th>
<th>Prob &gt; F</th>
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92% of the unoccupied sites (Table 5). Discriminant function coefficients are given in Table 6.

Stepwise multiple regression on all sites indicated PC1 and PC4 were significantly correlated to beaver numbers (Table 7). PC1 accounted for the greatest amount of variation in the dependent variable while PC4 accounted for a much smaller portion.

PC1 contrasted sites characterized by deep, wide streams with willow as the predominant vegetation (high negative loadings) with sites characterized by high, steep banks, relatively swift velocity and large substrate (high positive loadings). Scores for PC1 were negative for 23 of 24 occupied sites, associating these sites clearly with wide, deep streams and abundant willow (Figure 3). Random sites had positive scores for 21 of 24 sites.

PC4 factor loadings were weighted heavily on bank slope, bank height, hawthorne, and river confluence at one end and aspect, velocity, bank substrate, and rose at the opposite end. Scores for PC4 indicated that occupied sites were positively correlated with mild bank slope and height, low hawthorne availability, and the presence of a confluence. Unoccupied sites are positively correlated with higher velocity, larger substrate, and high availability of rose.

Stepwise multiple regression on occupied sites indicated PC1, PC2, PC7, and PC4 were significantly
Table 5. The numbers and percent of colony and random sites that were successfully classified into occupied and unoccupied sites using discriminant function analysis.

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<td>unoccupied</td>
<td>Total</td>
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<tr>
<td>Occupied sites</td>
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<td>25</td>
<td></td>
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<tr>
<td></td>
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<td>4.00</td>
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<tr>
<td>Total Percent</td>
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<td></td>
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<td>48.00</td>
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Table 6. Sample size, mean, standard deviation and estimated discriminant function coefficients for discriminating variables.

<table>
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<th>Variable</th>
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<th>DF Coefficients</th>
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<table>
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<td></td>
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</table>
Table 7. Results of stepwise multiple regression of principal habitat components and beaver numbers for all sites and occupied sites. Significance level to enter and to stay = 0.1500.

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<th>Variable name</th>
<th>Step number</th>
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<td>Occupied sites</td>
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Fig. 3. Ordination of colony and random sites on the first two principal habitat components. * Clearwater River colony sites, ○ Clearwater River random sites, ◆ Swan River colony sites, ◇ Swan River random sites, • Fish Creek colony sites, ○ Fish Creek random sites.
correlated to beaver numbers (Table 7). PC1, PC2, and PC7 accounted for similar portions of the total variance in beaver numbers while PC4 again accounted for only a small amount of the variation.

PC1 contrasted water depth, vertical water fluctuation, and slope distance (high positive loadings) with alder, and stream gradient (high negative loadings). A scatterplot of PC1 with animal numbers indicated that higher positive scores for PC1 correlated with greater beaver numbers (Figure 4). This indicated that deep water sites with a small amount of water fluctuation were relatively more important for beaver presence and abundance than sites with steep gradients and alder.

PC2 contrasted bank slope, bank height, and logjams (positive loadings) against river confluence with willow as the dominant vegetation (negative loadings). PC scores indicated that a majority of the colonies had negative scores, emphasizing the importance of confluence sites with willow.

PC7 contrasted stream velocity, rose, and aspect (positive loadings) to slope distance and alder (negative loadings). PC7 was negatively correlated with beaver numbers and indicated the relative importance of sites with alder and some slope distance to sites with high velocity and rose.
Fig. 4. Relationship between PCI scores for occupied sites and the log of beaver numbers for those sites. *Clearwater colony sites, #Swan colony sites, .Fish Creek colony sites.
PC4 contrasted availability of twinberry and alder (positive loadings) with availability of dogwood (negative loading). PC4 was negatively correlated with beaver numbers and indicated the insignificance of twinberry as a factor in colony size.

For all sites, a combination of deep water, wider streams and availability of willow appeared to be strongly correlated to beaver numbers.

For occupied sites only, a combination of deep water, a small amount of vertical water fluctuation and slope distance, the presence of a confluence, and willow as the dominant vegetation appeared to be positively correlated to colony size.

Stream characteristics that appeared to limit presence or abundance of beaver were steep gradient, swift velocity, high and steep banks, and coarse substrate. Hawthorne, rose, and twinberry did not seem to positively influence presence or abundance of beaver.

DISCUSSION

The discriminant function analysis delineated deep water, short slope distance from low to high water marks (a measure of water fluctuation), and availability of willow as variables with good predictive power for discriminating random sites from colony sites in northwestern Montana. These findings are generally supported by other beaver habitat studies.
It is generally agreed that availability of preferred forage is important for determining suitable beaver habitat (Hall 1960, Williams 1965, Boyce 1974). Aspen and willow head the list of preferred beaver foods (Denney 1952). In the absence of aspen, willow seems to replace aspen as the preferred forage (Townsend 1953, Hall 1960, Swenson and Knapp 1980). In this study, availability of willow (in the absence of aspen) was an important factor in the location of winter colony sites.

An adequate and stable water supply is also necessary for beaver habitat (Williams 1965, Slough and Sadleir 1977). Howard and Larson (1985) found all 4 of their water reliability measures (stream gradient, stream width, soil drainage class and watershed size) to be significantly related to colony site longevity in Massachusetts. They did not measure water depth or water fluctuation. This study is in general agreement, finding wide streams, low stream gradient, small substrate, deep water, and low water fluctuation to be important for the presence of winter colony sites in northwestern Montana.

Beaver probably respond to a mix of stream and vegetation characteristics and may be able to meet their behavioral and physiological requirements in a variety of habitats by substituting available habitat components for unavailable ones.
However, beaver probably require deep water, created by dams or naturally, for winter colony sites across all northern habitats. Deep water around the lodge or bank den and the cache allows both access to the cache throughout the winter and protection from predators.

It could also be argued from the results of this study that a minimum amount of water fluctuation (measured as bank slope distance) is required for winter colony sites and for which substitution is not possible. Severe high water from spring run-offs flood lodges and dens, forcing adults with young kits to vacate. Severe low water depths can expose lodge or den entrances leaving beaver vulnerable to predators.

Willow is a component for which beaver can substitute, although partial to complete substitution of a preferred forage by a less preferred forage may lower reproductive fitness (Huey 1956, Pearson 1960, Gunson 1970, Parsons and Brown 1979).

Discriminant function analysis delineated the habitat components that seem to be required for the presence of a winter colony site. Principal components regression was used to go beyond this broad range of presence/absence to elucidate habitat components that seemed to affect beaver abundance.

The stream and vegetation characteristics that apparently influenced beaver numbers were variables that
have been delineated in other research assessing suitable beaver habitat. Steep topography limits construction of channels which are used to obtain and transport food (Williams 1965, Slough and Sadleir 1977). In Wyoming, beaver were absent from areas of rivers exhibiting high velocities and extreme water fluctuations (Collins 1976). In Massachusetts, the "best" beaver habitat was found on wide streams with low gradients and small substrate (Howard and Larson 1985). In this northwestern Montana study, beaver were absent from areas exhibiting steep stream gradients, high velocity, and extreme water fluctuations. High and steep banks and coarse substrate were also negatively correlated to beaver presence and abundance. The "best" winter colony sites were those found on wide, deep streams with mild gradients and small substrate where willow was the dominant vegetation.

One of the keys to proper wildlife management is accurate assessment of habitat quality (Van Horne 1983). This study quantified stream and vegetation components that appeared to influence beaver presence and abundance on 3 northwestern Montana waterways. The importance of deep water, low water fluctuation and available willow was delineated through both the discriminant function analysis and the principal components regression analysis. Research conclusions can be viewed with more confidence if 2
different methods of analysis give the same results (Green 1979). The additional variables obtained from the principal components regression aided in defining the underlying habitat structure of beaver winter colony sites.

However, survival and reproductive characteristics are parameters that need to be examined to verify the conclusions drawn in this paper about what constitutes "high quality" beaver habitat. Stable populations with a dependable reproductive rate that are able to withstand outside influences should define quality habitat (Van Horne 1983).

The model of high quality habitat derived in this study should also be validated in a different geographic area in a different year (Johnson 1981) to provide a strong test of this hypothesis.
LITERATURE CITED


APPENDIX A

GENERAL SURVEYS
General distribution, habitat and relative densities of beaver were assessed on 550 km of northwestern Montana waterways June - October 1985 and June - August 1986 (Fig. 1). Habitat and beaver sign surveys were conducted every 2 - 3 km on each waterway. At each survey site, a habitat and sign transect 3 m wide and 50 m long was run along the high water mark (2 m below the mark and 1 m above the mark). A second habitat and sign transect 3 m wide started at the high water mark and ran inland (perpendicular to the bank) 25 m (Fig. 2). The raw data collected during these general surveys is shown in Table 1.

Generally, areas revealing common and abundant amounts of old and current beaver use exhibited stream and vegetation characteristics (deep, wide, meandering streams with slow velocity, small substrate, and abundant willow) that seemed to have the most influence on presence and abundance of northwestern Montana beaver.

Flint Creek and the Clark Fork River from Schwarz Creek to Turah were notable exceptions, with high stream scores (indicating good beaver habitat) but limited beaver sign (Table 2). This may be a reflection of the moderate to heavy grazing observed all along these survey sections (Table 1).

The North Fork of the Blackfoot River showed limited beaver use with a moderate stream score.
Fig. 1. Map of the northwestern Montana study area showing survey rivers and creeks. Surveyed sections of the waterways.
Fig. 2. Diagram of the bank (parallel) and inland (perpendicular) habitat and sign survey transects for general surveys.
Table 1. Raw habitat and beaver use data collected on 24 rivers and creeks in northeastern Montana. Meander factor is 1.0 (straight stretch of waterway) to 1.5 (waterway makes "S" configuration). Velocity is 1 = slow, 2 = moderate, 3 = fast. Bank substrate is S = sand, M = mud, D = dirt, G = gravel, SR = small rock > 2" x 2", MR = medium rock > 2" x 10", LR = large rock > 10" x 10". Fresh cut and old cuts are 1 = < 10G cut, 2 = 10 - 40G cut, 3 = > 40G cut. Other current and old evidence is 1dg = stick and mud lodges, dam = bank dam, dam = beaver dam, c = food cache, ts = track set, and = scent mount. NA = not available.

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1. Beaver Creek: Recreation, upstream 10 km: campingground, pack camp

- 1: 1200
- 2: 1700
- 3: 1500
- 4: 1500

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1. Meadow Creek: Recreation, Gorge to wilderness

- 1: 2200
- 2: 1500
- 3: 2000
- 4: 2500
- 5: 2000

2. Big Salmon: Recreation, Lake area: wilderness

- 1: 5000
- 2: 5000
- 3: 3500

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1. Avon to: moderate grazing

- 1: 2700
- 2: 1200
- 3: 1500
- 4: 1500
- 5: 1500

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1. Lindbergh Lake: Recreation, downstream, 15 km

- 1: 1200
- 2: 3000
- 3: 2500
- 4: 3000
- 5: 2500

2. Salmon Prairie: Homes, recreation to Holland, Lake

- 1: 3000
- 2: 3500
- 3: 4000
- 4: 1200
- 5: 1400

3. Porcupine: Recreation, Bridge to San wildlife refuge, Lake

- 1: 3000
- 2: 5000
- 3: 1500
- 4: 5500

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Table 2. Relationship of observed beaver sign to five habitat parameters on 23 northwestern Montana waterways. Relative amount of beaver sign is the total amount of sign found on a waterway averaged over all sites and ranked as 1 = scarce; 2 = common; 3 = abundant. Stream characteristics, averaged over all sites on a waterway are ranked as 1 = least preferred by beaver; 2 = moderate; 3 = most preferred. Availability of preferred food is the total amount of willow and cottonwood understory averaged over all sites on a waterway and ranked as 1 = < 10%; 2 = 10-25%; 3 = 26-40%; 4 = >40%. Mean section score is the total of all scores for that section divided by the 7 factors. Mean river score is the total of all section scores divided by the number of sections.

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<td>1) West Fork confluence to Clark Fork River</td>
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<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>West Fork of the Bitterroot</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1) Painted Rocks Lake to Bitterroot confluence</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Spotted Bear River</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1) Beaver Creek upstream 10 km</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Rock Creek</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1) West Fork confluence to Hogback Creek</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>1) Siria Camp to Interstate 90</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Waterway section</td>
<td>Beaver sign</td>
<td>Depth</td>
<td>Meander factor</td>
<td>Velocity</td>
</tr>
<tr>
<td>------------------</td>
<td>-------------</td>
<td>-------</td>
<td>----------------</td>
<td>----------</td>
</tr>
<tr>
<td>West Fork of Fish Creek</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1) Hole in the Wall to Fish Creek confluence</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Lolo Creek</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1) headwaters to Bitterroot confluence</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Jocko River</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1) Arlee to reservoir</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
</tbody>
</table>
beaver use of the Dry Gulch area may reflect both the lack of preferred foods and the coarse bank substrate that limits denning potential. The small amount of use seen above Scotty Brown's bridge may also reflect a lack of good denning habitat (Table 2).

The surveyed section of the Kootenai River showed no current beaver use, but old use was common. Severe water fluctuations caused by discharges from Libby Dam probably have a negative impact by flooding potential denning habitat (Table 2).

Three stream sections exhibited common amounts of old and current sign but low stream scores. The use seen on two of these rivers, the Swan River between Salmon Prairie and Holland Lake and the Spotted Bear River, was confined to cuttings indicating that these surveyed areas may have been suitable only as feeding sites. The surveyed sections of Rock Creek were not generally suitable for beaver colony sites. However, deep, meandery channels backed up by beaver dams in the Hogback Creek area created good beaver habitat (Table 2). The beaver fed along Rock Creek, creating moderate amounts of sign (only cuttings) in stream habitat that was ranked as low quality beaver habitat.

In summary, common and abundant historic and current use by beaver was seen on the surveyed sections of the Clearwater, Stillwater, Bull, Yaak, Bitterroot (Bell
junction to Stevensville), North Fork of the Flathead (Moose City to Ford Station), Swan (Salmon Prairie to Holland Lake and Porcupine bridge to Swan Lake), and the Spotted Bear rivers, as well as Rock Creek (Hogback Creek area) and Nevada Creek (Table 2). It should be noted that while the 2 survey sites on Nevada Creek revealed abundant old and current use, Nevada Creek runs through heavily grazed and agricultural land above and below these sites. The survey of Nevada Creek may not be representative.

Limited historic and current use was seen on the survey sites of Flint Creek, Rock Creek (Siria Camp to I-90), West Fork of Fish Creek, Fish Creek from the West Fork confluence to the Clark Fork, Lolo Creek, and the Whitefish, Clark Fork (Little Blackfoot confluence area and Schwarz Creek to Turah), North Fork of the Blackfoot, South Fork of the Flathead (Meadow Creek Gorge to Spotted Bear Ranger Station), and West Fork of the Bitterroot rivers.

Survey sections (see Fig. 1) that did not seem to be colonized by beaver to their full potential were the Yaak and Clark Fork river sections, the Blackfoot River just below Lincoln, and the Clearwater River above Seeley Lake, above Salmon Lake and above the Blackfoot confluence.

Possible overuse by beaver was noted on the Swan River Wildlife Refuge, the Clearwater River above Alva Lake and just below Seeley Lake, and the Stillwater River.