1990

# Beaver dispersal in western Montana

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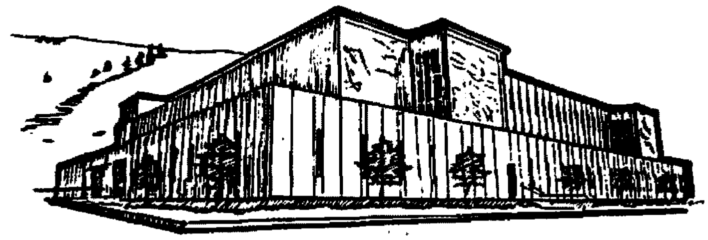

# BEAVER DISPERSAL IN WESTERN MONTANA

By

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B.S., Washington State University, 1986

Presented in partial fulfillment of the requirements for the

degree of

Master of Science

UNIVERSITY OF MONTANA

1990

Approved by:

Chairman, Board of Examiners

Dean, Graduate School

Date May 23, 1991

ABSTRACT

Jackson, Michael D., M.S., June 1990 Wildlife Biology

Beaver Dispersal in Western Montana. (79 pp.)

Directors: Dr. Lee H. Metzgar and Dr. Daniel Pletscher

A 3-part, 6-year study to determine the population status, distribution, and ecology of beavers throughout western Montana was initiated in July, 1985. This second phase of the 3 focuses on beaver dispersal. Field surveys, live trapping, and monitoring of captured beavers were initiated in July, 1987 and completed for this second phase of the study in March, 1989.

Four study areas were selected to represent relative beaver habitat quality and population density. Representative of secondary habitat were Cache/Fish creeks (low density) and Rattlesnake Creek (high density). Upper Willow Creek (low density) and Meadow Creek (high density) represented primary habitat. A total of 61 beavers were captured, and 4 of these were recaptured once. Intraperitoneal transmitter implant surgery was performed on 15 juvenile (1 to 2 years of age) beavers. Nine of these were monitored extensively during the 1987-88 field season. Two transmitter-equipped beavers, released at Cache Creek (which was not their site of capture) were considered 'artificial' dispersers. All other transmitter-equipped beavers, released at their site of capture, were considered natural dispersers.

Data analyses indicated a greater frequency and distance of moves by beavers from January to June; artificial dispersers moved more frequently and greater distances than natural dispersers; beavers in areas of low quality habitat moved greater distances more frequently than those of better quality habitat; and male beavers moved greater distances than females.

A discriminant function model for determining age classes of live beavers using morphological measurements was developed from the morphological measurements of 13 known-aged beavers. Beaver weight and tail width provided the greatest separation between age classes, indicating that these measurement may provide a relatively quick and simple means for estimating age of live beavers in the field.

Fourteen of 26 beavers captured in the Rattlesnake Creek study area were tested for the presence of Giardia lamblia. One, a 2-year old male captured on 11/10/88, tested positive.

## ACKNOWLEDGEMENTS

Many people and organizations were responsible for the completion of this work. Funding was provided by the Montana Department of Fish, Wildlife and Parks through the University of Montana Cooperative Wildlife Research Unit. Additional funding was provided by the Lolo National Forest. A special thanks to these organizations for making this project possible.

Drs. Lee Metzgar and Daniel Pletscher provided much needed and greatly appreciated enthusiasm, guidance, encouragement, and support as well as an occasional nudge to keep me at it. Drs. Bart O'Gara and Joe Ball reviewed much of the manuscript, provided insight into thesis preparation, constructive criticism, and continuing encouragement. Dr. Dave Patterson shared his knowledge of statistics in spite of a busy schedule, Dr. Kerry Forsman provided invaluable assistance in determining reproductive status of various trapped animals, and Dr. Les Marcum always expressed his interest and provided helpful information, especially pertaining to the Rattlesnake Creek area. Thanks are extended as well to those members of the faculty who expressed an interest in this project. A special thanks to Mr. Howard Hash who provided invaluable logistic support, advice, his knowledge of beaver, and the all important incentive to complete the project.

Field assistants Eric Schmidt and Steve Johnson provided excellent help and valuable contributions in data collection in spite of being dropped off in the wilderness and left to fend for themselves. Their enthusiasm and cheerfulness was always appreciated. Sarah Hall and Wendy Wilson provided helpful assistance as volunteers as well as pleasant company in the field.

Thank you Ginger Scwartz for taking such very good care of the financial aspects of the project and looking out for me, and Virginia Johnson for always turning on the copy machine for me. Thanks also to the Lutjke family, the Hansen-Bauer Ranch, trappers Harold McDowell and Bob White, Friends of the Rattlesnake, and the CASTOR organization for their cooperation and assistance. Mike Hillis and Greg Munther were instrumental in acquiring additional financial and logistical support, while Jack Fisher, Skip Rosquist, and Mike Paterno provided all permits required to operate on the Lolo and Deer Lodge Forests.

Very special thanks go to Therese, who in spite of nearly drowning while acting as my field assistant, continued to act as messenger, secretary, laundry worker, cook, major financial supporter, wife, mother, lover, and especially friend.

This is for Aaron in expectation that wildlife and wild places will be properly managed and conserved to provide him with at least the same enjoyment and wonderment that they hold for me now.

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# INTRODUCTION

A 3-part, 6-year study of western Montana beavers (Castor canadensis) was initiated in July, 1985. Original objectives included determination of the population status, distribution, and ecology of beavers throughout western Montana. The Montana Department of Fish, Wildlife and Parks provided funding through the Montana Cooperative Wildlife Research Unit at the University of Montana. The initial portion of the research, conducted by Andrea Easter-Pilcher (Easter-Pilcher 1987), included general surveys to assess population size, relative densities, distribution, and habitat of beaver populations in western Montana. That project produced data on forage utilization, habitat selection, and population indices for beavers in northwestern Montana (Easter-Pilcher 1987). My study represents the second project of the 3. The study plan initiated in this project was designed to be continued by a third and final graduate student. Additional funding was provided for this project by the U. S. Forest Service, Lolo National Forest, Missoula, Montana.

The beaver is of economical, ecological, and recreational importance in western Montana. It is of economic importance not only for the value of its pelt, but because it can become a pest species at high populations densities and in localized situations. Dam building and feeding activities of beaver alter hydrology, channel geomorphology, biogeochemical pathways and community productivity (Naiman et al. 1986). These alterations can have both positive and negative impacts;

negatively impacting local economies by flooding fields, blocking culverts and irrigation channels, and by damaging harvestable timber and ornamental trees and shrubs; and positively impacting fishing, recreation resources, other wildlife and wildlife habitat (Munther 1983).

Beaver populations in northwestern Montana require management objectives that will prevent over-exploitation and provide a sustained yield while minimizing possible nuisances associated with high population levels. A knowledge of beaver population dynamics will provide managers with much of the information necessary to attain management objectives. Information is needed concerning beaver productivity, mortality, dispersal, and the impacts of harvest within the population to provide managers with an understanding of beaver population dynamics.

Beaver productivity and mortality provide the manager with information to help determine the rate of increase or decrease within a beaver population. Productivity estimates for beaver occur frequently in the literature. Ovulation rates, placental scar and fetus counts, and colony observation of kit activity have been used to determine the number of kits per colony (Leege 1968, Henry and Bookhout 1969, Bergerud and Miller 1977, Svendsen 1980). Mortality in beaver populations, other than that caused by predation, is generally due to trapping pressure. Mortality rates can be determined by estimation of survivorship by age class from carcass data or by live trapping (Caughley 1977).

This study was designed to investigate beaver population dynamics with an emphasis on dispersal. Dispersal is the process by which areas of previous overexploitation or habitat degradation are recolonized and thus is of primary importance in the dynamics of beaver populations (Slough and Sadleir 1977). Mortality rates can be high among dispersers due to lack of shelter, starvation, and predation (Boyce 1974, Lidicker 1975). Dispersers may also provide a source of replacement for adult mortality from trapping or predation (Aleksiuk 1968).

Specific objectives included: 1) quantify survivorship of dispersers and determine the direction and distance of beaver dispersal in selected drainages in western Montana; 2) determine the effects of habitat quality and beaver population density on beaver dispersal; 3) develop a model to estimate age-class membership of live-trapped beavers; and 4) estimate the probability and extent of <u>Giardia lamblia</u> spread by beaver dispersal in the Rattlesnake Creek study area.

The beaver is a highly specialized furbearer adapted to semi-aquatic habitats. It is the largest North American rodent. A typical beaver colony consists of the adult male and female, kits, and subadults from the previous year (Bradt 1938, Novak 1977, Bergerud and Miller 1977). Two-year old beavers usually leave the colony prior to the birth of the kits in spring (Leege and Williams 1967, Svendsen 1980). Beavers are monogamous and produce only one litter per year (Boyce 1974, Lyons 1979). Breeding usually occurs between January and March in cold climates (Grasse and Putnam 1950, Henry and Bookhout 1969, Bergerud and Miller 1977). Reported gestation periods vary from 70 to 90 days (Provost 1958, Bergerud and Miller 1977, Woodward 1977). Births occur between April and June in cold climates. Litter sizes average between 3 and 4, but may vary between 1 and 9 (Hodgdon 1949, Jenkins and Busher

1979, Hill 1982), depending on the condition of the female, the quantity and quality of available food, and the severity of winter.

Territorial boundaries of beaver colonies are marked by mounds of mud and castoreum from the castor glands of the beaver. Aleksiuk (1968) suggested that these scent mounds function in maintaining territorial rights; transient beaver appear to voluntarily avoid areas harboring scent mounds. Thus, territorial behavior may cause dispersing beavers to move into unoccupied areas.

Whether dispersal of beaver is caused by innate or environmental factors is unclear. Environmental dispersal is defined by Howard (1960) as the movement away from an animal's birthplace in response to crowded conditions. Innate dispersal is defined as a predisposition at birth to disperse. Innate dispersers often ignore available and suitable areas and voluntarily move into strange and often unfavorable habitat. Bergerud and Miller (1977) and Leege (1968) suggested that beaver disperse in response to an innate tendency to leave their home colony. Hodgdon (1978) and Svendson (1980) observed no aggression associated with dispersal; if dispersal was environmental, then aggressive behavior by the adults toward the subadult disperser in the colony might be expected. However, Gunson (1970) suggested that less dispersal of 2-year olds takes place in high quality habitat and Bradt (1938) reported that 2-year olds may be driven from the colony. Both reports suggest that dispersal is environmental.

Howard (1960) reported the following advantages to innate dispersal. Innate dispersal would: 1) reduce the likelihood of inbreeding; 2) further the spread of new genes; 3) extend the range of the species; 4) facilitate the recolonization of depopulated areas; 5) tend to reduce intraspecific competition; 6) bring about a more efficient utilization of habitat resources.

Lidicker (1975) discussed 2 types of dispersal that he termed saturation and presaturation dispersal. Saturation dispersal was defined as the outward movement of individuals from a population living at or near carrying capacity. This could occur through environmental or genetic mechanisms and would, presumably, involve those individuals least able to cope with local conditions. Pre-saturation dispersal is defined as an exodus from a population before the habitat becomes saturated. This type of dispersal is more probably genetically caused and would largely include innate dispersers. Supposedly, pre-saturation dispersers are in relatively good condition, not economically or socially destitute, and thus would be expected to have higher survival than saturation dispersers.

Variation in the distance of dispersal has been modelled by Murray (1967), Waser (1985), and Buechner (1987). These models contend that dispersal is driven by competition for available resources and thus would correspond to environmental dispersal. Each author admits that at least some data sets do not fit the models and thus innate dispersal may be indicated in some species. It seems that both environmental and innate dispersal occur in some species, and both types may occur in single species.

Hestbeck (1987) presented a model of population growth in which he included an emigration component based on the "social fence" hypothesis. This hypothesis states that dispersal is a function of aggressiveness within and between social groups. At low densities, aggression within the social group dominates and dispersal increases with increased density. When densities reach the point where the habitat is saturated, aggression between social groups dominates and dispersal decreases. This model may apply to beavers because dispersal of 2-year olds has been delayed in some high density populations (Novakowski 1965, Bergerud and Miller 1977). However, whether or not aggressiveness plays a part in their dispersal is not known.

Molini et al. (1980) suggested that beaver dispersal is a function of population density. Increases in density result in a decrease in the rate of dispersal. Dispersal may be delayed one or more years in a high density population (Novakowski 1965, Nordstrom 1972). Delayed dispersers would have a competitive advantage over younger dispersers because they would be physically larger and presumably more experienced. There would be no competitive advantage in delaying dispersal at low population densities.

Lidicker (1975) suggested that dispersal plays 3 different roles in the regulation of a population: 1) dispersal is one of several factors that account for the total losses of a population; 2) dispersal may be a key factor in stopping population growth at carrying capacity; 3) dispersal may prevent population numbers from reaching carrying capacity. Beaver populations may be an example of continuous regulation of population size below carrying capacity. Membership in the beaver colony is usually limited to the family group. Immigration is unlikely unless an adult dies. This limited immigration and the dispersal of young beavers limit colony size. As beavers exploit a resource that is only slowly renewable, increasing their numbers above carrying capacity would be a poor strategy. Beaver social stability is enhanced by combining dispersal with a resistance to immigration. The primary effects of immigration in beaver populations is the replacement of reproductive adults lost to mortality (Boyce 1974, Svendson 1980).

The limited information on dispersal in beaver populations is generally inconclusive. I will attempt to clarify the role of dispersal in beaver populations by determining the pattern of dispersal in selected drainages in western Montana through the use of radiotelemetry. Relative habitat quality and beaver population density will be used as a basis of comparison between study areas.

## STUDY AREAS

Four study areas were selected from secondary drainages within western Montana (Fig. 1): Cache and Fish creeks in Mineral County, Rattlesnake Creek in Missoula County, and Meadow and Upper Willow creeks in Granite County.

The Upper Willow Creek and Meadow Creek areas, located approximately 18 km west and 28 km southwest, respectively, of Philipsburg in the Deer Lodge National Forest, were selected to represent primary beaver habitat (Table 1). I defined primary beaver habitat as an area represented by relatively low stream gradient, high meander, and high availability of *Salix* spp. (willow), a major food source for beavers. These 2 drainages were also selected to represent

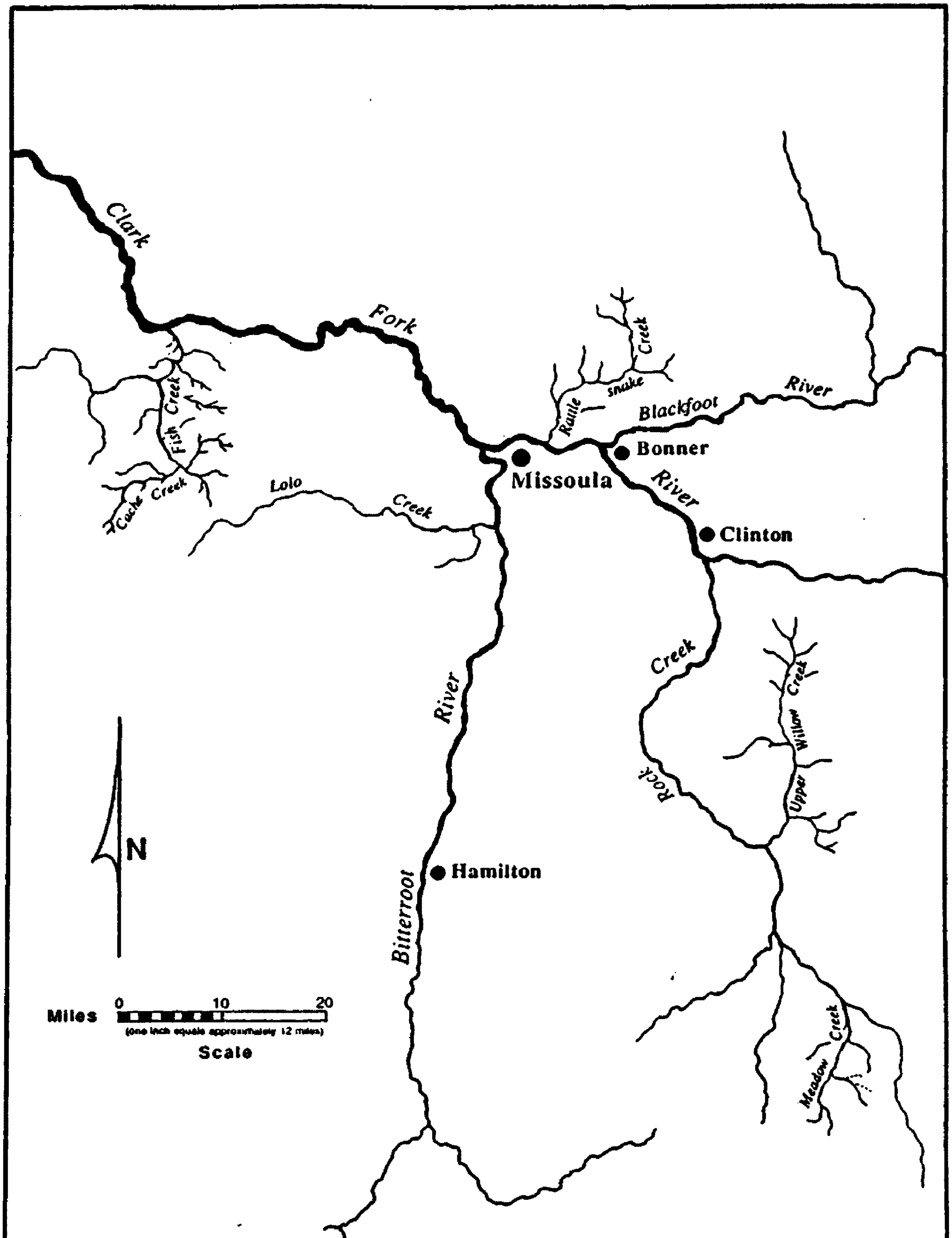


Fig. 1. Map of western Montana showing study area drainages - Cache/Fish creeks, Rattlesnake Creek, Meadow Creek, Upper Willow Creek.

Table 1. General characteristics of study area drainages.

| | Cache/Fish creeks | Rattlesnake Creek | Upper Willow Creek | Meadow Creek |
|---|---|---|---|---|
| Relative Habitat Quality | secondary | secondary | primary | primary |
| Relative Population Density | low | high | low | high |
| Flow* | | | | |
| Direction | NE/N | S | SW | NW |
| Distance (km) | 18.0/35.9 | 34 | 28 | 15 |
| Elevation Decrease* (m/km) | 43/11 | 35 | 21 | 56 |
| Bank Ht. | variable | variable | low | low |
| Substrate | medium rock | large rock | mud - sand, small rock | mud - sand, small rock |
| Turbidity | low | low | medium | medium |
| Gradient | moderate to steep | moderate to steep | low | low |
| Velocity | moderate to swift | moderate to swift | low to moderate | low to moderate |
| Shrub Cover | low to moderate | moderate | moderate to heavy | moderate to heavy |

* - flow and elevation decrease measurements are approximate and represent creek source to mouth; all other measurements are relative to each other and represent portion of creeks actually surveyed and trapped.

low (Upper Willow Creek) and high (Meadow Creek) density beaver populations. Relative densities were determined from the amount of trapping taking place the previous year and by stream surveys. A minimum of 48 beavers were trapped in the Upper Willow Creek drainage (upstream from Miner's Gulch Rd. bridge) in the 1986-87 trapping season (H. McDowell, pers. commun.), while little or no trapping was done in the Meadow Creek drainage. The Rattlesnake Creek and Cache/Fish creeks areas in the Lolo National Forest, located just north of and 64 km west of Missoula, respectively, were selected to represent secondary beaver habitat. I defined secondary beaver habitat as having greater stream gradient, less meander, and less willow and other food sources relative to primary habitat.

The Rattlesnake Creek drainage, which lies within the Rattlesnake National Recreation Area, was selected to represent a high density beaver population because survey results indicated a high number of colony sites for the available habitat, and I assumed either non-existent or little trapping pressure due to lack of vehicle access. The Cache Creek drainage was originally selected to represent a low density beaver population. One of the 4 beaver colonies within the drainage was trapped out during fall, 1987 to create an area of low density. Probable poaching activity during that fall and winter however eliminated all colonies within the drainage as well as decreasing the beaver population in Fish Creek. The combination of Cache/Fish creeks was consequently used to represent a low density beaver population.

Rattlesnake, Meadow, and Upper Willow creeks lie within the west-central forest region of Montana (Arno 1979). The west-central forest region is bounded to the west by the Bitterroot Range, which constitutes a barrier to Pacific Coast moisture. The general climate for this region is relatively mild and generally drier than the northwestern region. Mean annual precipitation for the study areas within this region ranges from approximately 36 to 41 cm. The Cache/Fish creeks drainage lies within the northwestern forest region (Arno 1979). Mean annual precipitation for the area ranges from approximately 36 cm at the mouth of Fish Creek up to 102 cm at the headwaters of Cache Creek. Temperatures for all study areas range from a mean minimum of -13 to -11 C in January to a mean maximum of 27 to 30 C in July (Arno 1979).

Dominant bank vegetation for all study areas is composed of willow (Salix spp.) intermixed with alder (Alnus spp.) and red osier dogwood (Cornus stolonifera). Black hawthorne (Crataegus douglasii) is found at the Rattlesnake Creek study area. Vertebrate fauna in each of the study areas is typical for western Montana and has been described by numerous authors. Predators of concern to beavers include black bears (Ursus americanus), bobcats (Felis rufus), cougars (Felis concolor), coyotes (Canis latrans), mink (Mustela vison), and river otters (Lutra canadensis) (Swank 1949, Young and Jackson 1951, Hakala 1952, Mech 1966, Gunson 1970, Boyce 1974).

The surrounding area at the Cache/Fish creeks and Rattlesnake Creek sites (Table 1) is composed primarily of montane forest consisting of a mosaic of western larch (Larix occidentalis), ponderosa pine (Pinus ponderosa), lodgepole pine (Pinus contorta), Douglas-fir (Pseudotsuga menziesii), Engelmann spruce (Picea engelmanii), subalpine fir (Abies lasiocarpa), and small stands of western redcedar (Thuja plicata).

Black cottonwood (Populus trichocarpa) is plentiful along the banks of Fish Creek, and isolated stands of aspen (Populus tremuloides) can be found along the upper reaches of Cache Creek. Less lodgepole pine and little western redcedar is present along Rattlesnake Creek.

The surrounding area at the Upper Willow and Meadow Creek sites (Table 1) is primarily sedge and hay meadows on the flat. Montane forest of subalpine and Douglas-fir, grand fir (Abies grandis), lodgepole pine, and Engelmann spruce occupies the adjacent uplands at Meadow Creek along with small stands of aspen along the creek and interspersed throughout the area. Montane forest of primarily lodgepole pine and Douglas-fir with some ponderosa pine and western larch occupies the adjacent upland at Upper Willow Creek.

## METHODS

Ground surveys were conducted of each drainage to locate active colony sites and determine live-trapping locations. Beaver were live-trapped using Hancock traps set in a variety of sites using a castor-based scent or fresh aspen as bait. Trapped animals were anesthetized with ketamine hydrochloride (HCL) combined with acepromazine maleate (APM) by intramuscular injection while the animal was still within the trap. A standard initial dose of 150-200 mg ketamine HCL plus 2.5 mg APM was used on all animals except kits, which were given 100 mg ketamine HCL plus 2.5 mg APM as recommended by Lancia et al. (1978). Beaver were then weighed and measurements were taken of total length; length, width, and thickness of tail; circumference of head, neck, and chest; length and width of the right hind foot pad; and the breadth of the zygomatic arch (Table 2). Inspection of tooth eruption and wear were used in conjunction with relative size of morphological measurements to estimate age class (Cook and Maunton 1954, Williamson 1959, Patric and Webb 1960, Van Nostrand and Stephenson 1964, Larson and Van Nostrand 1968). Beavers were separated into age classes as kits (up to 11 months), yearlings (12 - 23 months), 2-year-olds (24 - 35 months), and 3-years and older. Sex was determined by external palpation for the presence or absence of the os penis, cloacal examination (Osborn 1955, Svendsen 1980), or the presence of enlarged pectoral teats on lactating females (Lancia 1979). All trapped individuals were marked with colored plastic eartags (Miller 1964) in both ears and tattooed on the webbing of the hind foot pad. Standard-size colored rototags cut down to approximately half the original size and imprinted with the individual's tattoo number were used as eartags. Separate colors were used to distinguish male and female and adult and subadult. All captured beavers except those kept for surgery were held in the trap at a cool, protected area close to the trap site until they had fully recovered from anesthetizing (usually about 2 hours) and then were released at the trap site.

Fall-trapped yearlings and spring-caught 2-year old beavers were held for surgical implantation of radio transmitters. Beavers were held in a quiet, cool, and dark location to minimize stress. Food and water were withheld for at least 6 hours prior to surgery to allow for waste elimination.

Table 2. Morphological variable names and measurement description. All measurements taken by metric or common measure tape except where noted.

| Variable name | Measurement description |
| --- | --- |
| WT | Weight in kilograms: measured with a spring scale |
| LTH | Total body length in cm: measured from tip of nose over the back to tip of the tail |
| TL | Tail length in cm: measured from base of tail at fur line to tip of tail |
| TW | Tail width in cm: measured at point of greatest width |
| TTH | Tail thickness in cm: measured with calipers at thickest portion of base of tail |
| HC | Head circumference in cm: measured just anterior to ears |
| NC | Neck circumference in cm: measured immediately behind lower mandible |
| CC | Chest circumference in cm: measured immediately behind forelegs |
| ZYG | Zygomatic breadth in cm: measured with calipers at widest distance between zygomatic arches dorsally across the skull |
| RHPL | Length of right-hind footpad in cm: measured at longest point of base of foot between 2nd and 3rd digits |
| RHPW | Width of right-hind footpad in cm: measured at widest point of base of foot just behind digits |

I used cylindrical, surgically implantable transmitters, constructed by Telonics, Inc. (932 E. Impala Ave., Mesa, Arizona 85204). Each measured approximately 10 cm in length by 4 cm in diameter. The expected life was a minimum of 24 months at 32 pulses per minute. Transmitters were implanted intraperitoneally. Intraperitoneal transmitter implants have been shown to be well tolerated by beaver (Guynn et al. 1987). Surgical procedures for intraperitoneal transmitter implants have been described by many authors (Smith and Whitney 1977, Melquist and Hornocker 1979, Davis et al. 1984, Van Vuren 1989). Procedures used in this study most closely followed those of Melquist and Hornocker. All surgeries were performed under field conditions using as sterile a procedure as was practical. Transmitters and all surgical instruments were stored in surgical disinfectant (Betadine solution) for a minimum of 2 hours prior to surgery. Surgical drapes were sterilized with disenfectant prior to use and sterile surgeon's gloves were used by both surgeon and assistant. A scalpel was used to shave the incision site after most hair was removed from the site with handclippers. Nonabsorbable #2.0 or #3.0 suture materials were used in place of staples to close the skin.

Water was provided after surgery and beavers were allowed a recuperation time of 6–8 hours or were held overnight when possible. The transmitter-equipped beaver was then released at its capture site or in the case of artificial dispersers, at sites distant from the release site. Artificial dispersers were those dispersal-age beavers from other locations released within the study area to be used as a basis of comparison to dispersal-aged beavers trapped and released within the study area, or natural dispersers.

Transmitter-equipped beavers were located every 2 to 3 days initially after release and through the spring when dispersal activity was expected to take place. During summer locations were limited to once weekly as movement activity decreased. Only periodic locations were obtained in the fall because all monitored beavers had settled into a specific location, presumably to prepare for winter (Appendix A). All locations were made during daylight hours by walking to the site of transmission when possible. In those cases where exact site locations were impractical due to difficult access, a minimum of 2 bearings were recorded and locations were estimated by triangulation. If the location indicated movement had occurred. then walking in for an exact site location was done regardless of access difficulty. I assumed that daylight locations would minimize location error due to beaver movement. Locations were noted individually on prepared location sheets for each individual. Date, time of day, weather conditions, map coordinates, comments, and observer's name were recorded.

Data were tabulated for each monitored beaver. A move was recorded if a monitored beaver was located 20 m or more from its previous location. The frequency of no moves recorded (0 moves), detected moves of 20-500 m, detected moves >500 m, the mean of the total distance travelled between detected moves (mean distance), the greatest distance away from the release site a beaver was located (greatest distance), and the distance from the release site a beaver was located at the final location of the field season (last location) were recorded. Frequency data indicated in Figs. 2 - 4 were expressed as a percentage of locations. I computed them by dividing the number of 0 moves or detected moves by the number of radio locations taken for each beaver. Frequency data for analysis of direction were determined from the number of upstream or downstream moves and the total number of moves. Comparisons of all frequency data, actual number of 0 moves, detected moves 20-500 m, and detected moves >500 m, were evaluated using the Chi-square test (Statgraphics 1987) to evaluate the hypothesis that there were no differences in the proportion of detected moves for each grouping. To ensure an approximate Chi-square distribution, no more than 20% of categories used in the analysis had an expected frequency of less than 5 and no categories had expected frequencies of less than 1 (Ott 1984). Tabulated data were grouped for comparisons by time of year, study area, relative habitat quality (primary or secondary), relative beaver population density (high or low), sex of the beaver, the type of disperser (artificial or natural), and by the direction of a move (upstream or downstream). Upon rejection of the null hypothesis, the Bonferoni Z statistic was used to determine significance within groupings. The Student's t-test (Statgraphics 1987) was used to evaluate the hypothesis that the mean distance, the greatest distance, and the last location for each of the above groupings were equal.

Thirteen known-aged beavers, dead animals aged by premolar development and degree of molar basal closure (Williamson 1959, Van Nostrand and Stephenson 1964, Larson and Von Nostrand 1968), were used to generate a model that may provide a basis for separating live-captured beavers into age classes. Stepwise discriminant function analysis was used to determine the optimal separation of age groups based on linear transformations of the morphological variables. Appendix B presents the methods used and the results of this analysis.

## RESULTS

During the trapping seasons of fall, 1987, and spring and fall, 1988, I captured beavers on 65 occasions, including 61 different individuals and 4 recaptures. Five beavers from a single colony in the Cache Creek drainage were kill-trapped using Conibear 330 traps in fall, 1987 to create an area of lowered population density. Two mortalities were a direct result of handling techniques: 1 female in Meadow Creek died of stress due to heat and drug dosage, and 1 male in Rattlesnake Creek died of accidental drowning following an early release (within 1 hour after drug injection). Percent trapping success, defined as the number of beavers captured per trap night, was similar in all drainages, with the greatest success seen in those drainages having the higher density beaver populations (Table 3). Thirty-two males and 29 females, which included thirteen kits, 10 yearlings, 12 2-year olds, and 26 adults (3-years and older), were captured (Table 4).

Fifteen beaver were held for surgical implantation of radio transmitters. Transmitter-equipped beavers included 5 in Rattlesnake Creek, 3 in Cache/Fish Creek, 4 in Meadow Creek, and 3 in Upper Willow Creek. Three of these beavers, 2 in Meadow Creek and 1 in Upper Willow Creek, were not caught and transmittered until fall, 1988. One from Rattlesnake Creek died shortly after surgery, and 1 from Cache/Fish

Table 3. Trapping success by season and study area. Percent success (s) was determined by dividing the number of captures (c) by the number of trap nights (t).

| Study Area | Fall '87 c/t | Fall '87 s | Spring '88 c/t | Spring '88 s | Fall '88 c/t | Fall '88 s | Totals c/t | Totals s |
|---|---|---|---|---|---|---|---|---|
| Cache/Fish Creeks | 5/37 | 13.5% | 5/60 | 8.3% | 2/38 | 5.3% | 12/135 | 8.9% |
| Rattlesnake Creek | 13/91 | 14.3% | 6/43 | 14.0% | 8/91 | 8.8% | 27/225 | 12.0% |
| Meadow Creek | not trapped | | 7/32 | 21.9% | 10/101 | 9.9% | 17/133 | 12.8% |
| Upper Willow Creek | not trapped | | 5/48 | 10.4% | 4/93 | 4.3% | 9/141 | 6.4% |

Table 4. Estimated age classes of live-trapped beavers by study area and sex. Kit = 0-11 months, 1-year = 12-23 months, 2-years = 24-35 months, 3-years+ = 36 months and older.

| Study Area | n M/F | Kit M/F | Age Class 1-year M/F | 2-years M/F | 3-years+ M/F |
|---|---|---|---|---|---|
| Cache/Fish Creeks | 8/6 | 3/0 | 2/1 | 0/3 | 3/2 |
| Rattlesnake Creek | 15/11 | 4/1 | 1/3 | 2/2 | 8/5 |
| Meadow Creek | 8/6 | 2/2 | 1/1 | 2/0 | 3/3 |
| Upper Willow Creek | 3/4 | 0/0 | 0/1 | 2/1 | 1/2 |
| Total | 34/27 | 9/3 | 4/6 | 6/6 | 15/12 |

creeks died shortly after release, leaving a total of 10 possible dispersers, 5 males and 5 females, for the spring 1988 field season (Table 5). Two beaver released in Cache Creek were artificial dispersers. One of these was incorrectly located due to equipment malfunction. This beaver (F405) was later correctly located upstream from its release site in Cache Creek and is now being monitored (T. Van Deelen, pers. comm.). All location data for each monitored beaver during the 1987-1988 field seasons were summarized and tabulated (Table 6).

Monthly movement data were placed into two categories (locations made from March to June and locations made from July to November) based on indicated trends seen in Figs. 2 - 5. Beavers moved significantly greater distances more frequently during the period from April to June, and lesser distances more frequently during July to November (Table 7).

Comparisons between study areas (Table 7) indicated that the monitored beaver in Cache/Fish creeks had a significantly smaller proportion of locations in which no move was detected and moved all distances more frequently than those in the other study areas. Monitored beavers in Rattlesnake Creek moved greater distances more frequently than those in Meadow and Upper Willow creeks, and lesser distances more frequently than those in Meadow Creek. Monitored beavers in Meadow Creek moved lesser distances more frequently than those in Upper Willow Creek.

The artificial disperser (Cache/Fish creeks) had a significantly smaller proportion of locations in which no move was detected and moved all distances more frequently than did natural dispersers (Table 8).

Table 5. Radio-telemetry monitored beaver in 1987-88. ID# reflects study area. R = Rattlesnake Creek, F = Fish/Cache creeks, M = Meadow Creek, W = Upper Willow Creek.

| ID# | Release Date | Sex | Frequency |
|---|---|---|---|
| R301 | 10/23/87 | F | 151.780 |
| R608 | 10/29/87 | F | 151.920 |
| R715 | 04/07/88 | M | 152.020 |
| R618 | 04/14/88 | M | 151.840 |
| F204* | 05/10/88 | F | 150.930 |
| F405* | 05/09/88 | F | 150.900 |
| M101 | 06/07/88 | M | 151.870 |
| M306 | 06/01/88 | M | 150.870 |
| W103 | 05/13/88 | F | 151.890 |
| W305 | 05/18/88 | M | 151.000 |

* - artificial dispersers released in Cache Creek, captured in lower Fish Creek.

Table 6. Dispersal distance and direction of transmitter-equipped beavers. ID# reflects study area. W = Upper Willow Creek, M = Meadow Creek, F = Cache/Fish Creeks, R = Rattlesnake Creek; up = upstream, dn = downstream. Move = minimum 20m distance from last radio location. Total distance moved = sum of successive moves.

| ID# | Number of Locations | Number of Moves 20-500 m | Number of Moves >500 m | Total Distance Moved | Distance/Direction from Release Site: Greatest | Distance/Direction from Release Site: Last location |
|---|---|---|---|---|---|---|
| W103 | 34 | 3 | 2 | 3390m | 1600m/up | 40m/up |
| W305 | 32 | 11 | 1 | 3220m | 2045m/up | 1860m/up |
| M101 | 28 | 9 | 1 | 2640m | 480m/up | 400m/up |
| M306 | 30 | 7 | 0 | 350m | 100m/dn | 0 |
| F204 | 21 | 15 | 7 | 15840m | 7960m/up | 7960m/up |
| F405 | 1 | 1 | 1 | 1080m | 1080/up | 1080m/up |
| R301 | 38 | 10 | 8 | 6890m | 890m/dn | 260m/dn* |
| R608 | 33 | 8 | 0 | 580m | 340m/up | 340m/up** |
| R715 | 22 | 8 | 8 | 11020m | 1980m/dn | 1980m/dn*** |
| R618 | 36 | 11 | 4 | 31630m | 7820m/dn | 100m/up |

* Predation mortality - 7/27/88
** Predation mortality - 6/22/88
*** Predation mortality - 6/06/88

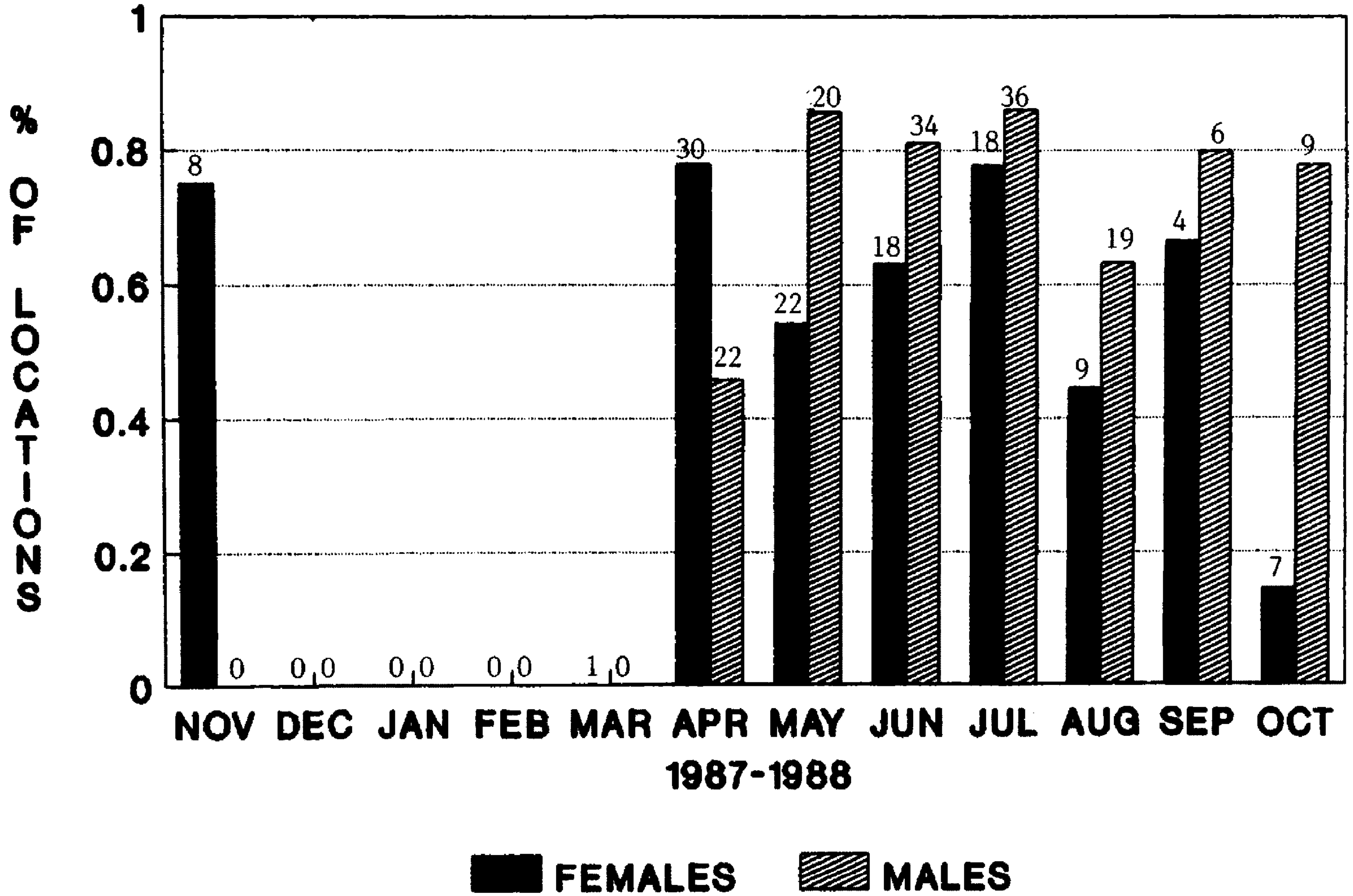


Fig. 2. Seasonal distribution of 0 moves (no move detected) for transmitter-equipped beavers in western Montana. Numbers above block represent the number of locations (radio fixes) made.

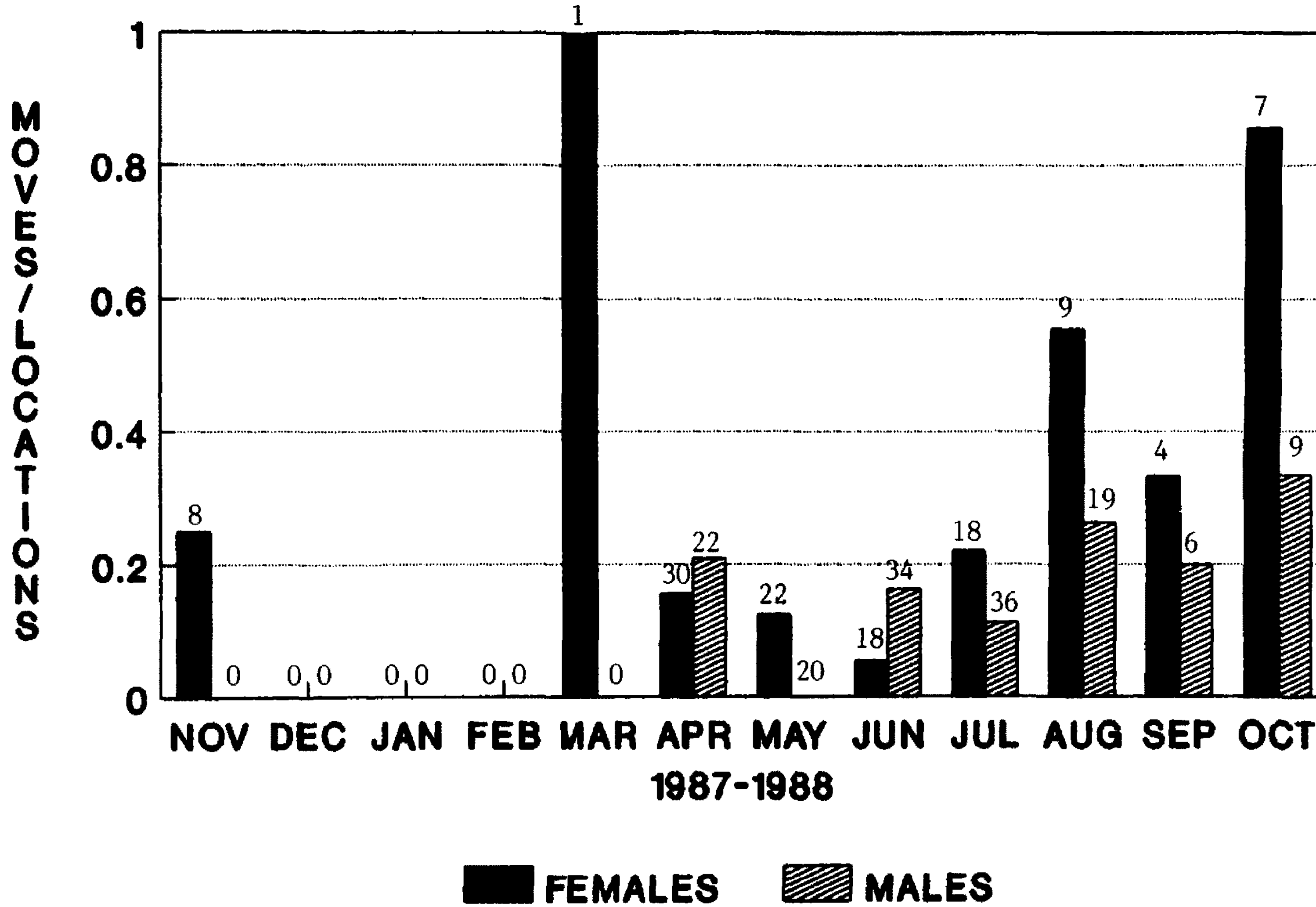


Fig. 3. Seasonal distribution of moves 20-500 m by transmitter-equipped beavers in western Montana. Numbers above blocks represent the number of locations (radio fixes) made.

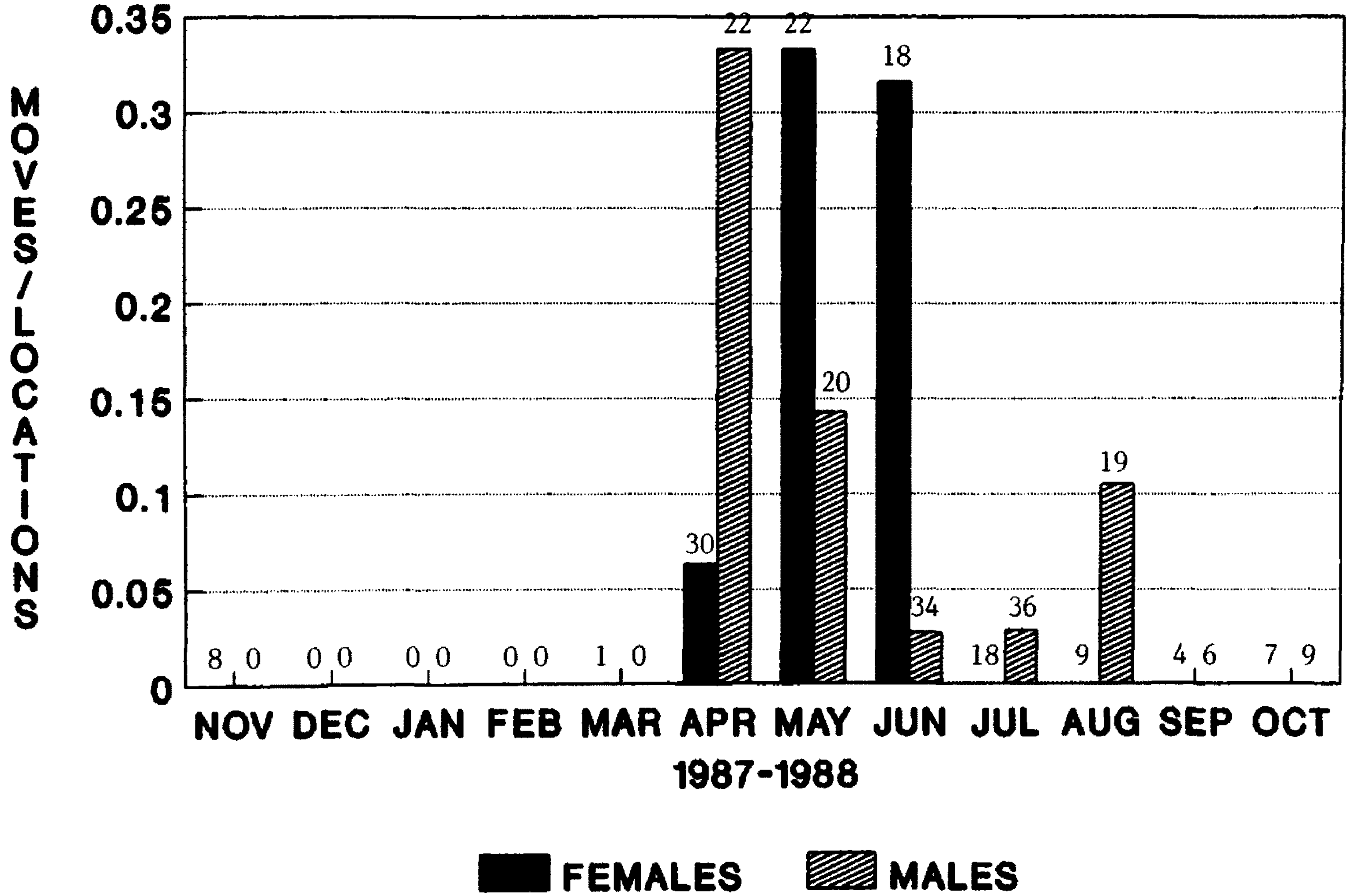


Fig. 4. Seasonal distribution of moves >500 m by transmitter-equipped beavers in western Montana. Numbers above blocks represent the number of locations (radio fixes) made.

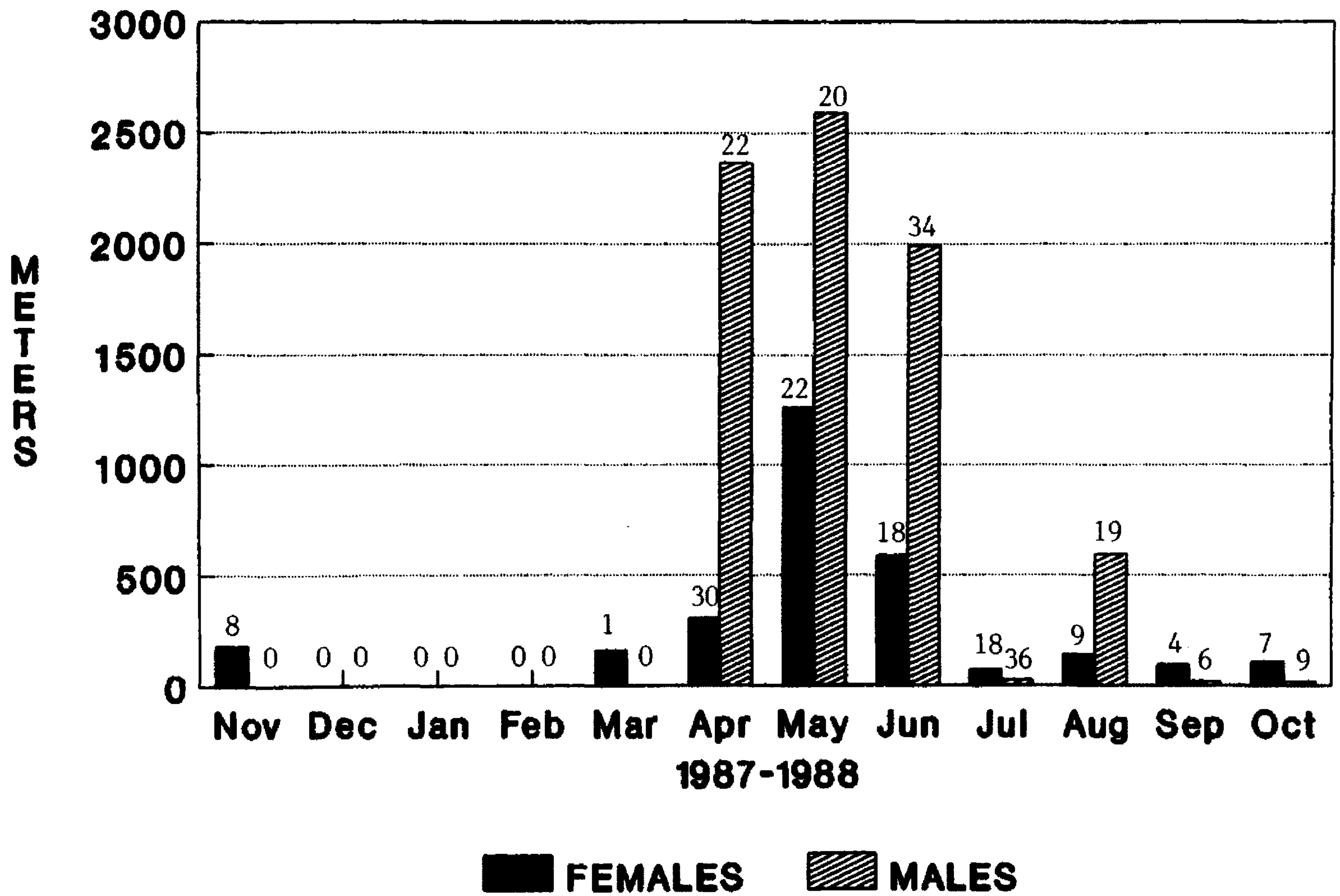


Fig. 5. Seasonal distribution of the mean distance travelled between detected moves by transmitter-equipped beavers in western Montana. Numbers above blocks represent the number of locations (radio fixes) made.

Table 7. Frequency of movement data by type of move for transmitter-equipped beavers in western Montana. Significance tests are within underlined groupings below. - less than expected by chance. + greater than expected by chance. ** - p < 0.01 *** - p < 0.05

| Variable | Observed Moves (O) | Expected* Moves (E) | Index (O/E) | Signi-ficance |
|---|---|---|---|---|
| Time of Year | | | | |
| January-June | | | | |
| 0 moves | 99 | 101.2 | 0.98 | |
| moves 20-500 m | 20 | 28.5 | 0.70 | |
| moves >500 m | 28 | 17.3 | 1.62+ | ** |
| July-December | | | | |
| 0 moves | 82 | 79.8 | 1.03 | |
| moves 20-500 m | 31 | 22.5 | 1.38+ | ** |
| moves >500 m | 3 | 13.7 | 0.22- | ** |
| Study areas | | | | |
| Rattlesnake Creek | | | | |
| 0 moves | 81 | 81.2 | 1.00 | |
| moves 20-500 m | 17 | 22.9 | 0.74 | ** |
| moves >500 m | 20 | 13.9 | 1.44 | ** |
| Meadow Creek | | | | |
| 0 moves | 42 | 39.9 | 1.05 | |
| moves 20-500 m | 15 | 11.2 | 1.34 | ** |
| moves >500 m | 1 | 6.8 | 0.15- | ** |
| Upper Willow Creek | | | | |
| 0 moves | 52 | 45.4 | 1.15 | |
| moves 20-500 m | 11 | 12.8 | 0.86 | *** |
| moves >500 m | 3 | 7.8 | 0.39- | ** |
| Cache/Fish Creek | | | | |
| 0 moves | 6 | 14.5 | 0.41- | ** |
| moves 20-500 m | 8 | 4.1 | 1.95+ | ** |
| moves >500 m | 7 | 2.5 | 2.80+ | ** |
| Disperser Type | | | | |
| Artificial | | | | |
| 0 moves | 6 | 14.5 | 0.41- | ** |
| moves 20-500 m | 8 | 4.1 | 1.95+ | ** |
| moves >500 m | 7 | 2.5 | 2.80+ | ** |
| Natural | | | | |
| 0 moves | 175 | 166.6 | 1.06 | |
| moves 20-500 m | 43 | 46.9 | 0.92 | |
| moves >500 m | 24 | 28.5 | 0.84 | |

Table 7. Continued.

| Variable | Observed Moves (O) | Expected* Moves (O) | Index (O/E) | Significance |
|---|---|---|---|---|
| Relative Habitat Quality | | | | |
| Primary | | | | |
| 0 moves | 94 | 89.7 | 1.05 | |
| moves 20–500 m | 26 | 22.0 | 1.18 | |
| moves >500 m | 4 | 12.3 | 0.33– | ** |
| Secondary | | | | |
| 0 moves | 81 | 85.3 | 0.95 | |
| moves 20–500 m | 17 | 21.0 | 0.81 | |
| moves >500 m | 20 | 11.7 | 1.71+ | ** |
| Relative Population Density | | | | |
| High | | | | |
| 0 moves | 42 | 44.0 | 0.95 | |
| moves 20–500 m | 15 | 12.2 | 1.23 | |
| moves >500 m | 1 | 1.9 | 0.53 | |
| Low | | | | |
| 0 moves | 52 | 50.0 | 1.04 | |
| moves 20–500 m | 11 | 13.8 | 0.80 | |
| moves >500 m | 3 | 2.1 | 1.43 | |
| Sex | | | | |
| Females | | | | |
| 0 moves | 67 | 69.4 | 0.97 | |
| moves 20–500 m | 20 | 17.1 | 1.17 | |
| moves >500 m | 9 | 9.5 | 0.95 | |
| Males | | | | |
| 0 moves | 108 | 105.6 | 1.02 | |
| moves 20–500 m | 23 | 25.9 | 0.89 | |
| moves >500 m | 15 | 14.5 | 1.03 | |
| Direction | | | | |
| Upstream | | | | |
| moves 20–500m | 24 | 22.0 | 1.09 | |
| move >500 m | 12 | 14.0 | 0.86 | |
| Downstream | | | | |
| moves 20–500 m | 14 | 16.0 | 0.88 | |
| moves >500 m | 12 | 10.0 | 1.20 | |

* Expected moves computed by multiplying the proportion of observed moves to total moves for that category (i.e. January–June) by the total moves for both categories (i.e. January–June and July–December).

The artificial disperser (Cache/Fish creeks study area) was eliminated from the remaining analyses of frequency of movement data because differences in disperser type could have biased results.

Monitored beavers in the study area identified as secondary habitat (Rattlesnake Creek) moved significantly greater distances more frequently than those in primary habitat (Meadow and Upper Willow creeks).

No significant differences were seen in the comparisons of relative population density, sex of disperser, and the direction of a move (Table 8). Comparisons by relative population density were made only within primary habitat (Meadow Creek/Upper Willow Creek) due to Cache/Fish creeks being dropped from the analysis. The Rattlesnake Creek study area was not included because of habitat differences.

Analysis of distance moved data indicated that the artificial dispersers (Cache/Fish creeks) moved the greatest distance between detected moves and were found further away from their release site than the natural dispersers (Table 9). The artificial dispersers were eliminated from the remaining analyses of distance moved data for the greatest distance and last location variables to eliminate any bias that might result from the differences seen between disperser types. A significant difference ($p < 0.035$) in mean distance travelled by female artificial and natural dispersers resulted in elimination of the artificial dispersers for the mean distance variable analysis by sex.

The mean distance travelled between detected moves was greatest for males and greater in the study areas considered of secondary habitat quality. Beavers in the high relative density study area (Upper Willow

Table 8. Distance moved data for transmitter-equipped beavers in western Montana. Distance moved is the distance moved between detected moves. Greatest distance is greatest detected distance from release site. Last location is distance from release site at last location of the year.

| Variable | Means | | df | t value | Significance |
|---|---|---|---|---|---|
| Time of Year | | | | | |
| | (Early/Late)** | | | | |
| Distance Moved | 1541.7 | 227.2 | 76 | 3.379 | 0.001 |
| Greatest Distance* | 3345.0 | 620.0 | 6 | 1.707 | 0.139 |
| Disperser Type | | | | | |
| | (Artificial/Natural) | | | | |
| Distance Moved | 1056.0 | 947.9 | 7 | -0.206 | 0.837 |
| Greatest Distance | 7960.1 | 1982.5 | 8 | 3.172 | 0.013 |
| Last Location | 4520.0 | 622.5 | 8 | -2.621 | 0.031 |
| Relative Habitat Quality | | | | | |
| | (Primary/Secondary) | | | | |
| Distance Moved | 320.0 | 1374.2 | 76 | 2.586 | 0.012 |
| Greatest Distance* | 1040.0 | 2925.0 | 6 | 1.055 | 0.332 |
| Last Location* | 575.0 | 670.0 | 6 | -0.153 | 0.883 |
| Relative Population Density | | | | | |
| | (Low/High) | | | | |
| Distance Moved | 774.1 | 1083.9 | 76 | 0.726 | 0.470 |
| Greatest Distance* | 1775.0 | 305.0 | 2 | 6.624 | 0.022 |
| Last Location* | 950.0 | 200.0 | 2 | 0.805 | 0.505 |
| Sex | | | | | |
| | (Male/Female) | | | | |
| Distance Moved* | 1361.9 | 395.9 | 61 | -2.049 | 0.045 |
| Greatest Distance* | 2550.0 | 1036.7 | 6 | -0.791 | 0.459 |
| Last Location* | 504.0 | 820.0 | 6 | -0.503 | 0.633 |
| Direction | | | | | |
| | (Upstream/Downstream) | | | | |
| Distance Moved | 834.0 | 1143.1 | 76 | 0.744 | 0.459 |
| Greatest Distance* | 2541.7 | 2542.0 | 9 | -0.0001 | 0.999 |
| Last Location* | 548.0 | 1120.0 | 5 | 0.792 | 0.464 |

* Artificial dispersers eliminated from the analysis.
** Early = January - June, late = July - December.

Creek) moved greater distances than those in the low density study area (Meadow Creek). No significant differences in the distance from the release site at the last location or in the distance travelled up or downstream (direction) were seen (Table 9).

DISCUSSION

The data analyses indicate that the majority of long distance movement by beavers takes place during the months of January to June, that beavers in lower quality habitat travel farther and make long moves more frequently than those in better quality habitat, that males travel greater distances than females, and that artificial dispersers will travel more frequently and to greater distances away from their site of release than will natural dispersers. The difference seen in the greatest distance travelled in the better quality habitat by a beaver from the higher density beaver population may not have been of great importance because the mean distances travelled in both low and high density populations were not significantly different.

Patterns seen here generally agree with the literature. Many authors have reported that dispersal activity takes place in the spring prior to the adult female's giving birth and coincides with spring thaw and high water (Bradt 1938, Cook 1943, Leege and Williams 1967, Svendson 1980, Hodgdon and Lancia 1983). Townsend (1953) reported late summer as a time of settling for potential dispersers. Little has been done to assess the affect of habitat quality on beaver dispersal. Gunson (1970) suggested that beavers in high quality habitat may delay dispersal. My data tend to support this contention because the greater amount of activity was seen in the lower quality habitats. This makes intuitive sense as one might expect an individual in a lower quality habitat to travel further and more often in order to locate suitable areas with better food and homesites. That males move more often and greater distances than females has been reported by Leege (1968) among others. Increased movement by transplanted beavers has been reported by Hibbard (1958), Berghofer (1961), and Leege (1968).

A number of confounding factors may have influenced the analysis and should be addressed. I originally planned to monitor an equal number of artificial and natural dispersers within each study area. However, realities of time, access, and trapping success limited the possibilities. Consequently, sample size and equal variance assumptions for the Student's t-test were not met in some instances. Where this was the case, I utilized the t' test statistic for unequal variances (Ott 1984). The lack of equal representation within each study area forced me to limit comparisons within and between study areas as mentioned in the results section. I feel that this limits the extent of the analysis and my results indicate possible patterns. Hopefully, these will be clarified with increased sample size as the project continues.

Particular attention should be given to the fact that no significant differences were seen in the final location of the year except for the differences seen between natural and artificial dispersers. This location could indicate actual dispersal as it represents the distance from the release site (original colony location for natural dispersers) a beaver was found at the last location of the year. Except for the 3 mortalities in Rattlesnake Creek, I assumed that this location represented where a beaver settled for the winter of 1988-89. The final location for these animals was recorded as the last known location prior to discovery of the mortality. Assuming that the last location of the year represents actual dispersal distances, then actual dispersal could only be determined for 7 of the 10 monitored beavers. The artificial dispersers (F204 & F405) represented obvious differences in dispersal distance. It is difficult to assess the significance of the distance moved by these beavers. Both artificial dispersers were released at an unoccupied colony site within 1 hour of each other. This site had been trapped out the previous fall to create an unoccupied site. No sign of recent beaver use was apparent at the time of release. Both released beavers moved through the unoccupied site without settling. The differences detected in the frequency and distance of movement for these beavers indicate that the distance of dispersal may have been the result of disorientation and insecurity from being released at an unfamiliar location.

One beaver (W305) in Upper Willow Creek showed a significant difference ($t = 12.7$, $p < 0.01$) in possible dispersal distance (distance from release site at last location of the season) when compared to the surviving natural dispersers. This beaver relocated approximately 1860 m upstream from its capture/release site. All other surviving potential natural dispersers were last located within 500 m of their release site. Reported beaver home ranges on streams have varied from 0.6 km (Bergerud and Miller 1977) to 2.2 km (Novakowski 1965) of stream length. Thus, I assumed that distances within 500 m of the home colony did not represent movement away from the colony and could not be considered dispersal.

W305's movement may not have actually represented dispersal. She was captured near an active colony almost 2 km away from her final location. The actual capture site was approximately 200 m from the only active lodge location in the area, making it unclear whether she was a member of this local colony or a passing potential disperser from another colony. Confounding the confusion is the fact that the site of her last location was an occupied colony from which 3 beavers, a female yearling, an adult male, and a lactating female adult, were captured. This suggests that W305 may have been an original member of this colony and that her capture near the first colony was coincidental during a exploratory movement away from her home colony. Similar exploratory movement away from the home colony was seen in Rattlesnake Creek by beavers R301, R715, and R618. This exploratory or predispersal movement has been suggested by Molini et al. (1980) as a means by which potential dispersers assess population density.

If in fact W305's movement did not represent dispersal, then dispersal by natural dispersers may not have been seen during this study. Although admittedly a small sample size, this contradicts reported time of dispersal in much of the literature. Bradt (1938), Cook (1943), Townsend (1953), Beer (1955), Aleksiuk (1968), Leege (1968), and Svendsen (1980) have reported that beavers dispersed at 2-years of age. Novakowski (1965), Bergerud and Miller (1977), Payne (1982), and Peterson and Payne (1986) have reported that beavers delayed dispersal 1 - 2 years under some conditions. Novakowski (1965) and

Nordstrom (1972) suggested that dispersal was delayed in high density populations and Molini et al. (1980) have produced a model of beaver population growth based on the probabilities of dispersal varying as a function of population density. The data presented here certainly support the contention that beaver delay dispersal under certain conditions. However, whether high density was a factor in delaying dispersal was not conclusively shown in this study.

A number of factors including date of capture, possible incorrect estimates of age, mortality of potential dispersers, lack of sufficient sample size, and classification error related to population densities may have influenced the lack of dispersal shown in this study.

Date of capture was a concern primarily in the Meadow and Upper Willow Creek areas during the spring trapping season because snow made access difficult. Monitored beaver in these study areas were not trapped until May and June. Captured beavers may already have been in the process of dispersing or have been on a predispersal exploratory movement and thus have been captured away from their home colony. This may have been the case with M101 and W305. W305 has already been discussed. M101 was the only beaver trapped in that particular colony site and was the only single capture of a potential disperser from any colony site. This suggests he may have been the only beaver in the colony, which in turn suggests he may have already dispersed and settled into the colony area where he was captured. Consequently, no dispersal could be documented. Continued monitoring through the final phase of the project should clarify M101's status as a potential disperser. Concentrating on yearlings in place of 2-year olds should eliminate this problem, however it would require an increased trapping effort the season before monitoring.

The possibility of incorrectly aging possible dispersers in this study was a major concern. An incorrect estimate of age could have resulted in the monitoring of either a pre- or postdispersal beaver with the end result of no dispersal seen in both instances. Appendix B presents a possible technique for refining the methods used for estimating age in live-trapped beavers and confirms the estimated ages for the potential dispersers used in this study. Recovery of transmitter equipped beavers 2 years after implantation (minimum transmitter battery life) during the remaining phase of this project would provide further verification of the reliability of age estimation. In addition, the 2-year life expectancy of transmitters provided a means by which potential dispersers incorrectly aged as older than they actually were (kits or yearlings aged as yearlings or 2-year-olds) could be monitored through their second or third year of life in the final phase of the project.

Three of the 4 potential dispersers in the Rattlesnake Creek study area were confirmed mortalities. Transmitters and some remains were recovered for each of these beaver - R301, R608, and R715. Although I cannot discount the possibility that these beavers may have been killed by some other means and then scavenged, evidence suggests that all three beavers died as a result of predation. Bear scat, hair, and the remains of probable bear kills at the site of transmitter and carcass recovery suggests that R608 and R715 may have been black bear kills. Black bears had been sighted in the area several times. Evidence at the site of

R301's last location prior to recovery of the transmitter and carcass suggests that a black bear may also have been responsible - tracks, hair, and trampled grass at the lodge site.

Black bears have generally been discounted as predators of beaver (Semyonoff 1951, Hakala 1952, Gunson 1970), although Novak (1987) cites information indicating occasional black bear predation on beavers, and scavenging by bears on beaver carcasses has been documented by Banfield (1954). The possibility that these beavers had died as a result of surgery and had been scavenged by black bears seems unlikely because all 3 beavers had shown movement after surgery. R301 and R608 were killed 8 months after surgery, while R715 was probably killed within 6 weeks of surgery. The amount of movement by R715 after surgery (Appendix A), however, indicates he was probably in good condition. The evidence in Rattlesnake Creek suggests that black bear predation may be a significant mortality factor, especially on dispersal-aged beavers. Continued trapping and survey efforts in Rattlesnake Creek by T. Van Deelen (pers. commun.) have indicated that a major decline in the beaver population may be occurring. This decline may be a result of concentrated bear predation within this drainage. Although we cannot rule out the possibility of increased trapping pressure, T. Van Deelen (pers. commun.) has been in touch with local trapper organizations that had no knowledge of trappers working the Rattlesnake Creek study area.

The limitations of sufficient sample size are obvious and have been addressed earlier. Continuation of the project and an increased trapping effort should provide an increased sample size sufficient for observations of actual dispersal and for meaningful statistical analysis.

The possibility of observer bias in the determination of relative population densities could have resulted in an apparent lack of dispersal if the study areas used did not reflect both low- and high-density populations. If beavers in high density populations delay dispersal 1 or 2 years as has been suggested, and if the study areas represented only high-density populations, no dispersal would have been detected. This was a possibility as what seemed a low density population to the observer may not have seemed the same to a beaver. I felt confident in my selection of low- and high-density populations (see Study Areas Pp. 9-10), and the percent trapping success (Table 3) for each drainage supported my classification.

The above discussion assumes that beaver have a mechanism for determining population density. Molini et al. (1980) suggested 2 mechanisms for assessment of population density: predispersal exploratory movements and a propensity to pass through resident colonies either during the dispersal process or the predispersal movement. Density would be assessed based on the intensity or number of scent-marking signals encountered. The data presented here tend to provide support for these mechanisms. Major movement was seen by 5 of the 8 natural dispersers and by 1 of the artificial dispersers, all of which had to pass through at least one active colony. R618 was located with R301 within a few hundred meters of the active lodge site for R301's natal colony. All surviving potential natural dispersers returned to the area of their natal colony (see above discussion for W305).

The lack of major movement seen in the Meadow Creek study area may have been an indication of differences in population densities although the only difference seen was in the greatest distance moved. The beavers in the lower density population (Upper Willow Creek) made longer moves than those in the higher density population. However, this difference reflects only 3 moves by the 2 beaver in Upper Willow Creek. If representative of density differences, then the Meadow Creek beavers may represent a return to the natal colony upon encountering a neighboring colony site. Another possibility, however, may have been the lack of cover along much of the lower reaches of Meadow Creek. Annual grazing along the lower reaches of Meadow Creek has resulted in the loss of much of the stream-side vegetation. This lack of vegetative cover did not occur to the same extent in the other study areas. Upon encountering this area of no cover, potential dispersers may have returned to their natal colonies.

Of additional importance in this study was the taking of a marked female in November 1988 by a trapper in Rock Creek near its confluence with the Clark Fork River. This individual (W204) was an adult female originally captured near the upper end of Upper Willow Creek. This represents a move of at least 80 km. Analysis of tooth development, basal closure of the mandibular molars and examination of the reproductive tract indicated she was a 3-year old who had given birth to 3 kits that spring (K. Foresman, pers. commun.). This individual was trapped 15 May 1988, was considered to be in poor physical condition, and was not lactating at the time. A movement of 51.5 km by a transplanted beaver was documented by Berghofer (1961) and Libby (1957) reported a movement of greater than 242 km by a 2-year old male. This movement is of interest as it obviously does not represent a normal dispersal and may have been the result of predation of the other colony members and/or destruction of the original lodgesite (actual lodgesite was never located for this individual).

If the amount of exploratory activity by potential dispersers is indicative of predispersal movement, then the results of this study support the contention that dispersal is an innate tendency of subadult beavers. Environmental factors probably play a role in determining the age of a beaver at dispersal.

## MANAGEMENT RECOMMENDATIONS

If the data presented here are representative of movement and dispersal patterns of beavers, then the possible implications on beaver management are as follows. The amount of movement seen after the release of artificial dispersers in new areas indicates that subadult or dispersal-aged beavers may not be useful for artificial reintroduction of beavers into relatively small uninhabited areas. I suspect that reproducing adult beaver pairs would be most useful for artificial reintroduction, although I do not have data to support this.

If beavers delay dispersal in high density populations, then trapping regulations could be designed to manipulate population densities and control movement within or between areas of suitable beaver habitat by trapping 1 or 2 individuals within a colony to maintain the current situation; to encourage dispersal by trapping a high proportion of beavers within each colony to decrease population density; or to discourage dispersal by eliminating trapping for a set period of time to increase population density.

Determination of dispersal rates among beaver populations is of importance to the wildlife manager in order to acquire an understanding of beaver population dynamics. A beavers' ability to disperse provides a means by which uninhabited areas may be occupied. This is of primary importance when dispersing beavers move into an area where they may become a nuisance, when a population has been decimated due to overtrapping, or when an area may benefit from the damming activities of beavers. Continued monitoring of radio-equipped individuals and the trapping of new individuals for monitoring to increase the sample size for the remaining phase of this project should provide verification of the trends seen in this study.

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# APPENDIX A

## SUMMARY OF MOVEMENT DATA
## FOR INDIVIDUAL TRANSMITTER-EQUIPPED
## BEAVERS

Intraperitoneal transmitter implant surgery was performed on 15 juvenile (1 to 2-years of age) beavers during the 1987 and 1988 field seasons. One of these 15 beavers, R405 died of an internal obstruction the night following surgery. Another (W106) was found dead the week after release - cause of death was assumed to be stress related to surgery, 3 days in captivity, and relocation into Cache Creek from Upper Willow Creek. F405, a female trapped in Fish Creek and relocated to Cache Creek, was lost due to receiver malfunction. This animal was later relocated upstream from the release site during spring, 1989 (T. Van Deelen, pers. commun.). Three of the remaining 12 beavers, 2 from Meadow Creek and 1 from Upper Willow Creek, were not captured until fall, 1988 and consequently were not monitored for dispersal until spring, 1989. The remaining 9 beavers were monitored extensively to determine if dispersal would take place. Table A1 indicates each monitored beavers' history of detected moves. A detected move is defined as a minimum 20m distance away from the previous radio-location. Data are presented for each month the beaver was monitored, the number of locations, the number of detected moves >20m, the number of detected moves >0.5km, the sum of all detected moves, and the greatest distance each beaver was located away from their release site.

Table A1. Summary of movement history for 9 radio transmitter-equipped beavers in western Montana, 1987 - 1988.

| | | |
|---|---|---|
| ID# | - | M101 |
| SEX | - | MALE |
| CAPTURE DATE | - | 6/7/88 |
| CAPTURE LOCATION | - | MEADOW CREEK |
| SURGERY DATE | - | 6/7/88 |
| RELEASE DATE | - | 6/8/88 |
| RELEASE LOCATION | - | MEADOW CREEK |

| MONTH | # OF RADIO LOCATIONS | # OF MOVES >20M | # OF MOVES >.5KM | SUM OF CONSECUTIVE MOVES | DISTANCE - DIRECTION FROM RELEASE SITE* |
|---|---|---|---|---|---|
| JUNE | 10 | 3 | 0 | 960m | 200m - up |
| JULY | 11 | 3 | 1 | 890m | 310m - dn |
| AUGUST | 5 | 2 | 0 | 710m | 480m - up |
| SEPT | 1 | 0 | 0 | 0 | 0 |
| OCT | 1 | 1 | 0 | 80m | 400m - up |

* Refers to greatest distance away from release site; final entry in column is distance from release site at last location of year.

Movement History:

| | |
|---|---|
| 6-20-88 | 200m upstream |
| 6-21-88 | 380m downstream |
| 6-27-88 | 380m upstream |
| 7-05-88 | 510m downstream |
| 7-06-88 | 330m upstream |
| 7-20-88 | 50m downstream |
| 8-03-88 | 230m upstream |
| 8-10-88 | 480m upstream |
| 10-06-88 | 80m downstream |

Table A1. Continued.

ID# - M306
SEX - MALE
CAPTURE DATE - 5/30/88
CAPTURE LOCATION - MEADOW CREEK
SURGERY DATE - 6/1/88
RELEASE DATE - 6/1/88
RELEASE LOCATION - MEADOW CREEK

| MONTH | # OF RADIO LOCATIONS | # OF MOVES >20M | # OF MOVES >.5KM | SUM OF CONSECUTIVE MOVES | DISTANCE - DIRECTION FROM RELEASE SITE* |
|---|---|---|---|---|---|
| JUNE | 12 | 2 | 0 | 100m | 50m - dn |
| JULY | 11 | 1 | 0 | 25m | 25m - dn |
| AUGUST | 5 | 2 | 0 | 125m | 100m - dn |
| SEPT | 1 | 1 | 0 | 50m | 50m - dn |
| OCT | 1 | 1 | 0 | 50m | 0 |

* Refers to greatest distance away from release site; final entry in column is distance from release site at last location of year.

Movement History:

| | |
|---|---|
| 6-23-88 | 50m downstream |
| 6-28-88 | 50m upstream |
| 7-26-88 | 25m downstream |
| 8-10-88 | 25m upstream |
| 8-31-88 | 100m downstream |
| 9-09-88 | 50m upstream |
| 10-06-88 | 50m upstream |

Table A1. Continued.

ID# - W103
SEX - MALE
CAPTURE DATE - 5/12/88
CAPTURE LOCATION - UPPER WILLOW CREEK
SURGERY DATE - 5/13/88
RELEASE DATE - 5/13/88
RELEASE LOCATION - UPPER WILLOW CREEK

| MONTH | # OF RADIO LOCATIONS | # OF MOVES >20M | # OF MOVES >.5KM | SUM OF CONSECUTIVE MOVES | DISTANCE - DIRECTION FROM RELEASE SITE* |
|---|---|---|---|---|---|
| MAY | 6 | 0 | 0 | 0 | 0 |
| JUNE | 7 | 0 | 0 | 0 | 0 |
| JULY | 10 | 1 | 0 | 50m | 50m - up |
| AUGUST | 4 | 2 | 2 | 3.39km | 1.6km - up |
| SEPT | 2 | 0 | 0 | 0 | 40 - up |
| OCT | 5 | 0 | 0 | 0 | 40 - up |

* Refers to greatest distance away from release site; final entry in column is distance from release site at last location of year.

Movement History:

| | |
|---|---|
| 7-08-88 | 50m upstream |
| 8-11-88 | 1650m upstream |
| 8-18-88 | 1690m downstream |

Table A1. Continued.

| | | |
|---|---|---|
| ID# | - | W305 |
| SEX | - | FEMALE |
| CAPTURE DATE | - | 5/16/88 |
| CAPTURE LOCATION | - | UPPER WILLOW CREEK |
| SURGERY DATE | - | 5/18/88 |
| RELEASE DATE | - | 5/18/88 |
| RELEASE LOCATION | - | UPPER WILLOW CREEK |

| MONTH | # OF RADIO LOCATIONS | # OF MOVES >20M | # OF MOVES >.5KM | SUM OF CONSECUTIVE MOVES | DISTANCE - DIRECTION FROM RELEASE SITE* |
|---|---|---|---|---|---|
| MAY | 4 | 1 | 1 | 1.86km | 1.86km - up |
| JUNE | 7 | 1 | 0 | 125m | 1.985km - up |
| JULY | 10 | 2 | 0 | 245m | 2.045km - up |
| AUGUST | 4 | 1 | 0 | 185m | 2.045km - up |
| SEPT | 2 | 1 | 0 | 185m | 1.86km - up |
| OCT | 5 | 5 | 0 | 620m | 1.985km - up<br>1.86km - up |

* Refers to greatest distance away from release site; final entry in column is distance from release site at last location of year.

Movement History:

| | |
|---|---|
| 5-29-88 | 1860m upstream |
| 6-29-88 | 125m upstream |
| 7-08-88 | 60m upstream |
| 7-11-88 | 185m downstream |
| 8-18-88 | 185m upstream |
| 9-09-88 | 185m downstream |
| 10-06-88 | 185m upstream |
| 10-12-88 | 60m downstream |
| 10-17-88 | 125m downstream |
| 10-25-88 | 125m upstream |
| 10-26-88 | 125m downstream |

Table A1. Continued.

| | | |
|---|---|---|
| ID# | - | R301 |
| SEX | - | FEMALE |
| CAPTURE DATE | - | 10/20/87 |
| CAPTURE LOCATION | - | RATTLESNAKE CREEK |
| SURGERY DATE | - | 10/22/87 |
| RELEASE DATE | - | 10/23/87 |
| RELEASE LOCATION | - | RATTLESNAKE CREEK |

| MONTH | # OF RADIO LOCATIONS | # OF MOVES >20M | # OF MOVES >.5KM | SUM OF CONSECUTIVE MOVES | DISTANCE - DIRECTION FROM RELEASE SITE* |
|---|---|---|---|---|---|
| NOV | 4 | 1 | 0 | 180m | 180m - up |
| APRIL | 15 | 3 | 2 | 1.68km | 580m - dn |
| MAY | 7 | 4 | 4 | 3.53km | 890m - up |
| JUNE | 4 | 2 | 2 | 1.5km | 890m - up |
| JULY** | 4 | 0 | 0 | 0 | 260m - dn<br>440m - dn |

* Refers to greatest distance away from release site; final entry in column is distance from release site at last location of year.
** Found dead 7/27/88. Possible bear predation.

Movement History:

| | |
|---|---|
| 11-02-87 | 180m upstream |
| 4-25-88 | 80m upstream |
| 4-26-88 | 840m downstream |
| 4-29-88 | 760m upstream |
| 5-11-88 | 760m downstream (with R618) |
| 5-16-88 | 1070m upstream |
| 5-20-88 | 1000m downstream |
| 5-31-88 | 700m upstream |
| 6-06-88 | 710m upstream |
| 6-13-88 | 790m downstream |

Table A1. Continued.

| | | |
|---|---|---|
| ID# | - | R608 |
| SEX | - | FEMALE |
| CAPTURE DATE | - | 10/27/87 |
| CAPTURE LOCATION | - | RATTLESNAKE CREEK |
| SURGERY DATE | - | 10/29/87 |
| RELEASE DATE | - | 10/29/87 |
| RELEASE LOCATION | - | RATTLESNAKE CREEK |

| MONTH | # OF RADIO LOCATIONS | # OF MOVES >20M | # OF MOVES >.5KM | SUM OF CONSECUTIVE MOVES | DISTANCE - DIRECTION FROM RELEASE SITE* |
|---|---|---|---|---|---|
| NOV | 4 | 1 | 0 | 180m | 180m - up |
| MARCH | 1 | 1 | 0 | 160 | 340m - up |
| APRIL | 15 | 4 | 0 | 240m | 340m - up |
| MAY | 7 | 2 | ? | ? | ? - up |
| JUNE** | 3 | 0 | 0 | 0 | 340m - up<br>620m - up |

* Refers to greatest distance away from release site; final entry in column is distance from release site at last location of year.
? Unable to establish exact location 5/25/88.
** Found dead 6/22/88. Probable bear predation.

Movement History:

| | |
|---|---|
| 11-02-88 | 180m upstream |
| 3-23-88 | 160m upstream |
| 4-04-88 | unable to locate |
| 4-19-88 | 80m downstream |
| 4-20-88 | 80m upstream |
| 4-25-88 | 40m downstream |
| 4-26-88 | 40m upstream |
| 5-25-88 | unable to locate |

Table A1. Continued.

| | | |
|---|---|---|
| ID# | - | R715 |
| SEX | - | MALE |
| CAPTURE DATE | - | 4/5/88 |
| CAPTURE LOCATION | - | RATTLESNAKE CREEK |
| SURGERY DATE | - | 4/6/88 |
| RELEASE DATE | - | 4/7/88 |
| RELEASE LOCATION | - | RATTLESNAKE CREEK |

| MONTH | # OF RADIO LOCATIONS | # OF MOVES >20M | # OF MOVES >.5KM | SUM OF CONSECUTIVE MOVES | DISTANCE - DIRECTION FROM RELEASE SITE* |
|---|---|---|---|---|---|
| APRIL | 13 | 8 | 8 | 11.02km | 1.98km - dn |
| MAY | 7 | 0 | 0 | 0 | 1.98km - dn |
| JUNE** | 1 | 0 | 0 | 0 | 1.98km - dn<br>2.06km - dn |

* Refers to greatest distance away from release site; final entry in column is distance from release site at last location of year.
** Found dead 6/6/88. Probable bear predation.

Movement History:

| | |
|---|---|
| 4-11-88 | 720m downstream |
| 4-19-88 | 720m upstream |
| 4-20-88 | 550m upstream |
| 4-21-88 | 1270m downstream |
| 4-22-88 | 720m upstream |
| 4-25-88 | 1980m downstream |
| 4-26-88 | 2530m upstream |
| 4-27-88 | 2530m downstream |

Table A1. Continued.

| | | |
|---|---|---|
| ID# | - | R618 |
| SEX | - | MALE |
| CAPTURE DATE | - | 4/12/88 |
| CAPTURE LOCATION | - | RATTLESNAKE CREEK |
| SURGERY DATE | - | 4/13/88 |
| RELEASE DATE | - | 4/14/88 |
| RELEASE LOCATION | - | RATTLESNAKE CREEK |

| MONTH | # OF RADIO LOCATIONS | # OF MOVES >20M | # OF MOVES >.5KM | SUM OF CONSECUTIVE MOVES | DISTANCE - DIRECTION FROM RELEASE SITE* |
|---|---|---|---|---|---|
| APRIL | 9 | 5 | ? | 260m? | 100m - up? |
| MAY | 7 | 3 | 3 | 23.32km | 7.82km - dn |
| JUNE | 4 | 2 | 1? | 7.92km? | 100m - up? |
| JULY | 4 | 0 | 0 | 0 | 100m - up |
| AUGUST | 5 | 1 | 0 | 30m | 130m - up |
| SEPT | 2 | 0 | 0 | 0 | 130m - up |
| OCT | 2 | 0 | 0 | 0 | 130m - up |

* Refers to greatest distance away from release site; final entry in column is distance from release site at last location of year.
? Unable to establish exact locations 4/27/88 and 6/13/88.

Movement History:

| | |
|---|---|
| 4-15-88 | 100m upstream |
| 4-19-88 | 100m downstream |
| 4-20-88 | 80m upstream |
| 4-27-88 | unable to locate |
| 5-11-88 | 7700m downstream (with R301) |
| 5-16-88 | 7700m upstream |
| 5-31-88 | 7920m downstream |
| 6-13-88 | unable to locate |
| 6-22-88 | 7920m upstream |
| 8-02-88 | 50m upstream |
| 8-16-88 | 60m downstream |

Table A1. Continued.

| | | |
|---|---|---|
| ID# | - | F204 |
| SEX | - | FEMALE |
| CAPTURE DATE | - | 5/8/88 |
| CAPTURE LOCATION | - | FISH CREEK |
| SURGERY DATE | - | 5/9/88 |
| RELEASE DATE | - | 5/10/88 |
| RELEASE LOCATION | - | CACHE CREEK |

| MONTH | # OF RADIO LOCATIONS | # OF MOVES >20M | # OF MOVES >.5KM | SUM OF CONSECUTIVE MOVES | DISTANCE - DIRECTION FROM RELEASE SITE* |
|---|---|---|---|---|---|
| MAY | 4 | 4 | 3 | 9.21km | 7.86km - up@ |
| JUNE | 4 | 4 | 4 | 5.93km | 7.86km - up |
| JULY | 4 | 2 | 0 | 200m | 7.96km - up |
| AUGUST | 5 | 4 | 0 | 400m | 7.96km - up |
| SEPT | 2 | 0 | 0 | 0 | 7.86km - up |
| OCT | 2 | 1 | 0 | 100m | 7.96km - up |

* Refers to greatest distance away from release site; final entry in column is distance from release site at last location of year.
@ Moved downstream to mouth of Cache Creek, then upstream on Fish Creek.

Movement History:

| | |
|---|---|
| 5-17-88 | 5500m downstream (to Fish Creek) |
| 5-19-88 | 140m upstream (Fish Creek) |
| 5-25-88 | 2220m upstream |
| 5-31-88 | 1350m downstream |
| 6-05-88 | 1010m downstream |
| 6-13-88 | 2220m upstream |
| 6-23-88 | 1350m downstream |
| 6-27-88 | 1350m upstream |
| 7-12-88 | 100m upstream |
| 7-20-88 | 100m downstream |
| 8-01-88 | 100m upstream |
| 8-08-88 | 100m downstream |
| 8-15-88 | 100m upstream |
| 8-22-88 | 100m downstream |
| 10-31-88 | 100m upstream |

APPENDIX B

A DISCRIMINANT FUNCTION MODEL

FOR ESTIMATING

AGE OF LIVE BEAVERS

A reliable means of estimating age of live trapped beavers was a major concern in this study. Proper classification of yearlings and 2-year olds was critical for determining which animals received transmitters. An incorrect estimate of age could have resulted in the erroneous monitoring of a beaver too old or too young to disperse.

Kits are relatively simple to age by tooth development, as they retain a rooted premolar until almost a year of age. The degree of basal closure in the 1st mandibular molar can be used to age yearlings through 3-year olds, and 3-year olds and older can be aged by cementum layers of molars (a cementum layer is added each year beginning the third year). These aging techniques, as well as many other methods sugested by various authors for beaver, are generally not suitable as they require the removal of a mandibular molar and/or the beaver carcass (Cook and Maunton 1954, Williamson 1959, Patric and Webb 1960, Van Nostrand and Stephenson 1964, Larson and Von Nostrand 1968). Removal of the mandibular molar was a technique I chose not to use, primarily because of the additional stress this would place on the captured beaver and because the literature was unclear as to whether a molar could be removed from a live beaver. I did not feel that additional stress was adviseable, particularly if the animal was to be held for surgical implantation of the radio-transmitter.

I used presence or absence of a rooted premolar for kits and relative morphological measurements (Table B1) to estimate the ages of the beavers captured during this study (Table B2). Beavers were classified as kits (0-11 months), yearlings (12-23 months), 2-year olds (23-35 months), and 3-year olds and older (36 months and older). Means

Table B1. Morphological variable names and measurement description. All measurements taken by metric or common measure tape except where noted.

| Variable name | Measurement description |
|---|---|
| WT | Weight in kilograms: measured with a spring scale |
| LTH | Total body length in cm: measured from tip of nose over the back to tip of the tail |
| TL | Tail length in cm: measured from base of tail at fur line to tip of tail |
| TW | Tail width in cm: measured at point of greatest width |
| TTH | Tail thickness in cm: measured with a calipers at thickest portion of base of tail |
| HC | Head circumference in cm: measured just anterior to ears |
| NC | Neck circumference in cm: measured immediately behind lower mandible |
| CC | Chest circumference in cm: measured immediately behind forelegs |
| ZYG | Zygomatic breadth in cm: measured with a calipers at widest distance between zygomatic arches dorsally across the skull |
| RHPL | Length of right-hind footpad in cm: measured at longest point of base of foot between 2nd and 3rd digits |
| RHPW | Width of right-hind footpad in cm: measured at widest point of base of foot just behind digits |

Table B2. Estimated age classes of live-trapped beavers by study area and sex. Kit = 0-11 months, 1-year = 12-23 months, 2-years = 24-35 months, 3-years+ = 36 months and older.

| Study Area | n M/F | Age Class Kit M/F | 1-year M/F | 2-years M/F | 3-years+ M/F |
|---|---|---|---|---|---|
| Cache/Fish creeks | 8/6 | 3/0 | 2/1 | 0/3 | 3/2 |
| Rattlesnake Creek | 15/11 | 4/1 | 1/3 | 2/2 | 8/5 |
| Meadow Creek | 9/6 | 2/2 | 2/1 | 2/0 | 3/3 |
| Upper Willow Creek | 3/4 | 0/0 | 0/1 | 2/1 | 1/2 |
| Total | 35/27* | 9/3 | 5/6 | 6/6 | 15/12 |

* includes male from Meadow Creek captured in spring and fall, 1988.

and standard deviations of each morphological measurement for each age class estimate were examined (Table B3) to provide a measure of which variables provided the greatest difference in mean measurement. Pearson's correlation coefficents were then run on the measurements. High correlations were indicated between all variables except RHPW. Histograms of each variable provided an indication of the distribution of measurements for each variable and provided a preliminary means for assessing possible groupings within variables.

Variables were then plotted against each other by age class. These plots illustrated the correlations between variables and clarified age groupings and the amount of overlap between groupings that were only hinted at in the histograms. Assuming that my estimates of age class were correct, I might expect that those variables showing the least amount of overlap between age groupings were suitable indicators of age in live beavers. The variables WT, LTH, and TW showed the least amount of overlap for all estimated age classes (Figs. B1 & B2). LTH ($r$ = 0.94) and TW ($r$ = 0.95) were highly correlated to WT. The only higher correlation seen was between HC and NC ($r$ = 0.96). This analysis was based on my estimation of age classes. Incorrect age estimation and observer bias could invalidate the procedure. A means of validating through the use of known-age animals would have increased the effectiveness of estimating the age of live beavers.

The morphological measurements of 13 beavers, mortalities during the course of the study and aged using the tooth development and basal closure methods, were used to generate a discriminant function

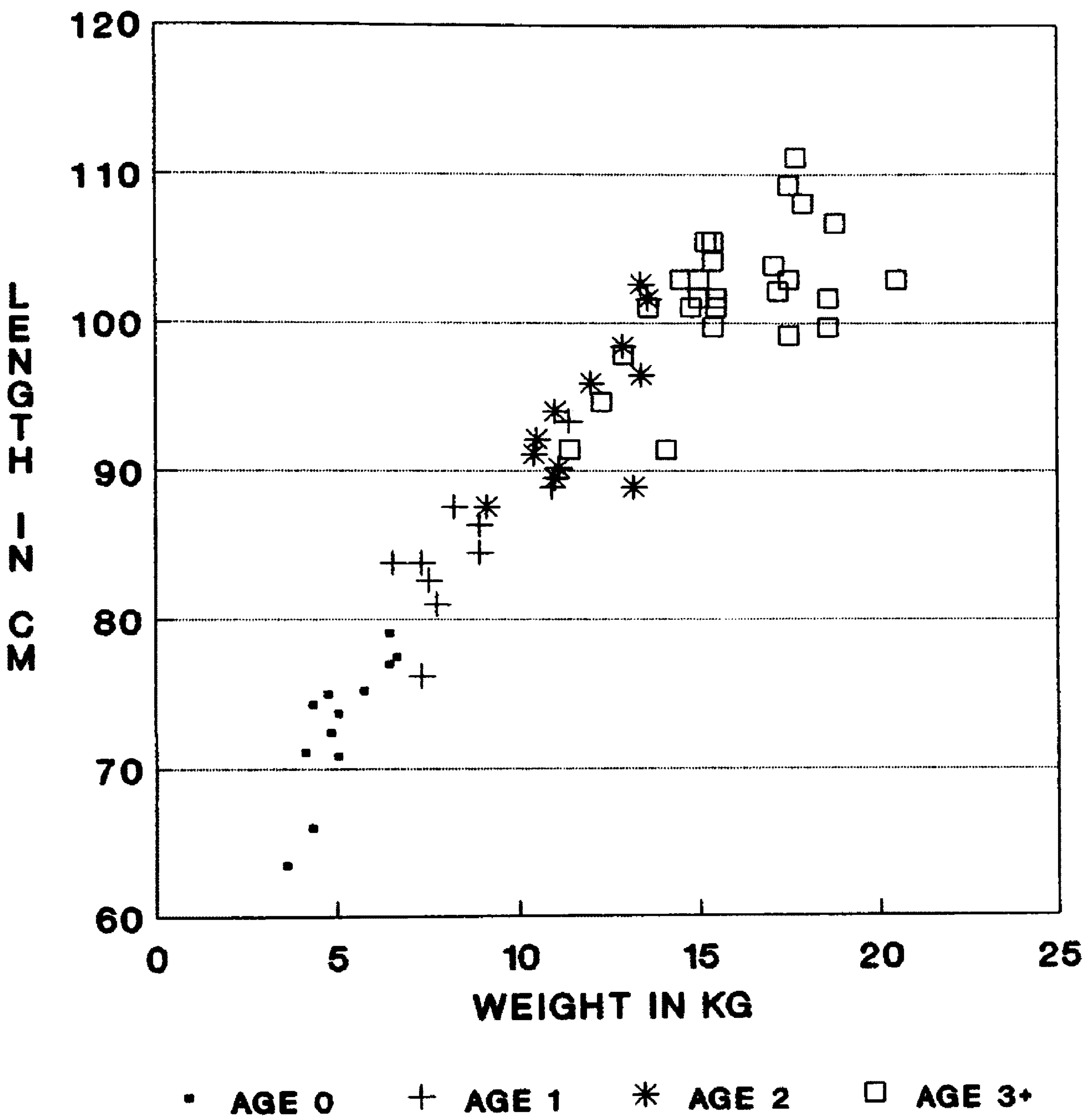


Fig. B1. Plot of body length with weight by estimated age of captured beavers in western Montana. Age estimated at time of capture.

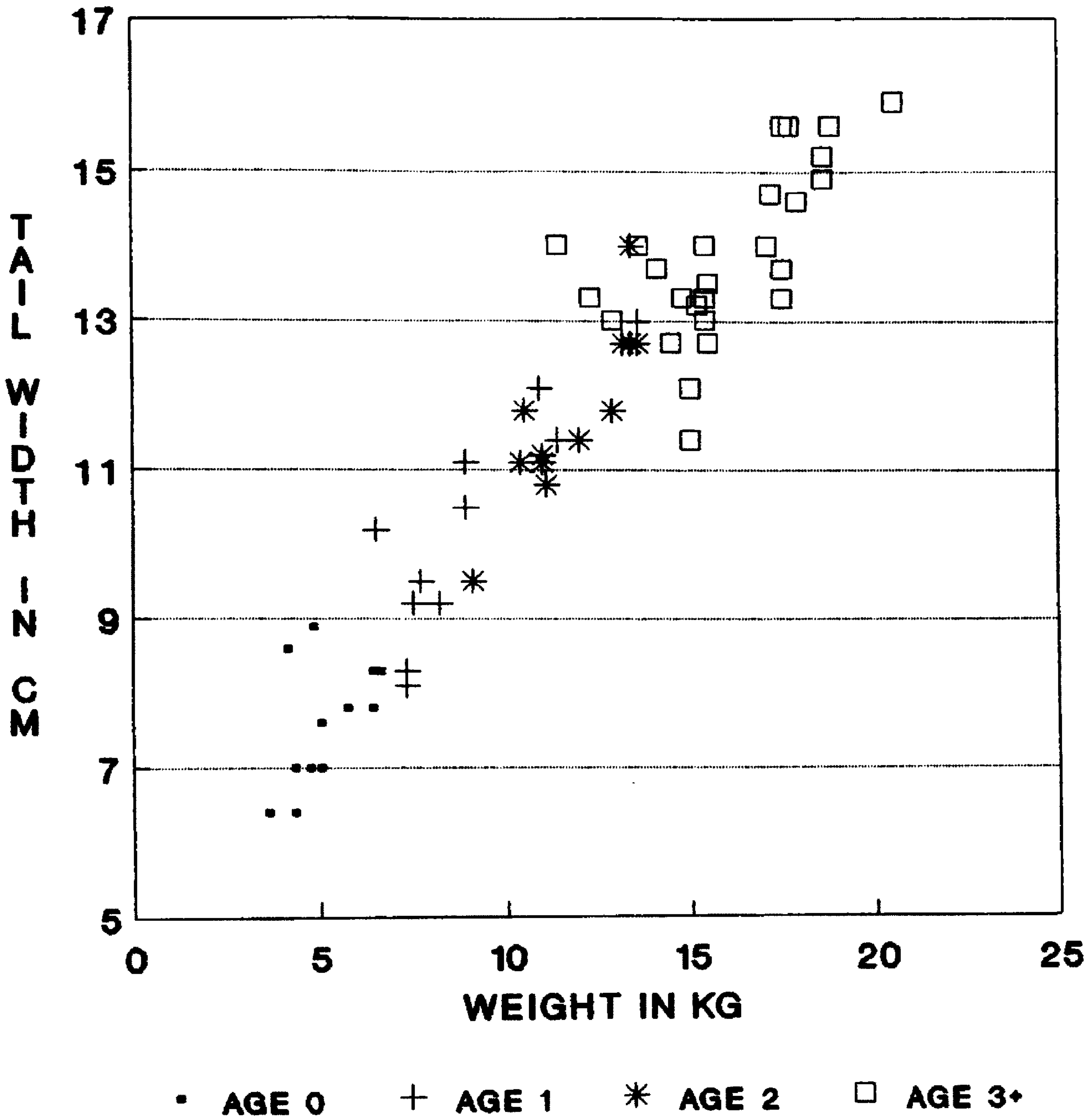


Fig. B2. Plot of tail width with weight by estimated age of captured beavers in western Montana. Age estimated at time of capture.

Table B3. Mean/standard deviation of morphological measurements by estimated age and location. M = Meadow Creek, R = Rattlesnake Creek, F = Cache/Fish Creeks, W = Upper Willow Creek. Values for n identical except where noted.

| Var. | Age | n | M | n | R | n | F | n | W |
|---|---|---|---|---|---|---|---|---|---|
| WT | 0 | 4 | 4.90/0.58 | 5 | 5.66/1.14 | 3 | 4.48/0.67 | 0 | n/c* |
| | 1 | 3 | 7.10/0.30 | 4 | 9.00/1.15 | 3 | 10.64/1.91 | 1 | 9.23/1.11 |
| | 2 | 2 | 12.60/0.85 | 4 | 11.48/2.00 | 3 | 12.47/1.21 | 3 | 10.17/0.97 |
| | 3+ | 6 | 16.88/2.68 | 13 | 15.93/2.26 | 5 | 16.62/1.24 | 3 | 14.67/0.95 |
| LTH | 0 | | 72.07/5.26 | | 75.42/3.47 | | 70.58/4.96 | | n/c |
| | 1 | | 83.40/0.69 | | 86.00/4.64 | | 90.04/8.25 | | 88.77/2.02 |
| | 2 | | 92.40/4.95 | | 92.84/6.55 | | 97.07/6.31 | | 90.90/3.20 |
| | 3+ | | 100.23/4.51 | | 101.70/5.56 | 4 | 105.65/1.74 | | 102.23/1.64 |
| TL | 0 | | 19.07/0.58 | | 20.52/1.64 | | 19.60/1.26 | | n/c |
| | 1 | | 21.13/0.57 | | 23.78/0.76 | | 5.52/2.80 | | 24.13/2.25 |
| | 2 | | 27.30/0.00 | | 25.40/1.65 | | 25.00/1.75 | | 25.30/1.85 |
| | 3+ | | 27.67/1.44 | | 27.58/1.08 | | 26.84/0.88 | | 27.93/0.65 |
| TW | 0 | | 7.27/0.46 | | 8.38/0.41 | | 6.85/0.57 | | n/c |
| | 1 | | 9.17/1.05 | | 10.73/0.97 | | 10.92/1.50 | | 9.93/1.02 |
| | 2 | | 12.05/0.92 | | 12.16/1.29 | | 11.77/0.95 | | 10.57/0.92 |
| | 3+ | | 14.08/1.50 | | 14.11/1.02 | | 13.76/0.57 | | 12.80/1.31 |
| TTH | 0 | | 2.10/0.12 | | 2.84/0.44 | | 2.16/0.40 | | n/c |
| | 1 | | 2.67/0.29 | 3 | 3.22/0.39 | | 2.67/0.28 | | 2.98/0.11 |
| | 2 | | 3.07/0.38 | 3 | 2.98/0.06 | | 3.00/0.20 | | 2.85/0.12 |
| | 3+ | | 3.13/0.18 | 11 | 3.69/0.52 | | 3.92/0.41 | | 3.52/0.51 |
| HC | 0 | | 25.40/1.30 | | 25.58/1.09 | | 25.00/1.37 | | n/c |
| | 1 | | 28.17/0.23 | | 29.58/0.92 | | 29.86/2.73 | | 28.97/3.27 |
| | 2 | | 30.80/2.26 | | 32.10/3.36 | | 33.77/1.65 | | 30.70/1.93 |
| | 3+ | | 34.20/3.03 | | 34.87/2.77 | | 35.12/2.65 | | 32.80/2.21 |
| NC | 0 | | 24.00/1.91 | | 23.80/2.00 | | 22.43/0.90 | | n/c |
| | 1 | | 26.70/0.00 | 3 | 29.50/0.42 | | 31.00/2.59 | | 29.63/5.06 |
| | 2 | | 33.05/0.91 | 3 | 33.57/5.47 | | 34.43/0.51 | | 31.97/2.85 |
| | 3+ | | 33.88/2.79 | 12 | 36.21/3.35 | | 37.02/2.31 | | 34.10/2.52 |
| CC | 0 | | 35.25/6.72 | | 34.56/2.82 | 2 | 29.08/4.21 | | n/c |
| | 1 | | 38.73/1.64 | | 44.75/1.12 | | 42.28/2.98 | | 43.10/6.02 |
| | 2 | | 44.75/3.18 | | 49.52/4.86 | | 47.23/2.65 | | 47.67/2.90 |
| | 3+ | | 52.60/5.54 | | 51.04/7.49 | | 53.96/3.09 | | 49.53/6.73 |

Table B3. Continued

| | | | | | | |
|---|---|---|---|---|---|---|
| ZYG | 0 | 7.16/0.08 | 7.58/0.59 | 2 | 7.29/0.30 | n/c |
| | 1 | 8.07/0.28 | 9.28/0.91 | | 8.79/0.61 | 8.87/0.44 |
| | 2 | 9.16/0.00 | 9.35/0.98 | 2 | 9.37/0.00 | 8.75/0.55 |
| | 3+ | 9.92/0.49 | 10.29/1.23 | | 10.31/0.27 | 9.31/0.67 |
| RHPL | 0 | 12.63/0.12 | 13.76/0.81 | | 12.30/0.62 | n/c |
| | 1 | 14.73/0.81 | 15.38/0.43 | | 15.36/0.55 | 15.37/0.68 |
| | 2 | 15.90/0.00 | 15.74/0.74 | | 15.87/1.25 | 15.80/0.17 |
| | 3+ | 6.93/0.63 | 16.97/0.99 | | 16.44/0.49 | 17.23/0.23 |
| RHPW | 0 | 4.40/0.40 | 4.18/0.52 | | 5.30/0.62 | n/c |
| | 1 | 4.80/0.52 | 5.15/1.25 | | 6.88/0.27 | 6.07/1.14 |
| | 2 | 7.30/0.42 | 5.28/0.73 | | 5.53/0.57 | 6.70/0.30 |
| | 3+ | 7.25/0.87 | 5.76/0.80 | | 5.64/0.25 | 6.70/1.77 |

* n/c – no captures

model. Stepwise discriminant function analysis was used to determine the optimal separation of age groups based on linear transformations of the morphological variables. Variables were included in the stepwise analysis based on the criteria of minimizing the sum of unexplained variation between groups. A variable was considered for entry into the model if the probability of its partial multivariate F-ratio was less than or equal to 0.05.

The variables WT and TW were selected for inclusion within the analysis. Two discriminant functions were derived that represent the largest and the next largest ratio of between-groups to within-groups sums of squares. These functions were used as multipliers of the selected variables to determine a discriminant score from which an assignment of age can be determined. The model generated takes the form:

Function 1

$$1.672(WT)-1.644(TW)-.025 = \text{Discriminant Score 1}$$

Function 2

$$-1.342(WT)+2.756(TW)-16.394 = \text{Discriminant Score 2}$$

Mean scores generated for each function and age group are as follows:

| Age group | Function 1 | Function 2 |
|---|---|---|
| Kit | -3.495 | -2.975 |
| Yearling | -2.263 | 0.921 |
| 2-year old | 1.308 | -0.580 |
| 3-year old | -0.301 | 3.944 |
| 4-year old + | 5.329 | -0.480 |

The group means were used as a basis for assigning beavers captured during this study but not included within the analysis to an age class based on their discriminant scores (Table B4). Assigned age

Table B4. Classification of beaver into age classes by study area and sex from discriminant function analysis. Kits = 0-11 months, 1-year = 12-23 months, 2-years = 24-35 months, 3-years = 36-47 months, 4-years+ = 48 months and older.

| Study Area | n M/F | Kit M/F | Age Class 1-year M/F | 2-years M/F | 3-years M/F | 4-years+ M/F |
|---|---|---|---|---|---|---|
| Cache/Fish creeks | 8/6 | 3/1 | 2/0 | 0/3 | 0/0 | 3/2 |
| Rattlesnake Creek | 15/11 | 2/1 | 5/2 | 2/2 | 3/2 | 3/4 |
| Meadow Creek | 9/6 | 3/2 | 0/1 | 3/0 | 1/0 | 2/3 |
| Upper Willow Creek | 3/4 | 0/1 | 1/0 | 1/1 | 0/1 | 1/1 |
| Total | 35/27* | 8/5 | 8/3 | 6/6 | 4/3 | 9/10 |

* includes male from Meadow Creek captured both spring and fall, 1988.

classes were then plotted by tail width and weight (Fig. B3) to illustrate the amount of overlap between age classes and as a means for comparison to those age classes estimated at capture (Fig. B2)

Twelve of 62 beavers were assigned age groups by the discriminant function model different from the ages I estimated at capture for them in this study. Two kits were classified as yearlings; 5 yearlings were classified as 3 kits and 2 2-year olds; 4 2-year olds were classified as 3 yearlings and 1 3-year old; and 1 3-year old was classified as a 2-year old. However, 1 yearling classified as a kit was captured on 5/8/88 and a beaver from Meadow Creek captured on 5/27/88 and recaptured on 10/22/88 was classified as a kit and a 2-year old for the 2 captures respectively. Because beaver are born in the spring and generally stay in the lodge until mid-summer, I assumed that the model incorrectly classified these 2 beavers to their respective age groups. This illustrates the importance of capture date in determining age class. Common sense dictates that a kit will not be captured in the spring, and a fall-caught yearling should be carefully examined to be certain it is not a kit.

The model generated here is based on an extremely small sample size. Additional carcasses for aging and analysis would provide a more reliable model and could generate additional or different variables. The variables weight and tail width generated within this model provide a relatively simple and quick means for estimating the age of live beavers in the field.

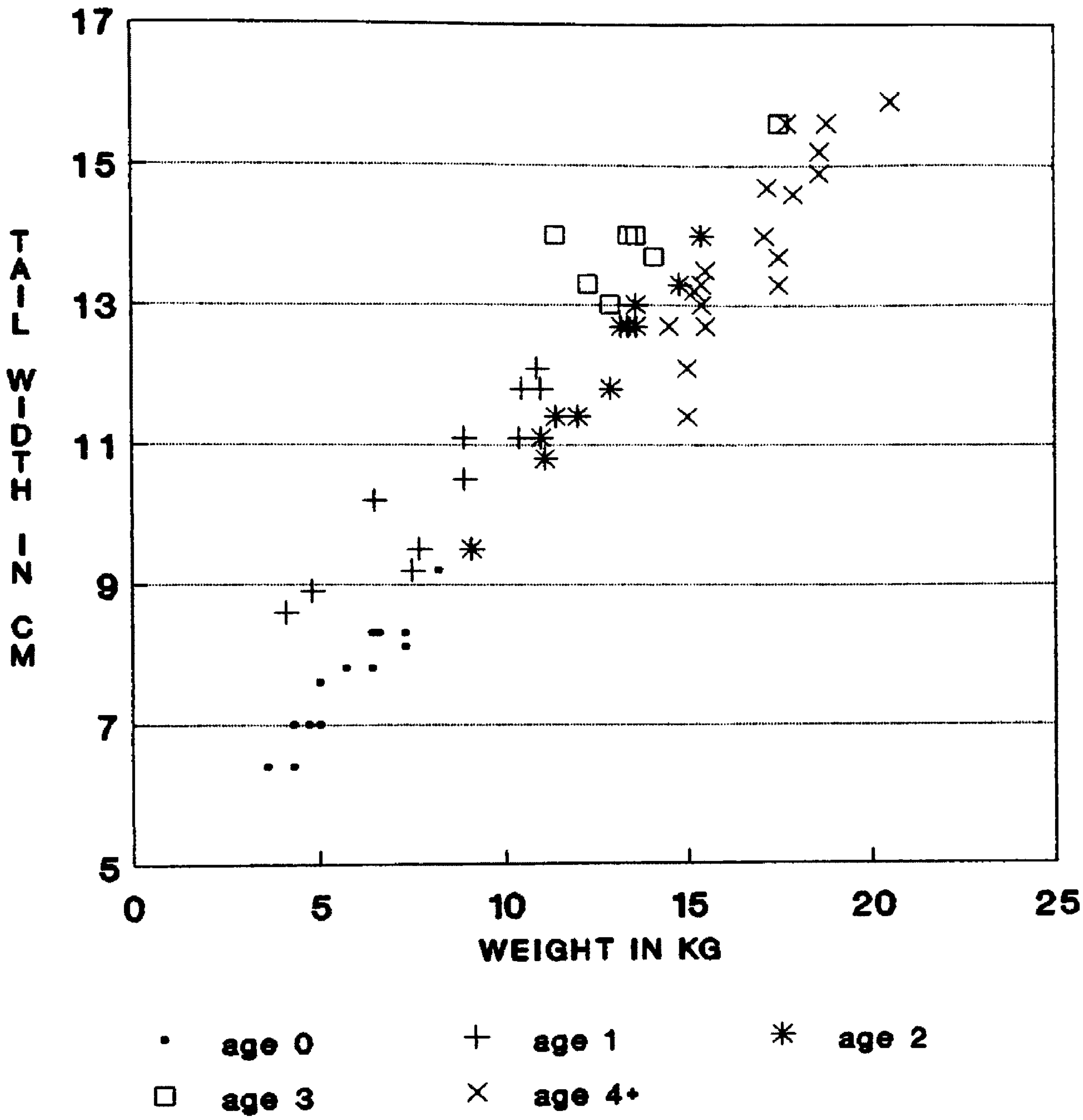


Fig. B3. Plot of tail width with weight by age of captured beavers in western Montana. Age determined from discriminant function model.

APPENDIX C

# POSSIBILITIES OF *Giardia lamblia* SPREAD BY BEAVER DISPERSAL IN THE RATTLESNAKE CREEK STUDY AREA

The presence of *Giardia lamblia* in the Rattlesnake Creek drainage is of primary importance to the city of Missoula, Montana. Rattlesnake Creek was the preferred source of Missoula's drinking water until an outbreak in 1983 of an intestinal disorder caused by *Giardia lamblia* called giardiasis. Since that time, underground wells have been used for Missoula's drinking water. The 1983 outbreak in Missoula was linked to an infected beaver above the intake reservoir for the city's water supply on Rattlesnake Creek. *Giardia lamblia* is a pathogenic protozoan with a 2-stage life cycle, the active trophozoite and the dormant cyst. Transmission is generally waterborne. Infection occurs with ingestion of live cysts. Cysts are periodically shed in the infected host's feces. The beaver has been suggested as a source of wildlife infections through water (Davies and Hibler 1979, Monzigo and Hibler 1987). An objective of this study was to assess the possibilities of the spread of giardiasis in the Rattlesnake Creek drainage by beaver dispersal.

A total of 26 beavers from 9 known colony sites (Fig. C1) were live-trapped in the Rattlesnake Creek study area (Table C1). Fecal samples were obtained from 14 of these beaver. One sample, collected from a 2-year old male captured 11/8/88 from colony 3, tested positive. This beaver was released after processing and has not been recaptured to date. Radio transmitters were surgically implanted intraperitoneally in 2 male (R715, R618) juvenile and 2 female (R301, R608) juvenile beavers. These four beavers were monitored extensively during the 1987-88 field seasons.

Extensive up- and downstream movements were detected from R301,

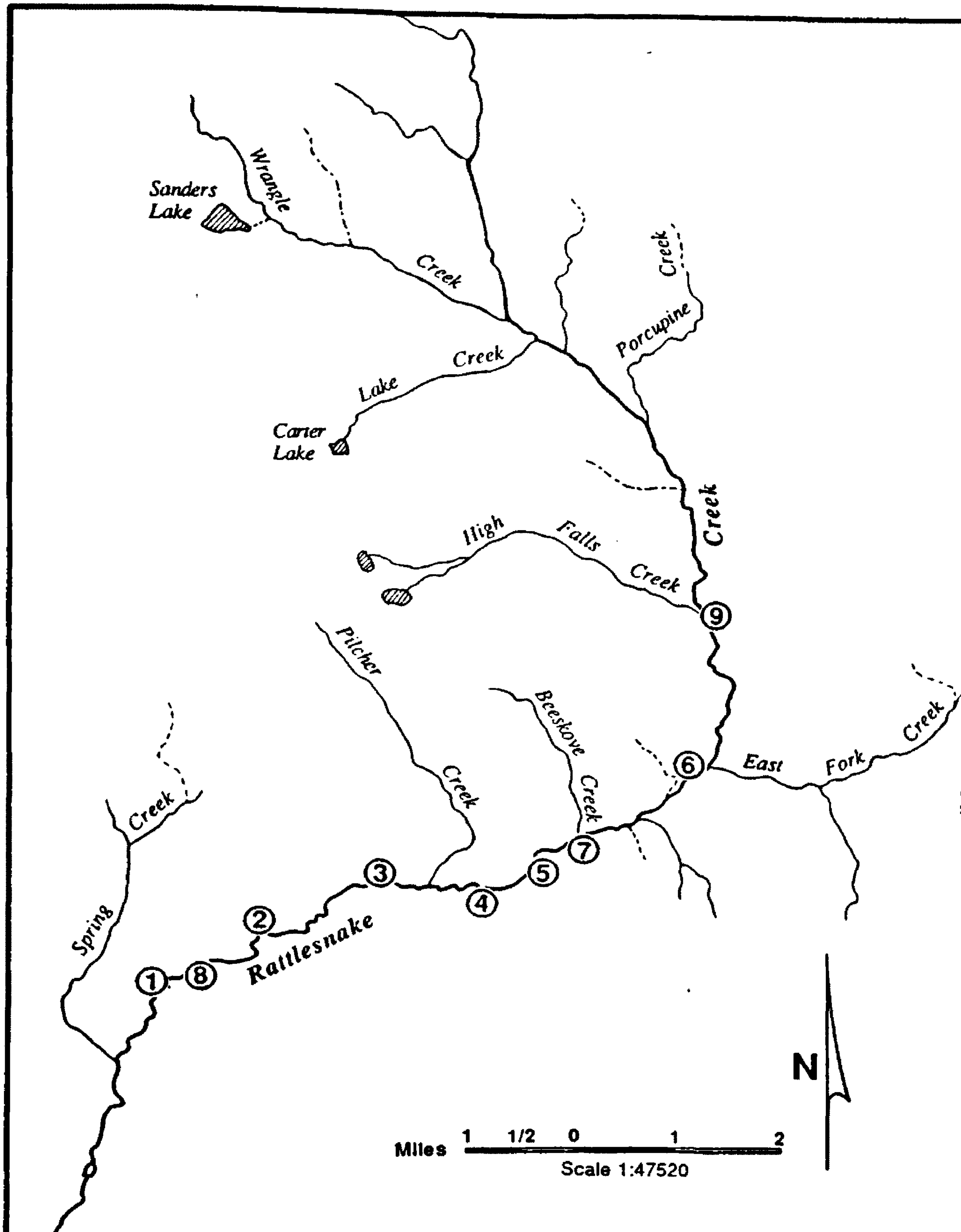


Fig. C1. Map of known beaver colony sites in the Rattlesnake Creek area. Colony numbers are in the order in which colony was located.

Table C1. Sex, age, and colony site of western Montana beavers captured in the Rattlesnake Creek study area. Colony numbers refer to the order in which colony was located.

| Years of Age | Sex | Colony Site 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | M | | | 2 | | | | | | | 2 |
| | F | | | 1 | | | | | | | 1 |
| 1 | M | | | | 2 | | 2 | 1 | | | 5 |
| | F | | | 1 | | | 1 | | | | 2 |
| 2 | M | | 2 | | | | | | | | 2 |
| | F | | | 2 | | | | | | | 2 |
| 3 | M | 2 | | | | | 1 | | 1 | | 4 |
| | F | | | 1 | | | 1 | | | | 2 |
| 4+ | M | | | | 1 | 1* | | | | | 2 |
| | F | 1 | | 2 | | | 1 | | | | 4 |
| Totals | M | 2 | 2 | 2 | 3 | 1 | 3 | 1 | 1 | 0 | 15 |
| | F | 1 | | 7 | | | 3 | | | | 11 |

* recaptured once at same site.

R715, and R618. Both males moved greater distances than the female and passed through known beaver colony sites. R715, captured in colony 7, passed through colonies 4 and 5. R618, captured in colony 6, passed through colonies 3, 4, 5, and 7, and was located twice with R301 (captured at colony 3) in the vicinity of colony 3. None of the detected moves by the females indicated that they had passed through a known colony site.

Three of the 4 monitored beavers (R301, R608, R715) died from predation. All mortalities took place between May and July, 1988. Evidence found at the site of beaver remains and transmitter recovery suggests predation by black bears. Evidence of black bear activity was detected throughout the study area and signs of concentrated activity were noted at colonies 2, 3, 4, 5, and 6.

Observations of colony sites during the summer and fall of 1987 indicated active colony sites for colonies 2 through 7. No activity was observed at colonies 1 and 9. Both adults and juveniles were observed at all colonies except colony 7, where 2 juveniles were observed. Capture information indicated high activity at colonies 3 and 7. Concentrated use at these 2 locations probably relates to site quality. These sites had greater amounts of available food, willow (Salix) and cottonwood (Populus), than other colony sites within the drainage.

The single surviving monitored beaver, R618, was located at his original site of capture (colony 6) on June 22, 1988. No moves out of the colony site were detected after that date. Continued monitoring during the 1989 field season by T. VanDeelen (pers. comm.) indicated that R618 was still at colony 6.

My data do not provide a definitive picture of the spread of giardiasis by beaver dispersal. Extensive movement by juvenile beavers demonstrates that an infected beaver could spread giardiasis between colony sites within a drainage. Contamination, however, would depend on the time an infected beaver spent within another colony. Only one beaver spent time in another colony during this study.

Although no measurements of habitat quality were made at individual colony sites, all colony sites other than colonies 3 and 6 appeared to lack adequate food. This could be the reason no dispersal was detected for the single surviving monitored beaver. The implications are two-fold: if dispersal is delayed 1 or 2 years, the possibilities of an infected disperser spending enough time in another area to shed Giardia cysts are limited; on the other hand, comparisons with other drainages of better quality habitat indicated that the beavers of Rattlesnake Creek moved more frequently and greater distances, evidently in search of areas of suitable habitat, thus providing the potential for the shedding of cysts throughout the drainage. However, beavers do not usually test positive for Giardia until mid to late summer and fall (Monzingo and Hibler 1987). All detected movement away from the home colony was observed prior to July 1 in this study. This suggests that the shedding of Giardia cysts may not take place when beaver are moving through other colony sites.
Lack of available colony sites may also discourage immigration by dispersing infected beavers from the Clark Fork River into the Rattlesnake Creek drainage.

The beaver population in the Rattlesnake Creek drainage appears to be declining (p. 48). Continued trapping and monitoring by T. VanDeelen (pers. comm.) suggests that colonies 3 and 6 may be the only active sites. Black bear predation as discussed above may be a cause of this decline. Increased movement due to lack of available food would cause increased vulnerability to predation. Heavy predation on beavers may eliminate sources of Giardia infection.

In summary, the potential for the spread of Giardia lamblia by dispersing beavers exists within the Rattlesnake Creek drainage. This potential is primarily due to the movement of beavers, primarily juvenile males, in search of potential colony sites or adequate food supplies. This potential for Giardia spread is limited, however, by the number of infected beavers within the drainage; the time of year most long distance movement by beavers takes place; the amount of time a dispersing beaver may spend at another colony site; and the possibility of mortality by predation of an infected beaver.

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Monzingo, D. L., and C. P. Hibler. 1987. Prevalence of _Giardia_ sp. in a beaver colony and the resulting environmental contamination. Journal of Wildlife Diseases 23:576-585.