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Population Status of Beaver on the Free-running Missouri River in Southeastern South Dakota

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POPULATION STATUS OF BEAVER ON THE FREE-RUNNING MISSOURI RIVER IN SOUTHEASTERN SOUTH DAKOTA

BY

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POPULATION STATUS OF BEAVER ON THE
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This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable as meeting the thesis requirements for this degree, but without implying that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Thesis Adviser

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I would like to dedicate this paper to the memory of my father, Harold O. Vanden Berge, who instilled in me the beginnings of a career in Wildlife and Fisheries Science.

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Abstract

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One hundred sixty two beaver (Castor canadensis) harvested by trappers from the free-running Missouri River in southeastern South Dakota were examined from fall 1974 to spring 1976. Ninety two were males and 70 were females (131:100 sex ratio). Age specific sex ratios were not significantly different ($P > 0.05$) from a 1:1 ratio for all age classes. The age structure of the sample was 69:26:45:15:4:3 for age classes zero through five, respectively.

Minimum breeding age for female beaver was 2.5 years. Seventy eight percent of all females (>2.5 years old) collected after the breeding season contained corpora lutea and viable fetuses. The mean number of corpora lutea was 4.91 per breeding female; the mean number of viable fetuses was 4.62 per breeding female. No statistical difference ($P > 0.05$) in corpora lutea or viable fetuses existed between the age classes. The observed overall resorption rate was 5.8 percent.

Survival estimates were calculated using time specific life table analysis treating the age structure of the harvested sample as representative of ages at death in the beaver population. Female survival was 60 percent in age class 0, 69 percent in age class 1,

and 34 percent in age classes 2-5. Male survival was 55 percent in age class 0, 74 percent in age class 1, and 31 percent in age classes 2-5.

Three estimates of the annual rate of population change were made: +17 percent (using a life equation), -39 percent (using a population model) and -15.3 percent (using a colony count index). Two estimates of colony size were applied to the mean number of colonies in the study area to estimate population density at 185-272 beaver in the study area. Mean colony density was significantly higher ($P < 0.01$) in the unstabilized subsection.

Comparison of physical features between the subsections of the river showed a significantly higher ($P < 0.01$) current speed 2 m from the shoreline in the stabilized subsection and no significant difference ($P > 0.05$) in river depth at 2 m from the shoreline. Distance from beaver dens to standing willows (*Salix* spp.) and cottonwoods (*Populus deltoides*) was not significantly different ($P > 0.05$) between the stabilized and unstabilized subsections. Beaver were selective for shoreline areas with slow current speed and deep water when choosing a den site, and beaver preferred low-tapered banks when compared to a high-cut, eroding banks or a granite-lined, stabilized banks.

POPULATION STATUS OF BEAVER ON THE FREE-RUNNING MISSOURI RIVER IN SOUTHEASTERN SOUTH DAKOTA

INTRODUCTION

Radical changes have been made in the Missouri River since the days of Lewis and Clark. Much of the change has taken place in the last 50 years under auspices of the U.S. Army Corps of Engineers to benefit river navigation and bank stabilization.

The most significant changes affecting the Missouri River in southeastern South Dakota were bank stabilization projects and the closure of the main stem dams in South Dakota. The Rivers and Harbors Act of 1945 authorized a 9-ft deep and 300-ft wide channel from the mouth of the Missouri River to Sioux City, Iowa. Kensler's Bend Project provided approximately 32 km of bank stabilization structures further upstream from Sioux City, Iowa to Ponca State Park, Nebraska, between 1946 and 1961. Since the closure of Gavins Point Dam near Yankton, South Dakota in 1955 and the subsequent formation of Lewis and Clark Lake behind the dam, downstream discharges into the free-running river have been much reduced in the winter (non-navigational) season, and regulated during the summer (navigational) season in relation to the amount of water entering the upper Missouri River watershed.

This study was designed to evaluate the current population status of beaver (Castor canadensis) on the free-running Missouri River in southeastern South Dakota. Comparison of beaver populations living where banks were not stabilized with those inhabiting areas where banks had been stabilized was possible. An understanding of the habitat requirements and ecological relationships of beaver to their environment and the changes brought about by bank stabilization will be useful in evaluating the impact of additional development by the Army Corps of Engineers. Information concerning population stability, natality, and mortality of the current beaver population are also essential in developing adequate management recommendations.

Specific objectives of this study were to:

1. Determine the age structure, sex ratio, and minimum breeding age of beaver taken by trappers along the Missouri River from Yankton, South Dakota to Sioux City, Iowa.
2. Estimate the number of beaver in the free-running portion of the Missouri River in southeastern South Dakota.
3. Estimate the productivity of the beaver population using life equation methods and to evaluate population stability using a general population model.
4. Test the hypothesis that there is no difference in population density of beaver in the unstabilized portion of the Missouri River as compared to the

stabilized portion of the free-running Missouri River in southeastern South Dakota.

STUDY AREA DESCRIPTION

The study area includes the Missouri River, high water mark to high water mark, between the Highway 81 bridge at Yankton, South Dakota and the South Dakota-Iowa border at Sioux City, Iowa. This includes 116 river kilometers. The shorelines of the lower 32 km (Ponca State Park, Nebraska to the Iowa border at Sioux City, Iowa) are stabilized with granite revetments and wing dams. The upper river (Yankton, South Dakota to Ponca State Park, Nebraska) remains in near native, unstabilized condition. Width of the Missouri River within the study area varies from 0.40 km to 2.4 km. Depth of the river is highly variable (0-10 m). A moderate current (0.9 to 2.5 m per second) carries a heavy silt load. Many small islands and constantly changing sand bars occur in the unstabilized subsection. The stabilized portion of the study area contains no small islands, and sand bars are stabilized by numerous wing dams and revetments.

Bank profile on the unstabilized subsection of the Missouri River study area is generally of two types. The first is a high-cut bank profile where current action has eroded a vertical bank from 2 to 6 m high. No permanently rooted vegetation occurs at the water line. The second type is low-tapered bank profile. This type is generally less than 2 m high and tapers gradually to the water line.

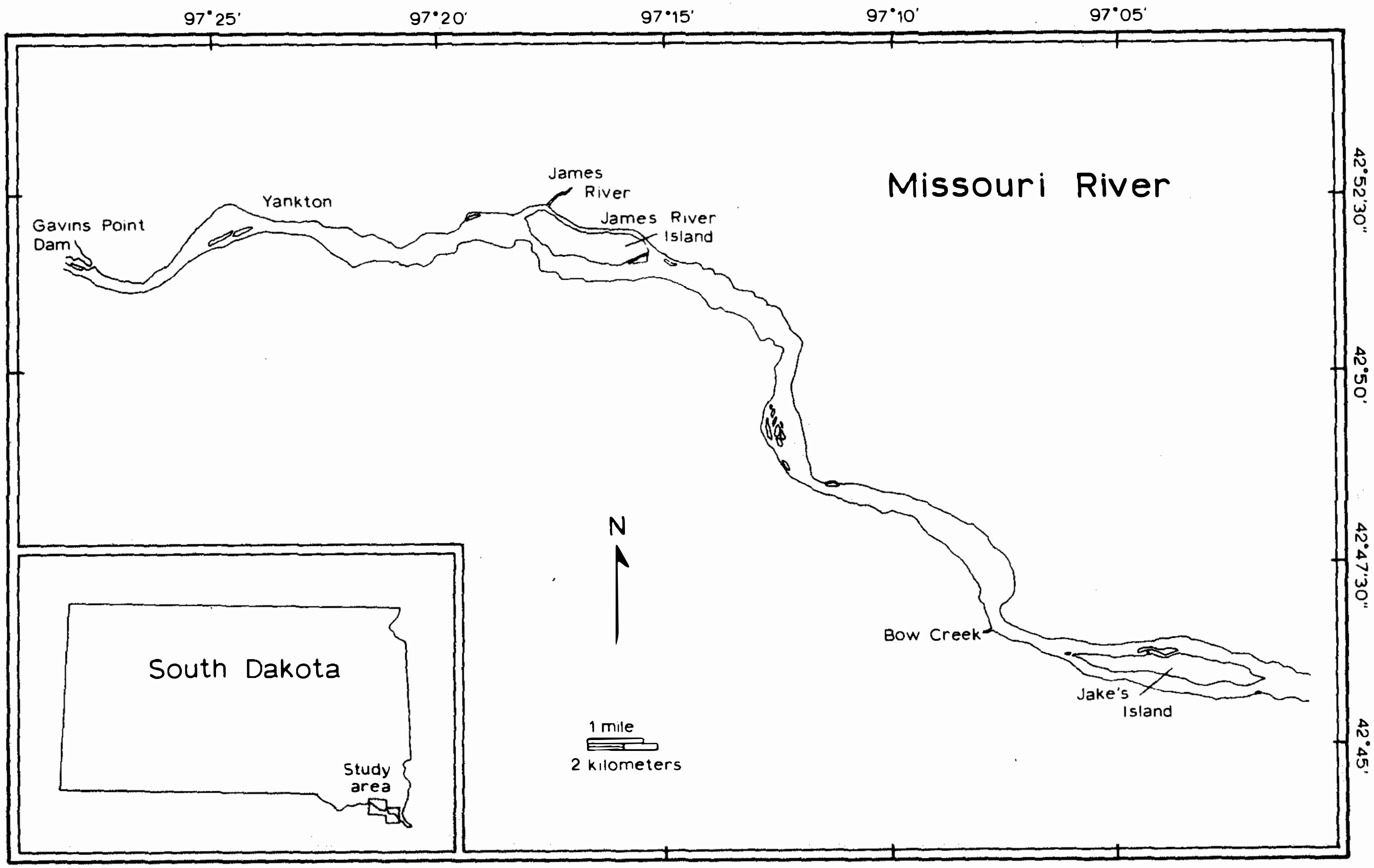

Fig. 1. Unstabilized subsection of Missouri River study area.

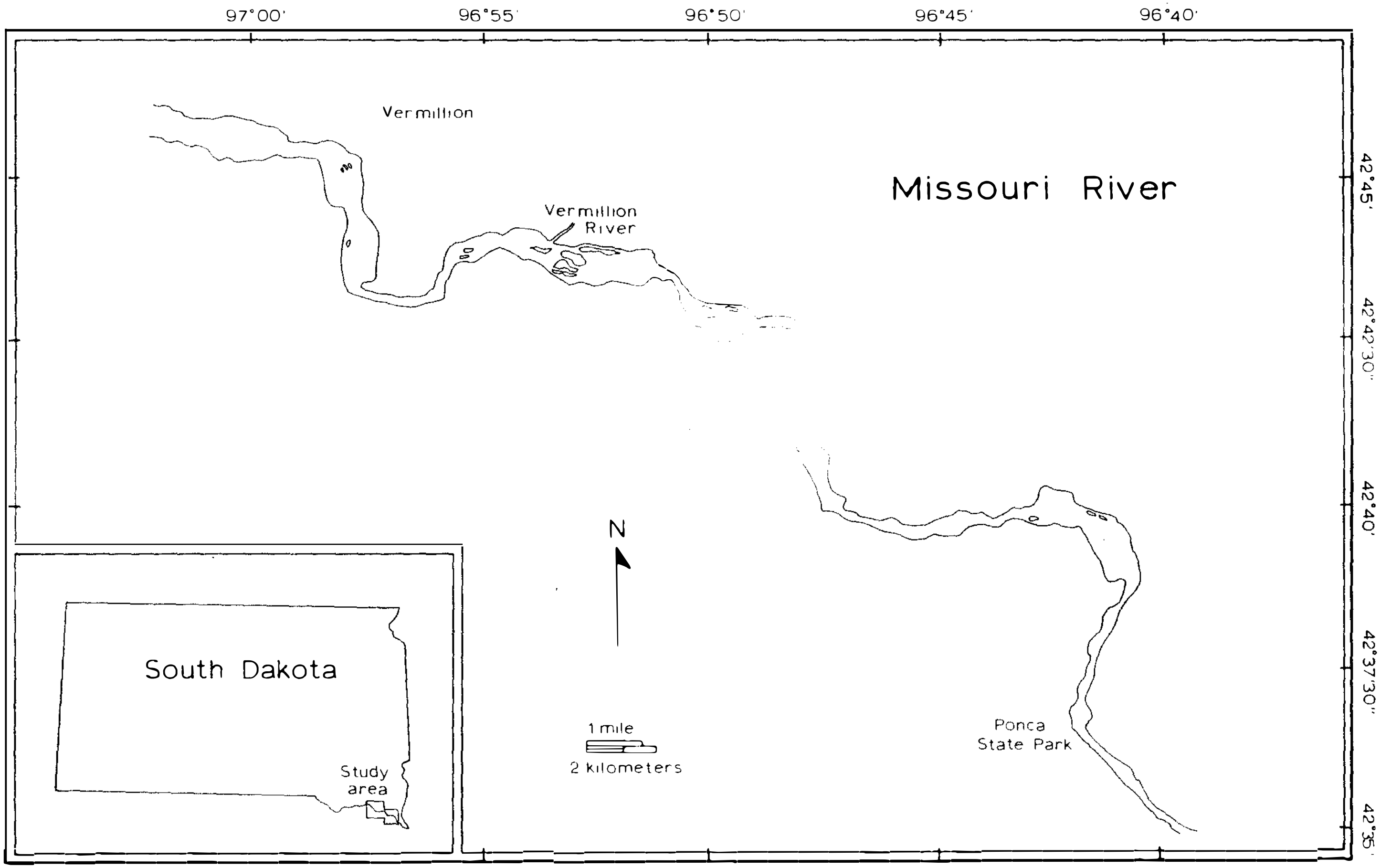

Fig. 1. Continued. Unstabilized subsection of Missouri River study area.

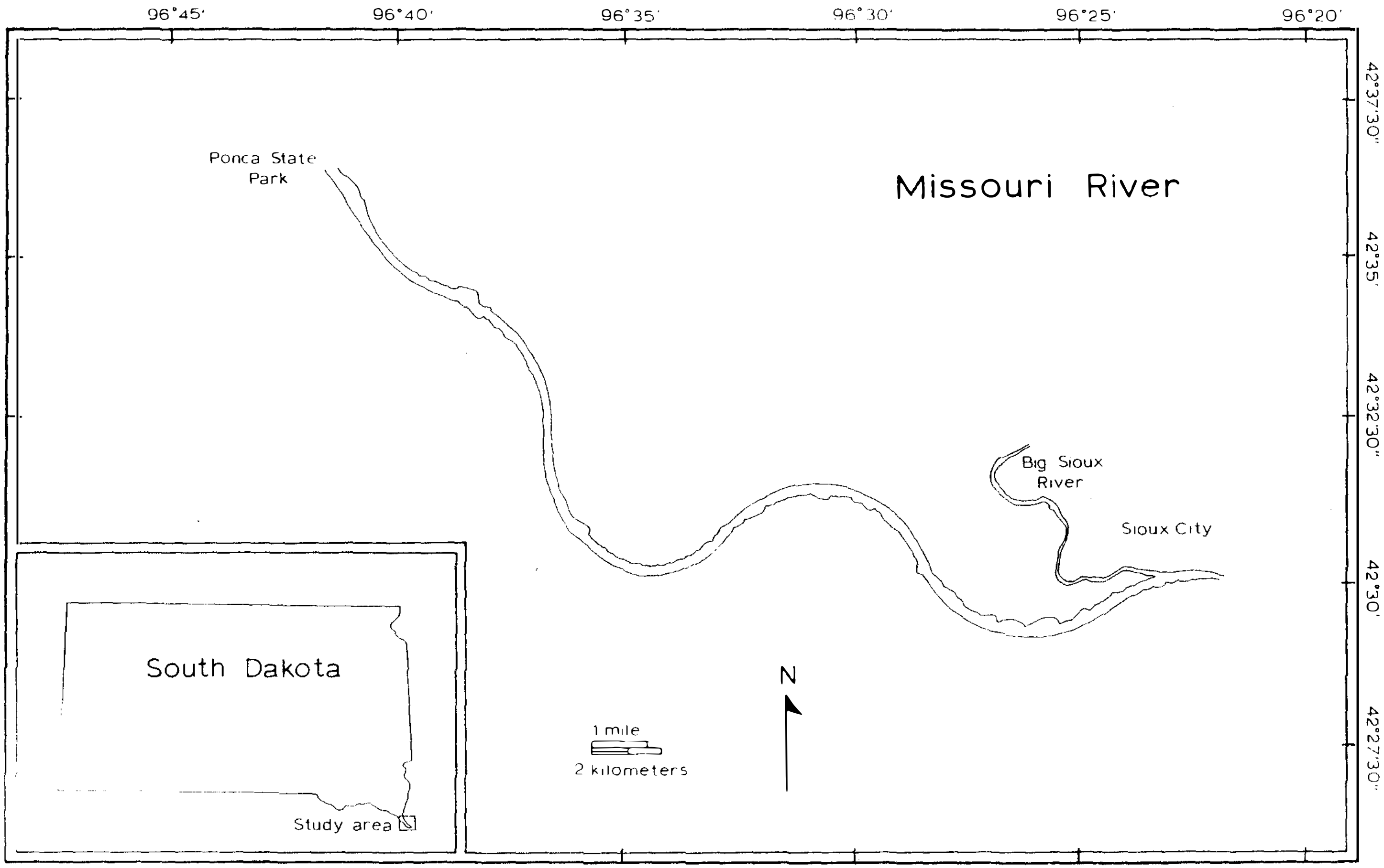

Fig. 2. Stabilized subsection of Missouri River study area.

Rooted vegetation grows to the water line in low-tapered bank profile.

In the stabilized subsection, bank profile is either a low granite revetment or low-tapered bank profile similar to that of the unstabilized subsection. Low-tapered bank profile exists primarily behind wing dams in the stabilized river. High-cut bank profile is almost nonexistent in the stabilized subsection because actively eroding areas have been stabilized with granite revetments.

The downstream discharge rate from Gavins Point Dam varies according to seasonal runoff into the upper Missouri River watershed and seasonal navigational requirements. Summer (navigational) season discharge rate is normally around 990 m^3 per second. The highest discharge rate recorded from Gavins Point Dam occurred during July and August 1975, and was 1700 m^3 per second. Winter (non-navigational) season discharge rates usually vary between 425-710 m^3 per second. The seasonal changes in discharge rate cause a fluctuation in river stage of 0.5 to 2.0 m depending on the extremes of summer and winter discharge and width of the river. The transitional periods from summer to winter and winter to summer river stages occur in late November, and March or April, respectively.

Winter freeze-up on the study area usually occurs during the first part of December and spring break-up takes place normally in February or March. During mild winters (such as 1975-76) the Missouri River may not completely freeze over.

MATERIALS AND METHODS

Carcass Collection

Carcasses of 162 beaver harvested on the Missouri River in southeastern South Dakota were collected during the 1974-75 and 1975-76 trapping seasons. Personal visits were made to solicit beaver carcasses because the number of trappers known to actively take beaver from the study area was small. Unusually persistent ice conditions during spring 1975 and low fur prices in both 1974-75 and 1975-76 reduced the number of trappers harvesting beaver from the study area. Three trappers supplied carcasses during the two collection periods. All beaver were weighed and measured (Appendix 1). One half of the lower mandible was removed from all specimens. The complete reproductive tract was removed from female carcasses.

Determination of Age

The ability to accurately determine the exact year class of each beaver is a prerequisite to use of age ratio data. The techniques used by Van Nostrand and Stephenson (1964) and by Klevezal' and Kleinenberg (1969) permitted valid separation of 11 year classes in their studies.

Each beaver was assigned an estimated age based on the method of Van Nostrand and Stephenson (1964:433). In addition, age classes for the 1975-76 sample (128 of 162 total specimens) were determined using the technique of Klevezal' and Kleinenberg (1969) to examine adhesion lines in the periosteal region of bone tissue.

Cementum annuli in the molars and adhesion lines in the periosteal zone of the mandible sections were seen as narrow, darkly stained bands. A count of cementum annuli or adhesion lines was made in each serial section of tooth or mandible, respectively, before an age class was assigned. The age class assigned to each specimen by this method was then cross checked against the age class assigned by the root canal closure technique. If a discrepancy existed, a second 10 mm cross section from a different region was processed using the same technique.

Final age class determination for each beaver was made only after evaluation of tooth replacement, root canal closure, and cementum annuli in the first molar or adhesion lines in the periosteal region of the mandible. No beaver of known age were available for comparison; however, correspondence occurred between the three methods.

Examination of Female Reproductive Tracts

Seventy female reproductive tracts were removed from carcasses and fixed in 10 percent formalin until examined.

Uteri

Horns of uteri with noticeable convolution or swellings were opened and embryos removed. Developing embryos were easily recognizable in specimens because the peak collection period (Feb. 15-March 15) was approximately one-half way through the 128 day gestation period. Embryos not developing properly (resorptions) were noted. No attempt was made to count placental scars.

Ovaries

Ovaries were removed from the reproductive tracts, fixed in 10 percent formalin for a minimum of 2 days, and mounted in paraffin for sectioning with a microtome. Ovaries were sectioned at a thickness of 8μ, and every tenth section was affixed to a glass slide. All serial sections were stained with Delafield's Hemotoxylin Stain Solution for 12 minutes and with Eosin Stain Solution for 10 seconds. No acid bath was used after the Hemotoxylin Stain Solution because dark sections were easier to read.

Each serial section was examined for the presence and number of corpora lutea. A total count was made from both ovaries on each specimen where corpora lutea appeared. Corpora lutea of pregnancy were distinguishable from other ovarian structures on the basis of size within a few days after ovulation and fertilization (Provost 1962).

Embryos

All embryos were removed from reproductive tracts, fixed in 10 percent formalin, and stored as distinct litters. Sex of individual embryos was determined where possible.

Colony Count

An enumeration of all active beaver colonies was made in the winter seasons of 1974-75 and 1975-76. An active beaver colony was defined as a group of beaver possessing at least one den or hut and one food cache. Undisturbed beaver colonies during the winter months normally contain an adult boar and sow, young of the year, and surviving yearlings from the previous year (Bradt 1938).

Three separate counts of active colonies were made each season. Counts in November and again in December were made to observe colonies when food caches were highly visible. A third count was made in late February with special emphasis on location of colonies without highly visible food caches. Colonies were included if entrances were littered with large amounts of stripped branches. Positions of colonies were plotted on aerial photos.

Five Percent Extermination Census

An extermination census of a randomly chosen 5 percent sample of the beaver colonies in the study area was planned for both trapping seasons (1974-75 and 1975-76). An estimate of population density could be calculated by multiplying the mean number of beaver per colony (from extermination census) X total number of colonies in the study area (from the colony count census). It was not possible to complete the random 5 percent extermination census because random dens were not always accessible. As a result, a larger sample of nonrandom dens was chosen on the basis of accessibility, adaptability to trapping technique, and in areas where trap theft was generally minimal. Connibear #330 traps and Victor #14 leg hold traps with drowning rig were used.

Eight colonies were trapped in the 1974-75 season; however, the number of trap days per colony was limited by ice conditions. Twenty three colonies were trapped in the 1975-76 season. Ice conditions on the study area were less severe in winter 1975-76, but it was still doubtful whether some of the colonies were exterminated.

Ecology of Beaver Colonies

Colony Density

The number of beaver colonies per kilometer in 31.6 km of the stabilized Missouri River study area was compared to the number of beaver colonies per kilometer in 31.6 km of unstabilized Missouri River immediately upstream from the stabilized subsection. The null hypothesis was that there is no difference in colony density between the stabilized and unstabilized subsections. This comparison was made for both the 1974-75 and 1975-76 periods.

Current Speed

Statistical comparison of random unstabilized and random stabilized points was an attempt to quantify physical differences between the subsections of the study area. Current speed was measured 2 m and 3.5 m from the shoreline at all beaver dens, at 50 random points in the stabilized subsection, and 50 random points in the unstabilized subsection. Distances from the shoreline (2 m and 3.5 m) roughly corresponded to placement of the winter food cache.

River Depth

River depth 2 m and 3.5 m from the shoreline was measured at all beaver dens, 50 random points in the stabilized, and 50 random points in the unstabilized subsections. Statistical comparison of mean river depth at 50 random points in each subsection and mean river depth at all beaver dens provided an indication of beaver selectivity for water characteristic of either subsection.

Distance from Beaver Dens to Food Supply

Food caches in the study area during the winter months were almost exclusively comprised of cottonwoods (*Populus deltoides*) and willows (*Salix* spp.). The distances from each den to the nearest standing cottonwood and willow trees were measured. The mean distance from each food species to the den in stabilized and unstabilized subsections was compared.

Bank Profile

The mean number of beaver colonies per km in high-cut and low-tapered bank profiles was compared to the ratio in which those bank profiles occur in the study area. The statistical comparison of bank profiles was made to determine whether beaver are selective for a certain bank profile when they choose a den site.

RESULTS AND DISCUSSION

Age and Sex Composition

Age Ratios

Thirty four beaver were collected during the 1974-75 trapping season, and 128 were harvested in the 1975-76 season. Both samples were combined to avoid loss of data from insufficient sample size in the 1974-75 season.

Age class 0 (Table 1) contained 42.6 percent of the total sample; however, the large proportion of individuals in age class 0 does not necessarily indicate an expanding population. Mortality factors affecting all age classes equally would have no net affect on the age ratio (Caughley 1974).

Table 1. Age composition of 162 beaver harvested by trappers on the Missouri River in southeastern South Dakota, 1974-76.

Age Class	Age (months)	No. of Individuals in Age Class	Percentage of Total Sample
0	6-12	69	42.6
1	18-24	26	16.0
2	30-36	45	27.8
3	42-48	15	9.3
4	54-60	4	2.5
5	66-72	3	1.8
TOTAL		162	100.0

Low frequency of age class 1 individuals in the age structure (Table 1) was noted in other beaver studies (Bradt 1947, Larson 1967). Larson (1967:410) suggested that two year old beaver have not had an opportunity to construct their own lodge complex, and thus may temporarily escape notice of most trappers. The low percentage of age class 1 individuals (Table 1) may also reflect extremely intense beaver harvest from the study area in 1973-74 caused by high fur prices, favorable weather conditions, and an unrestricted seasonal length.

Beaver have a physiological longevity of approximately 15 years (Bradt 1947), yet the harvested sample in this study has only six age classes represented. This suggests a high mortality rate, probably from fur harvest since beaver have practically no natural enemies in the southeastern South Dakota study area.

Sex ratios

The overall male:female ratio (131:100) observed in the combined samples was not significantly different from a 1:1 ratio ($\chi^2 = 2.99$, $P > 0.05$, 1 d.f.). Overall sex ratios of trapped samples, obtained from past studies, are normally not significantly different from a 1:1 ratio. Examples of sex ratios from other studies include 101:100 (Osborn 1953); 113:100 (Leege and Williams 1967); 108:100 (Bradt 1947); and 108:100 (Bond 1956).

Table 2. Sex ratios by age class for beaver harvested in southeastern South Dakota, 1974-76.

	1974-75		1975-76		Combined		Sex Ratio
Age Class	M	F	M	F	M	F	M : F
0	4	6	37	22	41	28	146:100
1	4	5	9	8	13	13	100:100
2	3	6	23	13	26	19	137:100
3	4	1	4	6	8	7	114:100
4	1	0	2	1	3	1	133:100
5	0	0	1	2	1	2	
TOTAL	16	18	76	52	92	70	131:100

The assumption of equal sex ratio at birth is usually made (Benson 1933, Grinnel et al. 1937). Bradt (1947) in Michigan observed a male:female ratio at birth of 109:100, and Osborn (1953) in Wyoming examined 22 liters containing 64 fetuses and observed a sex ratio of 129:100. Four litters containing 23 embryos sufficiently well developed for sexual determination were examined in this study. The male:female ratio (130:100 observed was not significantly different from a 1:1 ratio (χ^2 = 0.39, P > 0.05, 1 d.f.); however, the sample size was probably insufficient for adequate testing.

Sex ratios by age class (Table 2) showed a high proportion of males in all classes except age class 2, where the ratio was equal, and age class 5, where sample size was judged inadequate. The juvenile sex ratio (146:100) in this study was not significantly different from 1:1 (χ^2 = 2.45, P > 0.05, 1 d.f.). Other studies show sex ratios favoring males in the juvenile age class: 171:100 from Leege and Williams (1967) and 133:100 from Osborn (1953). The most common explanation is that juvenile males are more active than females causing higher relative vulnerability to trapping and other mortality factors.

Sex ratios of subadult and adult beaver in this study exhibited a leveling tendency toward a 1:1 male:female ratio; none were significantly different from a 1:1 ratio (χ^2's = 0.0 - 1.08, P > 0.05, 1 d.f.). No age class, except age class 5 where the sample size was judged inadequate, showed a sex ratio favoring females as observed in other studies: 88:100 (Osborn 1953); 88:100 (Leege and Williams 1967) and 78:100 (Henry and Bookout 1969). Grinell et al. (1937) suggested sex ratios favoring females in older age classes may reflect mortality incurred by adult male beaver fighting during mating season.

Reproduction

Minimum Breeding Age

No evidence of reproduction was found in any beaver less than 2.5 years old (Table 3). The data in this study agreed with Henry and Bookhout (1969:929) who found no placental scars in beaver less than 2.5 years old in a sample of 105 beaver trapped in northeastern Ohio in 1966-67. Bradt (1947) considers minimum breeding age as 2.5 years, and Benson (1933) examined 72 female beaver carcasses and found no breeding in yearling females.

Table 3. Female age structure, number of females breeding, and percentage of females breeding in the combined sample of 162 beaver collected on the Missouri River study area 1974-76.

Age Class	Age (months)	No. of Females Collected	No. of Females Breeding	Percentage Breeding
0	6-12	28	0	0
1	18-24	13[a]	0	0
2	30-36	19[b]	12	67[c]
3	42-48	7[b]	6	100[c]
4	54-60	1	1	100
5	66-72	2	2	100
TOTAL		70	21	

[a] Contains two females collected prior to the onset of the breeding season.

[b] Contains one female collected prior to the onset of the breeding season.

[c] Percentage of females breeding excludes one female collected prior to the onset of the breeding season.

All female beaver in age class 2, collected in February and March 1975, had conceived. In 1976, only 50 percent of the females collected in February and March in age class 2 were pregnant. Weather conditions in November and December 1974 were relatively mild, while in mid-November 1975, portions of the Missouri River froze during a severe blizzard and heavy ice flows occurred several weeks earlier than normal. Extreme weather conditions may have disrupted pairing and subsequent breeding activity by isolating the inexperienced first year breeders several weeks earlier than normal. However, a direct cause and effect relationship cannot be shown from the data presented in this study.

Bond (1956) suggested that presence of non-breeding, sexually mature females may have resulted from removal of males of mated pairs just prior to copulation. The trapping season in southeastern South Dakota generally begins the weekend closest to the middle of November, 14 to 30 days prior to the onset of the breeding season. Beaver at this latitude are not fully prime until middle or late December, and almost no beaver trapping is done before 15 February, when ice flows are reduced on the Missouri River. Thus, actual trapping practices do not remove males of mated pairs prior to copulation in this area.

All females older than 36 months and collected in February and March had conceived. Osborn (1953) observed 89 percent of a trapped sample of 39 adult females (>36 months) had conceived.

Thirty two percent of the entire female cohort collected in February and March were pregnant. This compares with 42 percent rate of pregnancy in a harvested sample of all females from Ohio (Henry and Bookhout 1969).

Corpora Lutea per Female

The mean number of corpora lutea was 4.91 for all breeding females (21) in the combined 1974-75 and 1975-76 trapping seasons (Table 4). In age classes 2, 3, 4 and 5, the mean number of corpora lutea per breeding female was 4.3, 5.5, 4.0, and 7.5 respectively. There was no significant age specific difference in number of corpora lutea per breeding female ($F = 3.09$, $P > 0.05$; 3, 19 d.f.).

Implanted Embryos

The overall mean of implanted embryos per breeding female was 4.62 for all breeding females in the combined sample in this study (Table 4). The range in number of implanted embryos was one to eight per breeding female. Osborn (1953) observed a mean of 3.12 embryos per breeding female with a range of one to six.

In age classes 2, 3, 4, and 5 the mean number of embryos per breeding female was 4.0, 5.5, 4.0, and 6.0 respectively. There was no significant difference between these age classes in mean number of embryos per breeding female ($F = 1.65$; $P > 0.05$; 3, 19 d.f.).

Bailey (1927) found that younger females produce one to two young, whereas older females produce four to six. In this study, 50 percent of 12 females breeding for the first time contained five or

Table 4. Number of corpora lutea per female having corpora lutea present, number of implanted embryos per female having implanted embryos, and the percentage of resorptions in the combined samples of beaver taken from the Missouri River in southeastern South Dakota, 1974-1976.

Age Class	No. in class	No. with Corpora Lutea	Mean No. per Breeding Female	Range	No. with Embryos	Mean No. per Breeding Female	Range	Percentage of Resorption
0	28	0	0.0	0-0	0	0.0	0-0	-
1	13[a]	0	0.0	0-0	0	0.0	0-0	-
2	19[b]	12	4.3	1-7	12	4.0	1-6	5.9
3	7[b]	6	5.5	4-7	6	5.5	4-7	0.0
4	1	1	4.0	4-4	1	4.0	4-4	0.0
5	2	2	7.5	6-9	2	6.0	4-8	20.0
Total	70	21	4.91	1-9	21	4.62	1-8	5.8

[a] Contains two females collected prior to the onset of the breeding season.

[b] Contains one female collected prior to the onset of the breeding season.

[c] Percentage of females breeding excludes one female collected prior to the onset of the breeding season.

six embryos. The lack of age specific differences in the mean number of implanted embryos per breeding female (potential litter size) may be a reflection of quality of beaver habitat and density of the population. Food is probably not a limiting factor on the Missouri River in southeastern South Dakota.

Resorptions

A resorption in this study was defined as any implantation failure or intrauterine death which causes a difference between the number of corpora lutea and the number of implanted embryos. The overall resorption rate in this study was 5.8 percent (Table 4).

Most resorptions take place early in gestation (Provost 1958) and must be considered if embryo counts are used as an index of productivity (mean number of pups per breeding female per year). Osborn (1953) observed a 27 percent resorption rate in 22 females. Provost (1962) noted a 15 percent resorption rate, and Henry and Bookhout (1969) observed resorptions in 12 percent of beaver with visible embryos.

Productivity

Annual Increment

Henry and Bookhout (1969:931) estimated the net rate of population increase using a life equation analysis of a harvested sample of beaver. The equation is: (((number of females of breeding age x ovulation frequency x average number of corpora lutea per female) -

prenatal mortality) ÷ (total number of animals in the sample)) - juvenile mortality = the net rate of population increase for the total number of animals in the sample. If this life equation is expanded to the population at large, the assumption must be made that the trapped sample is representative of the entire population. Prenatal mortality used in the equation is the overall resorption rate. Juvenile mortality in the equation is the percentage of juveniles appearing in the age structure of the sample; this assumes the frequency of ages at death due to fur harvest is the same as the frequency of ages at death due to all mortality factors.

Disease and starvation are not evident in the beaver population on the Missouri River in southeastern South Dakota. Some deaths of beaver may be caused by ice jamming and subsequent raising of the river level. Illegal shooting by a few boaters, fishermen, and waterfowl hunters probably adds to mortality, but fur harvest constitutes the majority of the beaver mortality in the study area. Since no data exist concerning magnitude or age class selectivity of non-harvest mortality, it was assumed that non-harvest mortalities occur randomly and are not age or sex specific.

Using data collected in this study (Tables 3 and 4), the life equation analysis (Henry and Bookhout 1969) estimates the beaver population to be growing at a rate of 17.3 percent. This estimate of population growth is considered high because the imprecise estimate of juvenile mortality does not allow for added mortality from sources other than fur harvest.

Recruitment Rate

Recruitment rate is defined as the number of pups per breeding female at the beginning of the spring trapping period (around 15 February - 15 March). Individual age specific recruitment rates were not calculated because there was no significant difference ($F = 1.63$-3.09, $P > 0.05$; 3, 19 d.f.) in the numbers of corpora lutea or implanted embryos per breeding females between age classes.

The recruitment rate was calculated by dividing the number of individuals in age class 0 of the combined age structure (Table 1, line 1) by the total number of breeding females (Table 3, line 7) in the combined sample. The recruitment rate was estimated to be 69/21 = 3.3 pups per breeding female.

If the recruitment rate of the sample is expanded to the population, the assumption must be made that the age structure of the sample is representative of the age structure of the population. Bradt (1947) in Michigan says it is doubtful that trappers can be selective during a short open season in late winter or early spring, and it may be assumed that trapping is generally indiscriminate. Precautions taken to minimize trap selectivity in this study included use of traps large enough to hold all beaver (Victor #14's or the equivalent with jaws and Connibear #330's), use of efficient drowning rigs on all leg hold sets to minimize the chances of larger individuals pulling themselves free, and intensive trapping throughout the study area.

A second assumption is that all females producing pups which survive to the spring trapping period also survive to the same trapping period. Females which produce pups are generally secure in a well established territory. The pregnant sow evicts the boar, the young of the year, and the yearlings prior to the birth of the current year's litter. The female remains in sole possession of the winter den, which is believed to be the most secure location within the territory. The adult boar generally remains within the territory in an accessory den and maintains the integrity of the territory, so we may reasonably assume mortality of females producing pups is minimal until the next trapping season.

The number of female pups per adult female will be used later in a population model (Henny et al. 1970). Since the sex ratio of age class 0 (Table 2) was not significantly different from a 1:1 ratio ($\chi^2 = 2.45$, $P > 0.05$, 1 d.f.), the female recruitment rate was 3.3/2 = 1.7 female pups per adult female.

Survival, Mortality, and Age Stability

Sample of the Dying

Age specific survival and mortality rates will be estimated using a time specific life table procedure. The age structure used in the life table analysis is the combined data from both 1974-75 and 1975-76 collecting seasons. The increase in sample size gained by combining age structures decreases variability due to chance. The averaging effect was desirable since the objective was to identify a general population trend. The age distribution of the combined sample (Table 2) was assumed to represent the age at death for members of the population.

The time specific life table analysis assumes that the population is stationary, age stable, and that the data on age structure used in the life table are representative of the age structure of the population (Caughley 1966). It was assumed that the beaver population on the Missouri River study area was stationary. Age stability was examined using a population model (Henny et al. 1970). The representativeness of the harvested age structure as a sample of age at death for members of the population depended on whether the frequencies of ages at death in the harvested sample were similar to frequencies of ages at death due to all mortality factors.

Fur harvest in some years (ie: 1975-76) exceeded 50 percent of the total beaver population in the study area. Mortality of beaver from causes other than fur harvest was thought to be minimal and was discussed earlier in this study.

Survival and Mortality Rates

Survival and mortality rates calculated in this study were rates of survival and mortality from the beginning of the spring trapping period (approximately 15 February - 15 March) in the first season to the beginning of the spring trapping period the following year. Age specific mortality rates of male and female beaver were calculated separately using the formula:

$$\bar{q}_x = \frac{d_x}{l_x}$$

where $\bar{q}_x$ = age specific, annual mortality rate,

d_x = number of beaver in age x of the combined, harvested sample.

l_x = number of beaver in age x, alive at the beginning of the spring sampling period.

The annual mortality rate of sexually mature beaver (age class 2-5) was averaged because the sample size in older age classes was insufficient. The average, annual mortality rates of male and female beaver in age classes 2-5 were calculated separately using the following formula:

$$\bar{q} = \frac{d_{2-5}}{l_{2-5}}$$

where $\bar{q}$ = average, annual mortality rate of beaver in age classes 2-5,

d_{2-5} = number of beaver in age classes 2-5 in the combined samples,

l_{2-5} = number of beaver in age classes 2-5 alive at the beginning of the spring sampling period.

Age specific, annual survival rates of male and female beaver were calculated separately using the following formula:

$$\bar{s} = 1 - \bar{q}_x$$

where $\bar{s}_x$ = age specific, annual survival rate of beaver in age x of the combined sample,

$\bar{q}_x$ = age specific, annual mortality rate of beaver in age x of the combined samples.

The average, annual survival rate of sexually mature male and female beaver were calculated separately using the formula:

$$\bar{s} = 1 - \bar{q}$$

where $\bar{s}$ = the average, annual survival rate of beaver in age classes 2-5 of the combined samples,

$\bar{q}$ = the average, annual mortality rate of beaver in age classes 2-5 of the combined samples.

Age specific, annual survival rates for male beaver in age class 0, 1, and 2-5 were 55, 74, and 31 percent, respectively (Table 5). Age specific, annual survival rates for female beaver in age class 0, 1, and 2-5 were 60, 69, and 34 percent, respectively (Table 6).

Table 5. Estimates of annual survival and mortality of male beaver calculated by time specific life table analysis using (d_x) entry of data.

Age Class	Frequency in Sample (d_x)	l_x	Survival Rate ($\bar{s}_x$)	Mortality Rate ($\bar{q}_x$)
0	41	92	0.55 $\bar{s}_0$	0.45 $\bar{q}_0$
1	13	51	0.74 $\bar{s}_1$	0.26 $\bar{q}_1$
2	26	38	0.31 $\bar{s}$ (ages 2-5)	0.69 $\bar{q}$ (ages 2-5)
3	8	12		
4	3	4		
5	1	1		

Table 6. Estimates of annual survival and mortality of female beaver calculated by time specific life table analysis using (d_x) entry of data.

Age Class	Frequency in Sample (d_x)	l_x	Survival Rate ($\bar{s}_x$)	Mortality Rate ($\bar{q}_x$)
0	28	70	0.60 $\bar{s}_0$	0.40 $\bar{q}_0$
1	13	42	0.69 $\bar{s}_1$	0.31 $\bar{q}_1$
2	19	29		
3	7	10	0.34 $\bar{s}$	0.66 $\bar{q}$
4	1	3		
5	2	2		

Trapping of beaver in spring in southeastern South Dakota occurs before young of the year and yearlings are driven out of the winter dens by adult sows. This may be reflected in the high juvenile ($\bar{s}_0$) and yearling ($\bar{s}_1$) survival rates for both males (Table 5) and females (Table 6). The disparity between the average, annual survival ($\bar{s}$) of breeding age beaver (Tables 5 and 6) and the age specific, annual survival rates ($\bar{s}_{0-1}$) of non-breeding beaver (Tables 5 and 6) may also reflect the timing of harvest. The low average, annual survival ($\bar{s}$) of breeding age beaver, coupled with the fact there are only six age classes represented in the combined sample, points to intensive trapping pressure on the Missouri River study area.

The average annual survival rates ($\bar{s}_{1-2}$) were .56 and .55 percent for males and females, respectively, when age classes 1 and 2 were combined to compensate for the low frequency of age class 1 individuals. The annual survival rates for age classes 0-2 in both male and female cohorts remains almost constant. The low average annual survival rate of breeding beaver ($\overline{s}$) may also be a reflection of insufficient sample size.

The inversion of frequencies of age classes 0-3 (Tables 5 and 6), and the disparity between survival rates of breeding and nonbreeding segments of the beaver population may violate the assumption of stability. It remains the best estimate possible from these data, and survival estimates from the life tables were adjusted by the assumed annual rate of change in population size before a final estimate of population stability was made (Tabor 1974).

Age Stability

Age stability of the beaver population in this study was estimated using formula 2 of the general population model as developed by Henny et al. (1970).

$$1 = m_1 s_0 (1 + \mu)^{-1} + m_2 s_0 s_1 (1 + \mu)^{-2} + m_3 s_0 s_1 s_2 (1 + \mu)^{-3} + \ldots$$

where m_x = age specific recruitment rate of female pups per breeding female per year,

s_x = age specific female survival rate,

μ = average annual rate of change in population size.

This population model is an evaluation of the balance between recruitment and mortality. An exact balance between recruitment and mortality for as many age classes as appear in the population equals 1 or an age stable population. Calculation of μ directly from the equation by entering only survival and recruitment rates and solving for μ was not appropriate because the survival estimates made using the time specific life table method could not be adjusted to correct for change in population size (Tabor 1974:40). Therefore, various values for μ must be assumed using a trial and error method. These assumed values of μ were plugged into the equation until one was found which balanced the equation. Using the trial and error method, it is not necessary to assume the population is stationary because it is possible to adjust the survival estimates from the time specific life table for any increase or decrease in population size.

Survival estimates, using the trial and error method, were modified by assuming each value of μ by the following formula used by Tabor (1974:41):

$$s'_x = \frac{\bar{s}_x}{(1+\bar{\mu})^{-1}}$$

where s'_x = adjusted, age specific, annual female survival rate used in the population model,

$\bar{s}_x$ = age specific, annual female survival rate as calculated by the life table procedure,

$\bar{\mu}$ = assumed, annual rate of change in population size.

The modified survival estimates (s'_x), the average annual recruitment rate (m), and an assumed value for $\bar{\mu}$ are plugged into formula (2) of the general population model (Henny et al. 1970).

Using survival estimates from the time specific life table (Table 6), a value of -0.39 for μ' balanced the population model. This indicated a 39 percent annual decline in the beaver population and conflicts with results obtained using the life equation method of Henry and Bookhout (1969) which indicated a 17 percent annual increase in the beaver population.

The general population model (Henny et al. 1970) uses more precise estimates of survival and evaluates annual stability for as many years as age classes appear in the harvested sample. The general population model is likely to provide more accurate estimates of population stability than the life equation model.

Age specific survival rates in the older age classes from the time specific life table (Table 6) may be underestimated due to the insufficient sample size, causing an overestimate of the percentage decline.

Colony Count Index

The colony count index provides another estimate of population stability for the period between the 1974-75 and 1975-76 sampling seasons. Fifty two colonies in the unstabilized subsection and five colonies in the stabilized portion of the study area were located during winter 1974-75. The colony count in winter 1975-76 yielded 48 colonies in the unstabilized subsection and only two colonies in the stabilized portion of the study area. This represents a 15.3 percent overall reduction in colony numbers, 11 percent in the unstabilized subsection and 60 percent in the stabilized portion of the study area from winter 1974-75 to winter 1975-76. Assuming the size of the beaver colonies remains constant, the colony count may be used as a rough index of population trend. This index indicates a 15.3 percent annual decline in the beaver population in the study area.

Colony Size

Undisturbed beaver colonies during winter months normally contain an adult boar and sow, the young of the year, and the surviving yearlings from the previous year (Bradt 1938). The mean number of beaver per colony in trapped areas varies with the population size, skill of local trappers, fur prices, and weather conditions.

Thirty one colonies trapped during the 1974-75 and 1975-76 seasons produced a mean of 3.4 beaver per colony. This figure was considered minimum as an estimate of colony size because colonies were not completely exterminated in most instances. Longley and Moyle (1963) in Minnesota found 5 to 6 beaver per colony in trapped areas. This agrees closely with 5.1 beaver per colony in Michigan (Bradt 1938) and 5.3 beaver per colony in Virginia (Swank 1949).

Population Density

Beaver population density in the study area was estimated by multiplying the mean number of colonies between the two sampling seasons by both the minimum estimate from the extermination census, and an estimate of colony size from previous studies. The mean number of colonies per year through both sampling periods was 51 in the unstabilized subsection of the study area. The beaver population calculated using 3.4 beaver per colony (from the extermination census) and 5.0 beaver per colony (from literature) was 173 and 255 beaver, respectively, in the unstabilized portion of the study area.

The mean number of beaver colonies in the stabilized subsection, over the two season sampling period, was 3.5 colonies. Applying estimates of colony size, the beaver population in the stabilized subsection of the study area was estimated at 12-17 beaver.

The overall estimate of population size combining the stabilized and unstabilized subsections is 185-272 beaver. In the 1975-76 trapping season, 128 beaver harvested from the study area were recorded by this study. Based on above population estimates, 128 beaver is 47-69 percent of the total population.

Bradt (1947:43) said maximum allowable annual loss is 50 percent provided the mortality is evenly distributed through all age and sex groups. An annual harvest of 25 percent should allow a steady increase, and a loss of 33.3 percent of the total population should be satisfactory to maintain the population or permit a slow increase. The annual harvest from the Missouri River study area, applying Bradt's percentages, should be approximately 50-75 beaver per year. The actual harvest of 128 beaver in 1975-76 was an overharvest and probably accounted for the 15.3-39 percent annual decline estimated in this study.

Ecology of Beaver Colonies

Placement of the study area permitted comparison of beaver populations living in stabilized and unstabilized subsections of the Missouri River study area. Little literature was devoted to the physical setting which a beaver colony selects for its den site in the lotic environment. Physical features as vertical shoreline profile, current speed, water depth, and distance to nearest food source were examined in this study.

Colony density

The colony density per river km is highly variable, especially in the native, unstabilized river. Overall colony density is considerably higher in the unstabilized portion than in the stabilized subsection. Probable causes for the difference in colony density were availability of den sites and differences in accessibility of food sources. To test the hypothesis that there was no difference in colony density between the stabilized and unstabilized subsections, the number of colonies per km in the stabilized subsection (31.6 km) was compared to the number of beaver colonies per km in 31.6 km of unstabilized river immediately above the stabilized area.

The mean number of beaver colonies in the stabilized subsection (1974-75) was 0.16 colonies per km and 0.75 colonies per km in the unstabilized sample area. The mean difference was highly significant ($t = 3.73$; $P < 0.01$; 19 d.f.). During the winter of 1975-76, the mean number of colonies dropped to 0.06 colonies per km in the stabilized subsection and 0.50 colonies per km in the unstabilized sample area. This difference was also highly significant ($t = 2.99$; $P < 0.01$; 19 d.f.).

Current speed

At 2 m from the shoreline, the mean current speeds were 0.42, 0.29, and 0.23 m per second for the random stabilized points, the random unstabilized points, and at all beaver dens, respectively. The mean current speed in the stabilized subsection was significantly different from both the unstabilized subsection ($t = 3.9$; $P < 0.01$; 49 d.f.) and the beaver den points ($t = 3.2$; $P < 0.01$; 87 d.f.). Comparing the unstabilized points and the beaver den points produced no significant difference ($t = 2.0$; $P < 0.05$; 87 d.f.).

Current speed measured 3.5 m from the shoreline at 50 random stabilized, 50 random unstabilized, and at all beaver dens provided means of 0.69, 0.49, and 0.42 m per second, respectively. There were no significant differences at 3.5 m from the shoreline ($t = 1.830$; $P < 0.05$; 49 d.f.) between means of the 50 random stabilized and 50 random unstabilized points. There was a highly significant difference ($t = 4.3$; $P < 0.01$; 87 d.f.) when current speed, 3.5 m from the shoreline, at beaver dens was compared to 50 random stabilized points, and a significant difference ($t = 2.0$; $P < 0.05$; 87 d.f.) when compared to 50 random unstabilized points.

These tests indicated that beaver were selective for areas with slower current speeds when building dens and food caches. The mean current speed in the bank stabilized subsection of the Missouri River study area was 1.5 times faster than the mean current speed in the unstabilized subsection. Possibly, the current speed of the stabilized subsection contributes to the lower density of beaver colonies.

River Depth

River depth 2 m and 3.5 m from the shoreline was measured at 50 random stabilized points, 50 random unstabilized points, and at points located at all beaver dens. Mean river depths 2 m from the shoreline were 0.63, 0.54, and 0.71 m, respectively, for the groupings. Mean river depth 2 m from the shoreline was deeper at the beaver dens than either the random stabilized or random unstabilized points. The shallowest mean river depth (2 m from the shoreline) occurred in the unstabilized section. There was a highly significant difference ($t = 2.8$; $P < 0.01$; 97 d.f.) between the mean depth at the beaver dens and the mean depth at the random unstabilized points. Comparison of the mean river depth in the random stabilized points to the mean river depth in the unstabilized subsection yielded no significant difference ($t = 1.5$p $P > 0.05$; 97 d.f.). There was no significant difference ($t = 1.29$; $P > 0.05$; 97 d.f.) between the mean river depth 2 m from shoreline at the 50 random stabilized points and the mean river depth at all beaver dens.

Measurement of river depth 3.5 m from the shoreline at 50 random stabilized, 50 random unstabilized, and at all beaver dens produced means of 1.13, 1.58, and 1.71 m, respectively. The mean river depth in front of the beaver dens was greatest. The difference in means was not significant (t = 1.0; P >0.05; 97 d.f.) when compared to the random unstabilized points, but was significantly different (t = 2.29; P > 0.05; 97 d.f.) from the 50 random stabilized points. The mean difference between the random stabilized points and the random unstabilized points was highly significant (t = 2.842; P < 0.01; 49 d.f.).

Mean river depths were greatest (2 m and 3.5 m from shoreline) in front of the beaver dens indicating that beaver prefer deeper water for den and food cache sites. There was no significant difference (2 m from the shoreline) in mean river depth between the stabilized subsection and the unstabilized subsection. This indicates that river depth was not related to the low beaver population density in the stabilized subsection of the study area.

Distance from Dens to Food Supply

Food caches in the study area were almost exclusively comprised of cottonwoods and willows. The distance from each den to the nearest stand of cottonwoods and willows was measured in both subsections of the study area. The mean distance from dens to cottonwood trees was 95 m in the stabilized subsection and 21 m in the unstabilized subsection. The difference in means was not significant (t = 0.972; P > 0.05; 55 d.f.), probably due to the small sample size (5 dens) and high standard deviation in the stabilized subsection.

The distance from beaver dens to willows was less than 1 m at 78 percent of all beaver dens in the study area. The mean distance from dens to willows was 1.4 m in the stabilized subsection and 6.4 m in the unstabilized subsection. This mean difference was not significant ($t = 1.79$; $P > 0.05$; 55 d.f.).

Bank Profile

Vertical bank profile on the unstabilized subsection of the Missouri River study area is of two types: high-cut (2-6 m, with no rooted vegetation) or low-tapered (<2 m, rooted vegetation usually to the water line). In the unstabilized subsection, the shoreline is comprised of 84.4 km of low-tapered and 105.6 km of high-cut bank profile; a ratio of 1:1.25.

Thirty three beaver dens occur on low-tapered bank profile, and 15 beaver dens were built on high-cut bank profile in the unstabilized subsection. The beaver dens exist at a ratio of 1:0.49 low-tapered to high-cut. The ratio of dens on low-tapered:dens on high-cut bank profile is significantly different ($\chi^2 = 11.5$; $P < 0.01$; 1 d.f.) than the ratio in which those bank profiles exist. Beaver apparently were selecting low-tapered bank profile for den placement in the unstabilized subsection of the study area.

Vertical bank profile on the stabilized subsection of the Missouri River study area consisted of either granite revetments and wing dams that solidly covered the shoreline or low-tapered bank profile similar to that in the unstabilized subsection.

Seven active beaver dens were located in the stabilized subsection of the study area during the two sampling seasons. Six dens were located in low-cut bank profile behind wing dams, and one was built on the face of a granite revetment. No statistical comparison was made because of the small sample size and the difficulty in measuring shoreline distances on wing dams. The low percentage of beaver dens built on the granite revetments does, however, suggest that beaver are selective for low-tapered bank profile in the stabilized subsection. The single beaver den built on the granite revetment was active only during one of the two seasons studied.

CONCLUSIONS

This study was undertaken primarily to determine the population status of beaver on the Missouri River in southeastern South Dakota. Three estimates of annual rate of population change were made. A 17 percent annual increase was estimated by a life equation analysis, but use of the juvenile segment of the harvested age structure as the sole estimate of overall juvenile mortality probably rendered the life equation unreliable. It is not known whether fur harvest is an added source of mortality or whether it is compensated for by reduction in other mortality factors. If fur harvest is added mortality, the life equation would grossly overestimate the annual rate of increase. This overestimate appears to have occurred in this study.

Population modeling provided a second estimate of beaver population stability in the Missouri River study area. Application of the model indicated a 39 percent annual decline in the beaver population. The population model used in this study had the advantage of evaluating stability for as many years as age classes appear in the sample. However, the large fluctuations in mortality from year to year caused by changes in fur price, changes in weather conditions, changes in trapping season length, or other factors may invalidate the use of life table methods to estimate the survival values needed in the population model.

The third estimate of annual rate of population change, the colony count index, showed a 15.3 percent decline in colony numbers between the sampling seasons. This estimate of population trend does not rely on assumptions dealing with the harvested sample. It does assume that there is no difference in den visibility from one year to the next. The degree of bias due to visability was not tested in this study; however, it was minimized by making three complete ground counts each year, two in the late fall and one in the early spring. Use of the colony count index requires the assumption that colony size remains constant from year to year. The difficulties in testing this assumption are well documented in this study. It still may be a reasonable assumption because pair bond formation takes place prior to the preparation of a winter den. Family units fragmented by removal of the adult sow or adult boar in the previous spring are restructured prior to the preparation of a new winter den and food cache for the upcoming winter.

The colony count index only measures change between two or more successive counts. This disadvantage is balanced by the low number of assumptions made in using it, and it may be the most accurate method. There is less time, money, and equipment involved in performing this count than in either of the other methods used to predict annual population change.

Appraisal of the three methods, their assumptions, and general reconnaisance on the river over the past years leads to the conclusion that the population declined from 1974-75 to 1975-76. Individuals experienced at trapping beaver on the study area agree with this conclusion.

The minimum breeding age of female beaver in the harvested sample as observed in this study was 2.5 years. Considering that only 14.3 percent of the females in the sample were 2.5 years old or older, the beaver population cannot expand with sufficient speed to offset a continual heavy removal of beaver during several years of high fur prices.

Since most beaver management consists of limiting the harvest by manipulation of the season length, the annual percentage of harvested beaver should be continually monitored, especially in years of high fur prices and mild weather conditions. Based on population estimates in this study, 47 to 69 percent of the beaver present in the study area at the beginning of the 1976 spring trapping period were removed. Weather conditions were ideal during spring, 1976, but the beaver fur price was only moderate. Restrictions in trapping season length should be implemented for at least two seasons following a year of high removal (in excess of 50 percent of the population).

River stabilization and high beaver populations do not occur together in southeastern South Dakota on the Missouri River. Further stabilization of the free-running Missouri River in southeastern South Dakota is currently being planned. It can be reasonably assumed from data presented in this study that river stabilization comparable to that in the stabilized subsection of the study area will virtually eliminate the current beaver population now existing on the free-running Missouri River in southeastern South Dakota. As stabilization proceeds, it may be necessary to completely restrict consumptive use of the remaining beaver population. The aesthetic value of beaver on the Missouri River is difficult to measure and should be protected for future generations.

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APPENDIX 1

APPENDIX 1

Table 1. Summary of beaver specimens 1974-76.

Specimen number	Date harvested	Sex	Age (years)	Total weight (kg)	Pelt size (cm)	Total length (cm)	Tail length (cm)	Tail width (cm)	Hindfoot length (cm)	Ear length (cm)	Corpora lutea	Fetuses
1	11/17/74[a]	M	4	23.4	174.0	114.3	27.9	15.8	20.1	3.2		
2	11/24/74[a]	F	1.5	14.0	154.9	101.6	25.4	13.3	16.5	2.9	0	0
3	11/29/74[a]	F	1.5	13.4	148.6	101.3	26.4	13.7	16.3	2.9	0	0
4	11/30/74[a]	F	2.5	17.2	161.3	108.0	26.7	12.7	17.8	2.9	0	0
5	3/1/75	M	4	20.0	168.9	107.2	27.7	13.0	18.0	3.2		
6	3/1/75	F	3	16.1	158.8	98.0	23.1	12.3	17.3	2.9	3	1
7	3/3/75	M	5	26.1	188.7	115.8	31.8	14.6	17.8	3.2		
8	3/3/75	M	4	24.3	181.6	115.8	31.8	15.5	17.8	3.5		
9	3/4/75	F	1	10.3	135.9	86.4	22.9	12.1	15.5	2.9	0	0
10	3/4/75	F	1	12.7	144.3	89.4	23.4	11.4	15.7	3.2	0	0
11	3/4/75	F	2	16.4	160.0	102.9	27.9	14.3	17.3	3.5	0	0
12	3/5/75	M	1	11.3	137.2	84.8	23.9	11.4	15.8	2.9		
13	3/5/75	M	1	7.2	119.4	77.5	19.0	8.9	14.7	2.9		
14	3/5/76	M	3	21.3	171.5	112.0	29.5	13.7	18.0	3.2		
15	3/6/75	M	1	11.1	133.4	90.2	22.9	11.4	15.8	3.2		
16	3/6/75	M	2	16.6	158.8	100.3	26.7	14.3	18.0	3.2		
17	3/6/75	F	1	10.4	137.2	86.9	23.4	10.8	15.8	3.2	0	0
18	3/8/75	F	2	14.9	156.2	100.3	25.4	13.0	18.0	3.2	0	0
19	3/9/75	M	2	16.4	157.0	97.0	23.4	12.1	17.5	3.2		
20	3/9/75	F	3	19.6	167.6	106.7	26.7	13.3	18.3	3.2	3	3
21	3/10/75	F	1	13.5	144.8	99.1	27.4	12.1	17.3	3.2	0	0
22	3/10/75	M	4	24.5	182.9	119.4	33.0	16.5	19.8	3.5		
23	3/10/75	F	1	13.5	148.6	94.5	25.9	12.4	16.8	2.9	0	0
24	311/75	F	1	12.6	143.5	96.0	24.9	12.4	17.3	3.2	0	0
25	3/11/75	F	3	25.4	182.9	115.3	29.0	15.6	19.0	3.8	5	5
26	3/11/75	F	3	23.1	174.0	110.2	26.4	15.2	18.8	3.5	3	3
27	3/11/75	M	3	21.3	171.4	110.7	28.2	13.7	18.8	3.5		
28	3/11/75	M	2	16.7	161.3	101.6	24.8	13.7	17.5	3.2		
29	3/12/75	M	1	12.5	142.2	94.0	25.4	12.1	16.8	2.9		
30	3/12/75	F	2	15.9	152.4	99.3	25.2	12.1	18.0	2.9	0	0
31	3/12/75	F	3	20.2	167.6	108.2	29.5	14.0	17.8	3.2	1	1
32	3/15/75	M	2	16.3	132.1	103.6	27.4	14.3	18.0	3.2		
33	3/15/75	M	3	19.3	168.9	104.1	26.7	14.3	17.8	3.2		
34	unknown[a]	F	3.5	21.1	168.9	111.5	27.7	13.3	17.8	3.2	0	0

[a] Collected prior to onset of ovulation and breeding season.

APPENDIX 1

Table 1. Continued

Specimen number	Date harvested	Sex	Age (years)	Total weight (kg)	Pelt size (cm)	Total length (cm)	Tail length (cm)	Tail width (cm)	Hindfoot length (cm)	Ear length (cm)	Corpora lutea	Fetuses
35	12/14/75	M	2	18.6	166.4	101.0	26.0	14.0	17.5	2.9		
36	12/14/75	F	1	6.1	116.8	76.2	19.7	7.9	14.0	2.5	0	0
37	1/24/76	F	2	16.0	157.5	101.6	25.4	12.1	17.8	3.2	0	0
38	1/24/76	M	1	7.1	116.8	81.9	21.6	10.8	14.6	3.2		
39	2/7/76	F	1	12.9	152.4	101.6	26.0	12.1	17.5	3.2	0	0
40	2/10/76	M	3	22.0	171.5	113.0	30.2	14.6	18.4	3.5		
41	2/10/76	M	2	16.0	156.2	101.9	26.3	14.3	16.8	3.2		
42	2/10/76	M	1	13.4	151.1	95.3	24.1	11.7	16.2	3.2		
43	2/10/76	F	3	21.0	167.6	104.5	27.0	15.6	17.8	3.2	4	4
44	2/11/76	M	1	12.6	142.2	93.0	23.2	12.1	16.8	2.9		
45	2/12/76	M	1	11.2	142.2	90.2	23.5	12.7	16.2	2.9		
46	2/12/76	M	3	22.7	179.1	112.4	29.8	16.5	18.7	3.5		
47	2/12/76	M	4	23.9	176.5	113.7	29.2	14.3	18.4	3.5		
48	2/13/76	M	2	18.2	167.6	101.6	25.4	12.7	17.5	3.2		
49	2/13/76	M	3	20.0	168.9	107.3	28.6	13.3	18.4	3.5		
50	2/14/76	M	4	27.5	184.1	112.1	28.3	17.5	19.1	4.1		
51	2/14/76	M	1	11.6	141.0	92.4	23.8	11.1	16.5	3.2		
52	2/15/76	F	3	17.3	166.4	109.5	28.3	12.7	17.8	3.2	0	0
53	2/15/76	F	3	21.8	171.5	112.4	29.8	15.9	18.7	3.2	0	0
54	2/15/76	F	4	25.0	176.5	110.5	27.9	14.3	18.4	2.9	5	5
55	2/15/76	F	1	11.3	141.0	84.8	22.5	10.8	15.9	3.2	0	0
56	2/16/76	F	3	22.4	168.9	108.3	25.7	15.2	17.8	3.5	6	6
57	2/16/76	M	3	20.0	160.0	104.5	25.7	14.0	18.1	3.2		
58	2/17/76	F	3	19.8	165.1	105.7	27.0	14.3	18.4	3.2	3	3
59	2/17/76	M	1	13.4	142.2	92.7	24.1	11.4	16.2	3.2		
60	2/17/76	M	3	21.4	167.6	107.3	26.0	15.9	18.7	3.2		
61	2/17/76	F	1	9.5	134.6	87.6	21.6	11.1	15.9	2.5	0	0
62	2/18/76	M	3	25.7	174.0	116.2	29.8	16.5	18.4	3.2		
63	2/18/76	M	3	25.1	175.3	117.5	30.5	18.1	19.7	3.2		
64	2/18/76	M	3	21.5	167.6	111.4	27.6	12.7	18.1	3.5		
65	2/18/76	M	1	6.9	121.9	78.7	19.7	8.9	14.3	2.5		
66	2/18/76	M	1	7.3	119.4	76.8	19.1	9.5	14.0	2.9		
67	2/18/76	M	3	22.5	171.5	109.2	27.9	17.8	18.7	3.2		
68	2/19/76	M	1	11.5	141.0	92.7	23.5	11.4	16.2	2.9		

APPENDIX 1

Table 1. Continued

Specimen number	Date harvested	Sex	Age (years)	Total weight (kg)	Pelt size (cm)	Total length (cm)	Tail length (cm)	Tail width (cm)	Hindfoot length (cm)	Ear length (cm)	Corpora lutea	Fetuses
69	2/19/76	M	1	13.7	142.2	93.7	23.2	11.4	16.5	3.2		
70	2/19/76	M	1	12.4	143.5	88.9	21.6	10.5	16.2	2.9		
71	2/19/76	M	1	13.4	147.3	93.3	22.2	14.9	15.9	2.5		
72	2/19/76	M	1	10.7	134.6	88.9	22.9	10.8	16.2	2.9		
73	2/19/76	F	3	25.2	181.6	115.3	28.9	16.5	19.1	3.2	7	6
74	2/19/76	F	2	17.4	160.0	108.6	29.8	13.7	17.8	3.2	0	0
75	2/19/76	M	5	28.0	193.0	115.9	24.4	16.8	17.8	3.2		
76	2/19/76	M	1	13.1	149.9	97.5	24.4	10.8	16.5	2.9		
77	2/19/76	M	2	15.6	152.4	104.5	27.0	13.3	17.5	3.2		
78	2/19/76	F	3	20.9	170.2	107.3	26.0	14.3	17.8	3.2	0	0
79	2/19/76	M	1	10.3	139.7	92.7	24.1	11.4	14.6	2.9		
80	2/19/76	M	1	11.8	138.4	92.7	24.1	11.4	16.5	3.2		
81	2/19/76	M	3	18.4	167.6	106.4	26.4	14.6	17.8	3.2		
82	2/19/76	M	1	12.2	143.5	92.7	22.9	10.8	16.2	3.2		
83	2/19/76	M	4	17.3	166.4	109.2	25.4	12.7	17.8	2.9		
84	2/19/76	M	3	15.5	170.2	107.0	25.7	16.5	17.8	3.2		
85	2/19/76	M	1	12.7	139.7	95.9	22.9	9.5	16.2	2.9		
86	2/19/76	M	3	20.0	166.4	106.7	26.7	14.6	17.8	3.2		
87	2/19/76	M	1	13.9	152.4	96.2	22.5	12.1	16.2	3.2		
88	2/19/76	F	3	23.9	176.5	112.1	27.0	13.0	18.1	3.2	6	6
89	2/19/76	M	1	13.6	144.8	95.3	24.1	11.4	16.5	3.2		
90	2/19/76	F	2	14.0	153.7	99.7	25.4	14.0	17.8	3.2	0	0
91	2/19/76	M	1	10.9	139.7	91.4	22.2	12.1	15.9	3.2		
92	2/19/76	F	4	27.3	181.6	123.2	31.1	16.8	18.7	3.2	7	7
93	2/19/76	M	2	14.0	153.7	97.5	25.1	12.1	18.4	2.9		
94	2/19/76	M	1	7.9	123.2	81.9	18.4	9.2	14.0	2.5		
95	2/10/76	F	1	5.9	114.3	83.8	20.3	8.6	14.3	2.9	0	0
96	2/21/76	M	1	12.3	146.1	94.0	22.2	10.8	15.9	2.9		
97	2/21/76	M	1	12.5	146.1	92.7	22.9	14.3	16.5	2.9		
98	2/21/76	M	1	13.1	144.8	93.3	23.5	11.4	15.9	2.9		
99	2/21/76	M	1	11.7	138.4	86.4	20.3	10.8	15.9	2.9		
100	2/22/76	M	1	9.8	129.5	83.8	22.9	11.4	15.2	2.5		
101	2/22/76	F	4	26.1	182.9	119.7	28.3	17.8	19.1	3.5	5	5
102	2/22/76	M	1	7.9	123.2	78.7	20.3	9.5	14.9	2.9		

APPENDIX 1

Table 1. Continued

Specimen number	Date harvested	Sex	Age (years)	Total weight (kg)	Pelt size (cm)	Total length (cm)	Tail length (cm)	Tail width (cm)	Hindfoot length (cm)	Ear length (cm)	Corpora lutea	Fetuses
103	2/23/76	M	2	18.4	160.0	104.1	25.4	15.2	17.8	3.2		
104	2/23/76	M	3	19.5	167.6	110.5	27.9	15.2	19.1	3.8		
105	2/24/76	F	1	11.8	138.4	92.7	25.4	11.4	16.8	2.9	0	0
106	2/24/76	F	1	12.5	141.0	91.4	22.2	11.1	16.8	2.5	0	0
107	2/24/76	M	3	21.8	170.2	105.4	26.7	14.6	18.1	2.9		
108	2/24/76	M	3	21.4	167.6	105.7	25.7	14.9	18.1	3.2		
109	2/24/76	F	1	12.3	146.1	90.8	22.2	12.1	15.2	2.5	0	0
110	2/24/76	F	3	18.9	163.8	104.8	26.0	15.2	17.8	3.2	0	0
111	2/24/76	M	2	12.0	151.1	95.9	24.8	13.7	17.8	3.2		
112	2/24/76	F	2	18.6	167.6	102.2	26.0	14.3	18.4	2.9	0	0
113	2/24/76	M	6	25.5	177.8	114.3	29.2	17.1	19.1	3.2		
114	2/24/76	M	3	22.3	174.0	106.0	26.0	14.3	18.4	3.2		
115	2/25/76	F	1	10.2	132.1	89.2	23.2	10.2	16.2	3.2	0	0
116	2/25/76	F	5	30.2	194.3	123.5	32.1	19.1	20.9	3.5	4	4
117	2/25/76	M	1	8.2	127.0	80.1	20.3	10.8	14.9	2.5		
118	2/25/76	F	1	8.5	128.3	81.0	20.0	10.8	14.6	2.5	0	0
119	2/26/76	M	1	13.9	144.8	82.5	24.1	12.4	16.2	2.9		
120	2/26/76	F	1	11.8	139.7	89.5	22.9	11.4	16.5	2.9	0	0
121	2/26/76	M	1	13.0	143.5	93.0	21.9	11.4	16.5	2.9		
122	2/26/76	F	1	6.8	116.8	73.7	17.8	8.6	14.3	2.5	0	0
123	2/27/76	F	1	11.8	141.0	91.7	23.2	11.4	17.1	2.9	0	0
124	2/27/76	M	3	18.0	167.6	108.6	26.7	12.7	19.1	3.2		
125	2/27/76	M	3	20.1	167.6	106.7	26.7	14.6	18.4	3.5		
126	2/27/76	F	1	10.7	139.7	92.1	24.8	11.4	16.5	2.9	0	0
127	2/27/76	M	2	15.8	154.9	99.7	25.4	13.3	17.1	3.2		
128	2/27/76	F	6	28.4	179.1	112.4	27.3	16.5	18.1	3.2	9	8
129	2/27/76	F	3	22.6	177.8	115.6	33.0	15.2	18.7	3.2	0	0
130	2/28/76	F	1	10.0	144.8	94.6	26.0	12.7	15.9	2.5	0	0
131	2/28/76	F	1	10.0	137.2	88.9	22.9	10.2	17.5	2.5	0	0
132	2/28/76	M	3	18.3	161.3	104.1	26.7	12.1	19.1	3.2		
133	2/28/76	M	1	11.0	142.2	94.9	25.1	11.4	16.8	2.9		
134	2/28/76	M	4	25.4	176.5	109.2	25.4	15.2	17.8	3.2		
135	2/28/76	F	4	30.0	182.9	119.4	29.2	16.5	19.4	3.5	7	7
136	2/28/76	M	3	17.7	163.8	113.0	27.9	14.0	17.8	3.2		

APPENDIX 1

Table 1. Continued

Specimen number	Date harvested	Sex	Age (years)	Total weight (kg)	Pelt size (cm)	Total length (cm)	Tail length (cm)	Tail width (cm)	Hindfoot length (cm)	Ear length (cm)	Corpora lutea	Fetuses
137	2/28/76	F	6	25.5	177.8	112.7	25.1	15.9	18.7	3.2	6	4
138	2/28/76	F	2	14.5	141.0	98.7	25.1	12.4	17.5	2.9	0	0
139	2/28/76	F	1	10.7	141.0	91.4	22.9	11.4	16.2	2.9	0	0
140	2/28/76	M	1	9.9	132.0	93.0	22.5	12.4	16.2	2.9		
141	2/28/76	M	1	7.2	114.3	79.7	18.7	7.9	13.7	2.2		
142	2/28/76	M	3	18.6	166.4	106.4	26.4	15.2	17.5	2.9		
143	2/28/76	F	1	12.5	142.2	96.2	23.8	10.8	15.9	2.9	0	0
144	2/28/76	M	1	13.2	142.2	96.5	24.1	12.4	17.5	3.2		
145	2/28/76	F	1	10.9	142.2	94.6	24.1	11.7	15.9	3.2	0	0
146	2/28/76	F	3	18.4	167.6	109.2	26.7	14.0	17.1	3.2	0	0
147	2/28/76	M	3	18.9	168.9	106.0	26.0	15.2	18.1	2.9		
148	2/29/76	F	1	12.9	144.8	95.3	25.4	12.7	17.1	2.9	0	0
149	2/29/76	M	1	11.8	141.0	92.7	21.6	11.1	16.2	2.9		
150	2/29/76	F	4	33.6	196.9	121.9	29.2	17.8	19.7	3.5	5	5
151	2/29/76	F	4	28.2	182.9	119.4	30.5	17.1	18.4	3.2	4	4
152	3/2/76	F	3	20.0	174.0	114.3	30.5	16.2	18.7	3.2	5	5
153	3/8/76	M	2	14.5	147.3	98.4	24.1	12.1	17.5	2.9		
154	3/8/76	F	3	18.5	158.7	102.9	24.8	13.7	18.1	3.2	5	5
155	3/8/76	F	2	14.2	149.9	97.8	25.4	13.7	17.5	3.2	0	0
156	3/8/76	F	1	11.1	141.0	90.1	23.5	12.1	15.2	2.9	0	0
157	3/8/76	F	2	13.8	148.6	104.1	29.8	12.7	17.8	2.9	0	0
158	3/9/76	M	1	9.6	137.2	92.1	24.8	10.5	15.9	2.9		
159	3/9/76	M	5	25.4	189.2	119.4	27.9	15.9	18.4	3.2		
160	3/13/76	M	3	22.2	172.7	110.5	26.7	15.2	19.1	3.5		
161	3/13/76	F	1	10.0	138.4	92.1	22.9	10.5	15.9	2.9	0	0
162	3/13/76	F	2	17.0	158.7	104.8	27.3	14.9	17.8	3.5	0	0