T H E S I S

BEAVER CARRYING CAPACITY OF CERTAIN MOUNTAIN STREAMS IN NORTH PARK, COLORADO

Submitted by

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Chapter I

INTRODUCTION

The beaver (Castor canadensis Kuhl)[1] has long been considered one of the more important wildlife species in the western states. Unique ability to alter its environment, and unusual adaptability to varied habitat types, give it an importance in bringing about ecological changes that surpasses that of perhaps any other animal. These changes affect not only the beavers themselves, but also exert a considerable influence upon other wildlife and plant associations, and upon watershed management. Therefore, the relative merits of the beaver in its relationships to man -- its harmful habits and beneficial attributes -- have been the subject of much discussion and controversy.

During the past half century, beaver populations in Colorado have increased substantially as the result of more or less suitable range and nearly complete protection. Beavers have now reached such numbers, especially on public lands, that some plan of management is essential in order that the animals may be kept within limits compatible with good land-use practices.

In any management plan involving animal life, it is essential to know the carrying capacity of the area involved. The beaver

1/ See Appendix A for a complete list of common and scientific names of plants and animals used in this dissertation.

is no exception; its present and potential food supply, involving both utilization and waste, must be determined. Thus, successful management requires not only that the amount of food be known, but also the replacement factors affecting the food supply. Only this sort of information permits evaluation of both use and production in determining the carrying capacity for beavers on any given range.

The problem

What are the food requirements of a colony of beavers for sustained occupancy of a section of stream?

Problem analysis.--The problem has been analyzed into the following questions:

1. What amount of food is required per beaver per year, including waste and use in construction?

2. What are the factors determining the availability of a beaver food supply?

3. What are the growth and reproduction factors involved in a beaver food supply?

4. What is the seasonal variation in beaver use of different food species?

5. How does the age of a beaver colony affect its food supply and hence the carrying capacity of the inhabited area?

6. How do the various physical factors of the site affect a beaver food supply?

7. How may knowledge of the various factors involved in beaver carrying capacity be applied to beaver management?

Delimitations.--The study has been limited to five beaver colony sites. These are located on four distinct streams or minor drainages found in the watershed of the North Fork of the North Platte River in the Routt National Forest, Colorado, at an elevation of approximately 8,600 feet above mean sea level. The study is further limited to the summer and fall seasons of 1954 and 1955.

Definition of terms.--Carrying capacity is the number of beavers which can exist indefinitely on a section of stream without depleting its food supply.

Colony, as used in this study, indicates a group of beavers occupying a section of stream in common and utilising a common series of dams, a common food supply, and inhabiting a common lodge or lodges.

Physical factors constitute such features of the habitat as stream gradient, stream flow, valley width, rock type, and slope.

Beaver food, for the purposes of this study, is limited to aspen (Populus tremuloides Michx.), willow (Salix spp.), alder (Alnus tenuifolia Nutt), birch (Betula glandulosa Michx.), and sedges (Carex spp.).

Stand table, as used in this study, is an estimate, in tabular form, of the total number and size of all woody plant species found on each colony site. This was determined from systematic line transects and cover maps.

Food preference, as used in this study, indicates the use of one species of food, or one size class of a food species, over another of equal or greater abundance.

Chapter II

REVIEW OF LITERATURE

This review of the beaver literature is an analysis of selected references pertaining to the animal's food and space requirements and, therefore, carrying capacity. Of the many studies related to carrying capacity, a great percentage are of local application. Some of the more important are considered here, and all pertinent investigations of general application known to the writer are included. In Chapter VI the findings of other workers will be compared, where applicable, with those of the present study.

Amount of food required by beavers

Several different approaches have been used in attempting to determine the food requirements of beavers. Perhaps the most indicative, all things considered (i.e. construction use, waste, etc.), are those studies which have enumerated the number of stems cut by beavers over a given period of time. Thus, Bradt (1938, 1947), Aldous (1938), Nash (1951), Lawrence (1954), Shadle and Austin (1939), Shadle et al.(1943), Stegeman (1954), Hodgdon and Hunt (1953), and Hazeltine (1950) conducted studies of this general nature. The results show great variation, as would be expected, and no attempt will be made to consolidate them. Instead, a few representative examples are cited below:

Bradt (1947) studied beavers on two Michigan lakes. The results are summarized in Table 1. Aldous (1938), in Minnesota, summarized data by diameter class and pounds of food available (the result of peeling and weighing studies), and percentage of waste. Results are given in Table 2.

Table 1.--FOOD UTILIZATION ON TWO MICHIGAN LAKES (Bradt, 1947).

House Lake, 1929; 345 trees cut by two beavers in 223 days; 0.772 trees per beaver per day, 282 trees per beaver per year.

House Lake, 1930; 1,040 trees cut by six beavers in 353 days; 0.491 trees per beaver per day, 179 trees per beaver per year.

Piper Lake, 1930; 283 trees cut by two beavers in nine months; 0.524 trees per beaver per day, 188 trees per beaver per year.

Averaging the figures from the above three counts: 0.592 trees per beaver per day, 216 trees per beaver per year.

Aldous (loc. cit.) further reported that in one year five colonies cut 456 aspens, or an average of 91.2 trees per colony.

Shadle and Austin (1939) credited two adults with cutting 116 trees from one to 13 inches in diameter in their first year of occupation of a given site. From August 11 to November 11 the same adults, plus two young, felled 266 trees from one to 15 inches in diameter. Nash (1951) determined the average annual cuttings per colony to be 130 trees, with a range of 40 to 240. He believed that averages would prove misleading. Data from Bradt (1938) showed that beaver colonies used 200 to 300 aspens per year, or approximately 0.6

trees per beaver per day. Haseltine (1950) listed a range of 21 to 514 trees cut in one year. The average per year for two flowages was 271.3 aspens; all species cut (except alder) averaged 589.6 on one area and 1,278 on the other. Inclusion of alder would have added at least 1,000 stems to each area.

Table 2.--ASPEN UTILIZATION ON FIVE MINNESOTA BEAVER COLONIES (Aldous, 1938).

Stump Diameter, inches	No. of Trees	Pounds of Available Food	Percent of Waste
1	9	19	20
2	57	276	12
3	66	730	50
4	72	1,474	63
5	87	2,020	63
6	69	4,080	65
7	45	3,943	66
8	29	3,238	70
9	9	1,080	74
10	9	1,080	54
11	4	480	59

Haseltine (loc. cit.) noted that the total number of trees cut by one colony did not increase with increase in animal numbers beyond the original pair of beavers. No explanation was suggested, although it is conceivable that, at least in part, the original construction needs may have accounted for the situation.

Another approach to food requirements has been the feeding of beavers in captivity. O'Brien (1938) conducted studies with captive animals, mostly in relation to species preference. He did find, however, that each captive beaver requires one two-inch tree per day.

A two-inch tree contained 5.4 pounds of beaver food. Bailey (1927) concluded that feeding captive beavers one one-inch aspen per day was sufficient, and a study reported by Bradt (1947) concurred with this statement.

A third phase of the problem is the amount of beaver food on trees of various diameters. Two studies, O'Brien (1938) and Aldous (1938), have provided information. Both investigators proceeded by peeling and weighing the bark and leaves of aspens of various diameters. Aldous peeled branches to a diameter of one-half inch, and O'Brien to a diameter of one-eighth inch. The results are summarized in Table 3.

Table 3.—AMOUNT OF BEAVER FOOD IN ASPENS OF VARIOUS SIZES (O'Brien, 1938 and Aldous, 1938).

Diameter, Inches	Average weight in pounds		No. of trees peeled	
	O'Brien	Aldous	O'Brien	Aldous
1	3.60	1.80	15	10
2	5.40	5.89	11	13
3	11.09	13.22	11	10
4	18.80	27.72	12	10
5	28.10	45.04	10	10
6	45.80	75.15	10	11
7	60.00	105.98	9	10

Much of the variation shown in the results of the two studies may be explained by the fact that O'Brien peeled twigs to a smaller diameter, and thus weighed less woody material.

Warren (1940) noted that in feeding beavers in a natural pond, with no other food available, one ton of green aspen was

required for each beaver per year.

Size distribution of trees cut

The size of trees cut by beavers obviously varies with the size of trees available. Most studies demonstrate, however, that the preference is definitely for smaller trees. Bradt (1947) determined an average diameter of 2.1 inches for trees cut. An important study in Maine, Hodgdon and Hunt (1953), showed the following, Table 4.

Table 4.--SIZE DISTRIBUTION OF TREES CUT (Hodgdon and Hunt, 1953).

All Species		Aspen Alone (44.6% of total)		
Diameter Inches	Percent Cut	Diameter Inches	Percent Cut	Number Cut
1	68.2	1	50	1,207
2	20.5	2	27	654
3	6.2	3	11	255
4	2.4	4	5	116
5	1.4	5	3	71
6	1.1	6	2	57
7	0.1	7	0.9	6
8	0.1	8	0.9	6
		9	0.1	1
		—	—	—
		—	—	—
		12	0.1	1
			100	2,374

The size distribution found by Aldous (1938), Table 2, shows cutting of a much larger average size of trees, which is best explained by availability.

Shadle et al.(1943) give similar data, summarized in Table 5.

Table 5.--SIZE DISTRIBUTION OF CUTTINGS ON SIX NEW YORK BEAVER COLONIES (Shadle et al. 1943).

Size Distribution, All Genera			Size Distribution, Aspen		
Diameter, Inches	Cut	Percent Cut	Diameter, Inches	Cut	Percent Cut
1	2,830	52.1	1	476	26
2	1,211	22.3	2	465	25
3	520	9.6	3	281	15
4	297	5.4	4	175	9.5
5	164	3.0	5	116	6.5
All larger	402	7.6	6	103	5.5
			7	58	3.5
			8	39	2.5
			9	34	2.0
			10	35	2.0
			11	10	0.5
			12	21	1.0
			13	11	0.5
			All larger	10	0.5

Mills (1913) stated that beavers prefer trees under six inches in diameter, and Shaw (1948) found the majority of trees used for food to be in the two-inch to six-inch classes. It is evident that these statements are well corroborated by the studies reported above. Variation in availability of various size classes probably constitutes the major source of difference in the several studies. No further generalizations can be drawn.

Amount of food wasted by beavers

Beavers are inclined to waste a considerable proportion of the woody food available to them. The amount has been found to vary considerably, and several factors appear to be responsible. Thus, almost invariably, waste is a factor that must be considered in

evaluating carrying capacity. The two most important factors in wastage are the failure of the animals to consume all the bark of trees cut, especially of larger trees; and the lodging of trees in dense stands.

Hazeltine (1950) noted that stems over four inches in diameter are seldom entirely stripped of bark. O'Brien (1938) found that beavers seldom use bark on that part of aspen trees over four or five inches in diameter. He hypothesized that the woody or "corky" bark may be unpalatable to the animals. Based on his tree-peeling studies, O'Brien (loc. cit.) estimated the wastage for trees six to eight inches in diameter as given in Table 6. In Table 7 his findings on the relationship of stem diameter to bark utilization are presented.

Table 6.--WASTE ON SIX TO EIGHT INCH TREES (O'Brien, 1938).

Diameter, Inches	No. of Trees	Av. Waste in Lbs.	Av. Consumption in Lbs.	Total Weight	Percent Waste
6	5	24.2	36.2	60.4	40.0
7	5	27.6	37.4	65.0	42.0
8	5	34.4	44.2	78.6	44.5

In a similar study, Aldous (1938) found that of 456 aspens cut, 27 percent were used completely, 44 percent used partially, and 29 percent were wholly wasted. He found the greatest proportion of complete waste in the four-inch to six-inch diameter classes. He further found that the food in one seven-inch tree one-half utilized equalled that in four three-inch trees completely used. Lawrence

Table 7.--RELATIONSHIP OF STEM DIAMETER TO BARK UTILIZATION (O'Brien, 1938).

Diameter, Inches	No. of Trees	Maximum Diameter Barked, Inches
2	6	Complete
3	11	"
4	8	"
5	8	4.5
6	9	5.5
7	5	5.0
8	7	5.5
9	2	5.5
10	3	6.5

(1954) classified food trees as utilized, partially used, and wasted. He found less lodging waste in trees over six inches in diameter, because their greater weight brought them through to the ground. Of 1,214 trees sampled, about seven percent were totally wasted. Shadle et al.(1943) cited 1.4 percent of the trees felled as total waste. They listed the factors of waste as: (a) poor felling, (b) trunks too large to handle and/or with corky bark, (c) limbs and trunks used for construction without removing edible portions, and (d) spoilage of food value by drying out. In a study in New York, Stegeman (1954) stated that the degree of utilization varies from 97.8 percent in one-inch trees to 64.4 percent in trees eight inches or larger. Gese and Shadle (1943) discovered that trees up to three inches in diameter are completely used, but that the greatest amount of available food, wastage considered, is afforded by six-inch trees. They further stated that the percentage of available food used depends on

varying wastefulness in the beaver's feeding habits. Most writers agree that the amount of waste depends in part on the abundance of food available.

Distance travelled for food

A definite limiting factor in the amount of food available to beavers is the distance they will forage for it. Reports in the literature vary considerably. The chief restriction seems to be local topography.

Hazeltine (1950) stated that, "Beaver apparently go farther to obtain food than to obtain construction material." (p. 31). Hodgdon and Hunt (1953) believed that only trees within 300 feet of the water should be considered as within the beaver's normal feeding range. Bradt (1947) found beavers travelling up to 650 feet from water for aspen. Swank (1949) referred to a beaver cutting 260 feet from the water and up a 40-percent slope. Hiner (1938) said that the distance travelled on water after food has no correlation with that on land, since towing presents no problem. When materials are cut up or down stream from the lodge, beavers transport them directly to the nearest water. The maximum distance of cuttings from the water observed by Hiner (loc. cit.) was 453 feet, with an average maximum for all colonies of 267 feet. The average elevation above the water was 39.5 feet. Longer forages were invariably made up steeper than average slopes. He believed that a beaver colony was able to subsist longer when the aspen supply grew on an incline. Warren (1927) found cuttings over 400 feet from the water, and Tevis (1950) told of beavers going 355 feet for aspen. Bailey (1927) gave 10 to 20 rods

(165 to 330 feet) as the normal limit of cutting, while Lawrence (1954) found beavers foraging a distance of five chains (330 feet) for food. Bradt (1938) gave 200 feet as the normal limit in foraging distance, 400 feet as the maximum, and one observation of 600 feet representing the extreme.

Where the topography is such that canal building is easy, beavers are enabled to harvest food a great distance from the colony site. Berry (1923) noted a canal 1,145 feet long, terminating at an aspen stand. This is perhaps the longest distance beavers have been observed to travel for food.

Growth and reproduction of food species

The rate at which various beaver foods, especially aspen and willow, will replace themselves after use is an important aspect of carrying capacity. Replacement must be considered both during beaver occupancy and after abandonment following exhaustion of the food supply.

Stegeman (1954), in an intensive study in New York, determined the growth rate of aspen and the size of trees producing the greatest amount of beaver food. It was indicated that the average growth rate of aspen up to one inch was 0.15 inches per year; and for larger trees, 0.249 inches. The amount of utilizable beaver food produced per acre per year for one-inch trees was 1,347 pounds; the average for all diameters was 530 pounds. The one-inch trees produced the greatest amount per year, and these trees averaged 6.6 years of age. Maximum height growth was in the three-inch trees.

The area under study was not considered a particularly good aspen site.

Gese and Shadle (1943), in a somewhat similar study, found maximum growth in four-inch trees. As mentioned under Amount of food wasted by beavers, the maximum amount of food with the minimum waste was in six-inch trees. Warren (1926b) stated that regeneration of aspen of usable size takes 20 to 50 years. Lawrence (1954) found that aspens two inches in diameter can be grown in 10 years or less. He further found an average of 13,000 root suckers per acre in beaver cuttings, and that they may develop up to 66 feet from the parent tree. Suckering of aspen is an aid in reproduction, but a pure aspen stand will not generally perpetuate itself. Grinnell et al.(1937) mentioned suckering of cut willow stumps in renewing the supply. Nash (1951) reported that in only one of 100 beaver-cleared areas was aspen reestablished.

Abandonment, reoccupation, and the influence of forest fires

Most writers are in agreement that beaver occupancy of a particular site is in many cases temporary. The obvious cause is that beavers tend to "eat out" their food supply. Where abundant suitable habitat exists, the animals simply move short distances and set up a new colony near to the abandoned one (Hodgdon and Hunt, 1953). Where over-populations of beavers exist, the problem of finding suitable habitat may be acute. In such areas Mills (1913) stated that beavers tend to harvest one more season's winter food before evacuating. Warren (1932) found that beavers will occupy, abandon

and re-occupy a site at various intervals (i.e., 1914, 1922, 1936). Swank (1949) noted a similar situation in which a colony site was eaten out and abandoned in 1941 and re-occupied in 1947.

Lawrence (1954) mentioned the effect of fire, logging, and wind-throw in creating the temporary forest succession stage of the aspen type, and thus controlling beaver distribution and abundance. He thought that forest fire control, and reduced logging in certain areas, tended to reduce future populations of beavers. Rutherford (1954) studied two streams in Colorado, one with, and the other nearly without, beavers. The chief reason for the presence of the animals on one stream was considered due to a "burn forest" of aspen and lodgepole pine; conversely, the slopes of the second stream were covered with a mature stand of Engelmann spruce and alpine fir in which fire had apparently never occurred. Stegeman (1954) also found that fire has a profound influence on beaver populations. Nash (1951) stated, "The poplar growth following a fire is a temporary or sub-climax sere and does not perpetuate itself." (p. 23). Packard (1947) found that deer and elk foraging may keep aspen reproduction down and otherwise decrease the beaver food supply.

Limiting factors

The chief limiting factors in beaver carrying capacity are inadequate food supply and insufficient water. Altitude also appears to be such a factor, since freezing in winter at high altitudes may be extreme. Packard (1947) listed one colony at 10,107 feet in Rocky Mountain National Park as probably the highest in the United

States. Olive (1951) noted a beaver colony at 10,800 feet in the north-central Colorado Rockies. The writer was informed by Don J. Neff (Colorado Cooperative Wildlife Research Unit graduate) of a beaver colony existing at more than 12,000 feet in central Colorado. This colony was above timber line, supported entirely by stunted willow growth. Baillie-Grohman (1882) thought 9,000 feet to be the altitudinal limit for beaver occupancy.

Townsend (1953) believed that population pressure may determine colony limits. Lawrence (1954) found home range to vary from seven to 33 chains (462 to 2,178 feet), but found it to be related to availability of food, not numbers of beaver. He believed that one-fourth mile approached the maximum proximity of colonies. He also found this factor to be of little value in determining carrying capacity. Stegeman (1954) found no known saturation point for beavers.

The chief effect of climate is on the food supply, as beavers will survive a temperature range of from -60° to 100+°F. (Nash, 1951). Cover is not considered a separate factor in carrying capacity, as it is an immediate requirement without which no beavers will be found (loc. cit.). Woody, rather than herbaceous, plants are considered in determining carrying capacity. Nash stated that ...

> ...due to the wide distribution of such plants, wherever the essential requirements of the beaver are found, the writer believes that they do not constitute a limiting factor to beaver distribution. Their importance probably varies inversely as the quantities of poplar available. (Nash, 1951, p. 31).

Stream gradient is definitely a limiting factor, and Wing (1951) found swift streams to be "...marginal habitat". Tappe (1942)

stated that fluctuation of the water level in streams is not critical.

Retzer (1955) made extensive observations on 61 streams in Colorado with the purpose of determining the effect of various physical factors on beaver occupancy. He studied rock type, valley grade, and valley width. He classified valley grade as follows:

EXCELLENT	Valley grades 0 to 6 percent.
GOOD	Valley grades 7 to 12 percent.
QUESTIONABLE	Valley grades 12 to 15 percent.
UNSUITABLE	Valley grades steeper than 15 percent.

Valley width was classified as:

SUITABLE	All valleys wider than the channel itself. The wider the valley the more satisfactory it is.
UNSUITABLE	All valleys that are only channel wide.

Rock type was classified as:

STABLE	Glacial till, granite, and schist.
LESS STABLE	Rhyolites
UNSTABLE	Shale, interbedded shale, and sandstone.

General

No writer has as yet attempted to provide an over-all determination of carrying capacity which can be applied to all types of habitat. Perhaps the following quotation from Nash is the best generalization so far made:

> There seems to be no better unit of carrying capacity than the "site", which, judging by those which the beaver occupies, should include a supply of calm water, soft banks for easy burrowing, willows or alders for building material, aquatic vegetation, a supply of aspen poplar, and no close neighbors. It appears to the writer that a good method of

> determining the carrying capacity is to make detailed reconnaissances of the area concerned in order to determine the number of such sites and to express the results in terms of colonies for that area. (Nash, 1951, p. 28).

Intensive management would call for more detailed analysis than outlined by Nash, but such analyses could only be of local application.

Chapter III

LOCATION AND DESCRIPTION OF STUDY AREAS

In this chapter the geographical location and physical characteristics of the study areas employed in this investigation are described.

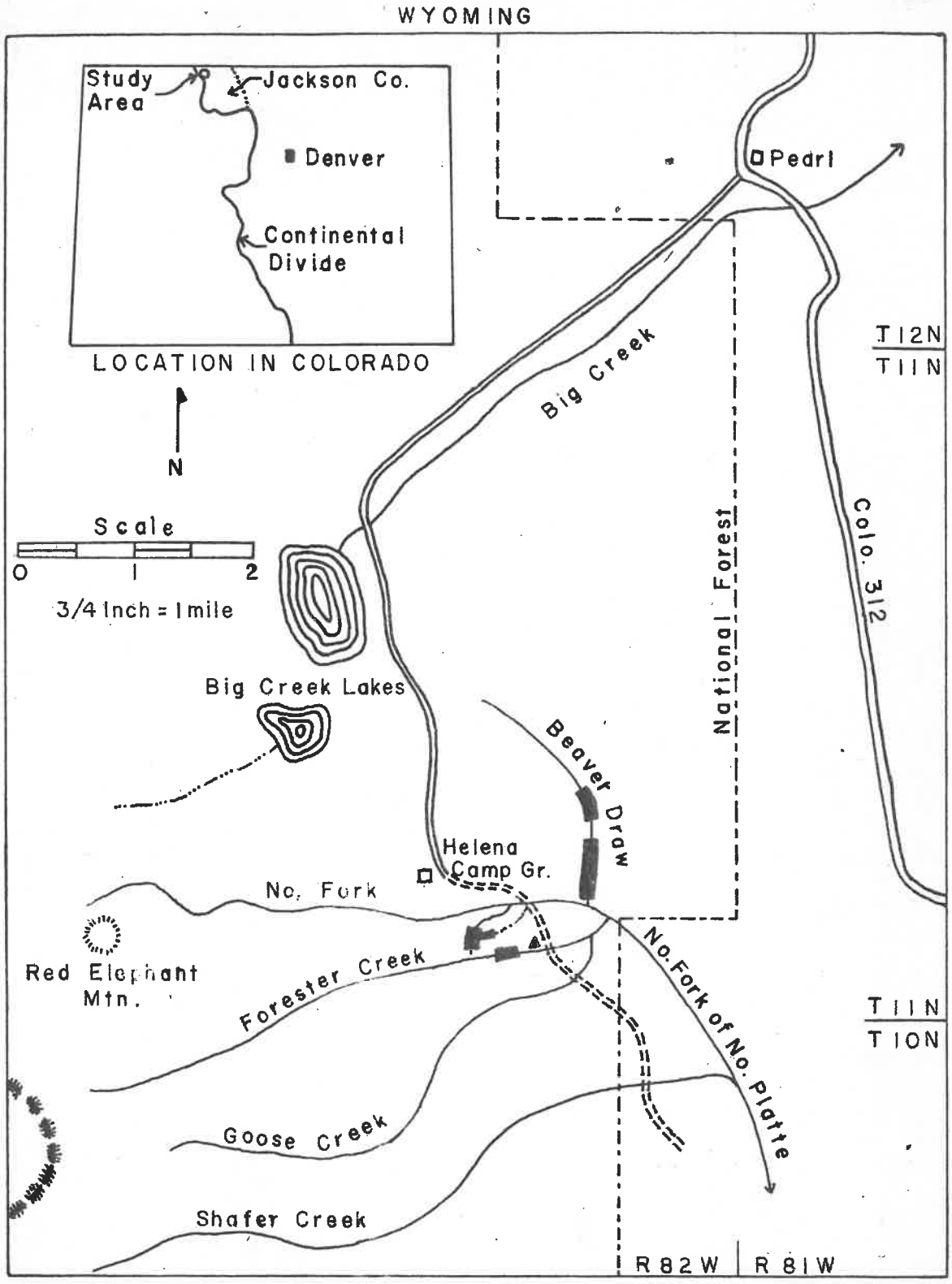
Location

This investigation of beaver food utilization was conducted wholly on the Routt National Forest, in North Park, Jackson County, Colorado. Geographically, the portion of the Forest concerned is situated on the eastern slope of the Park Range, approximately six miles south of Big Creek Lakes, near the eastern Forest boundary. The major drainage of the area is the North Fork of the North Platte River. All of the study areas occur within Township 11 North, Range 82 West of the Sixth Principal Meridian, at an elevation of 8,600 to 9,000 feet above mean sea level (Figure 1).

Five distinct colony areas were chosen for study. All were on tributaries of the North Fork. Two study areas were situated on Beaver Draw, one area on Forester Creek, one on Forester Seep, and one on Forester Seep Draw (Figures 2 through 6).

Description of areas

Beaver Draw is a small semi-permanent stream which flows south into the North Fork of the North Platte River. The lower portion, Area 2, is separated from the upper portion, Area 1, by a



LOCATION OF STUDY AREAS

LEGEND

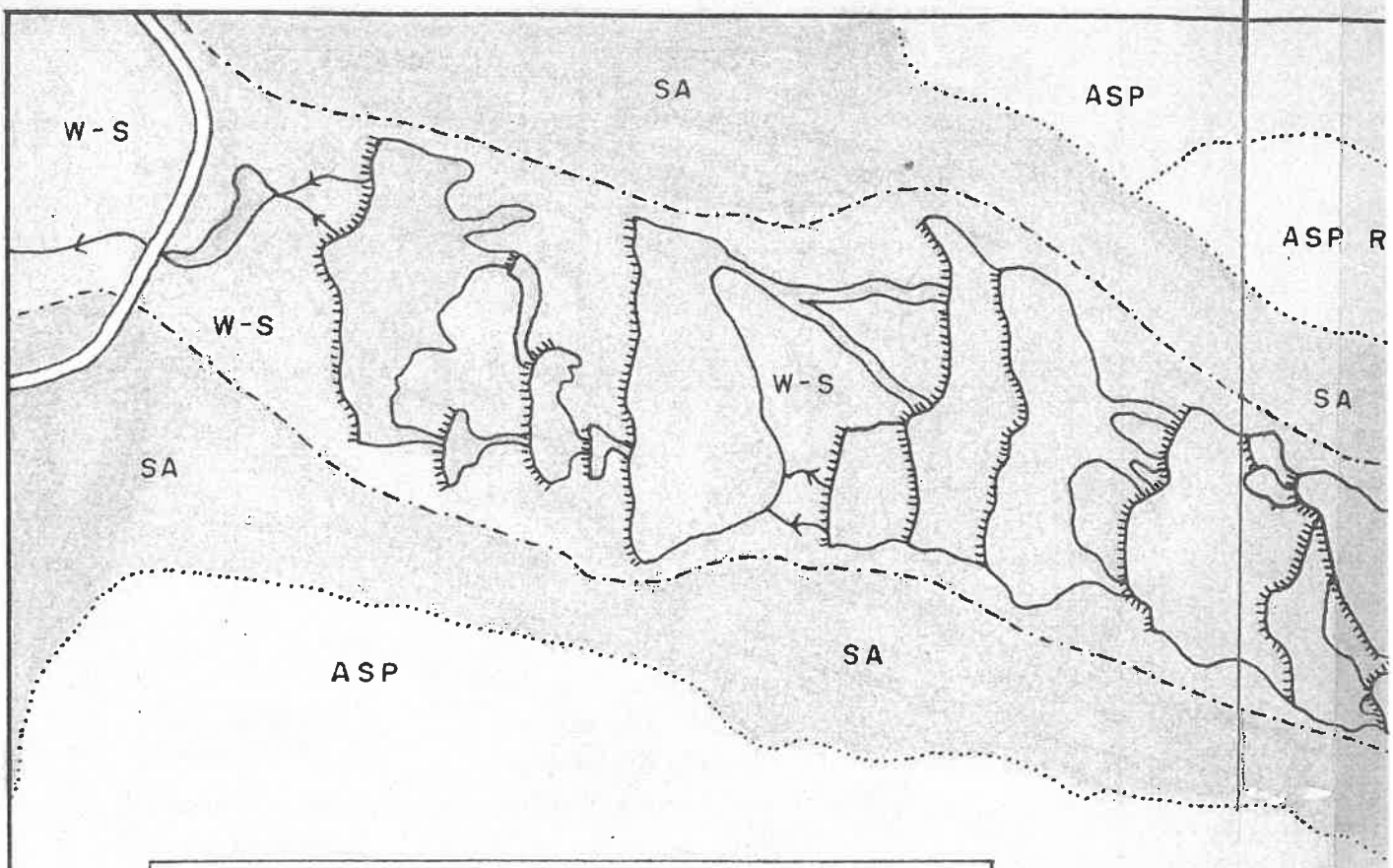
ROAD — STUDY AREA

ROAD (unimp.)==== CAMP

CONTINENTAL DIVIDE

6th. Principal Meridian

Figure 1



BEAVER DRAW AREA 2

LEGEND

SCALE

1 INCH = 120 FEET

DAM

LODGE

POND

FLOODPLAIN

WATER COURSE

ROAD (UNIMPROVED)

VEGETATIVE TYPE

ASPEN - ASP

SAGE - SA

WILLOW - W

LODGEPOLE - LP

SEDGE - S

ASPEN REPRO. - ASP R

JACKSON COUNTY, COLORADO - 1955

T 11 N R 82 W 6TH P. M.

N

Figure 2

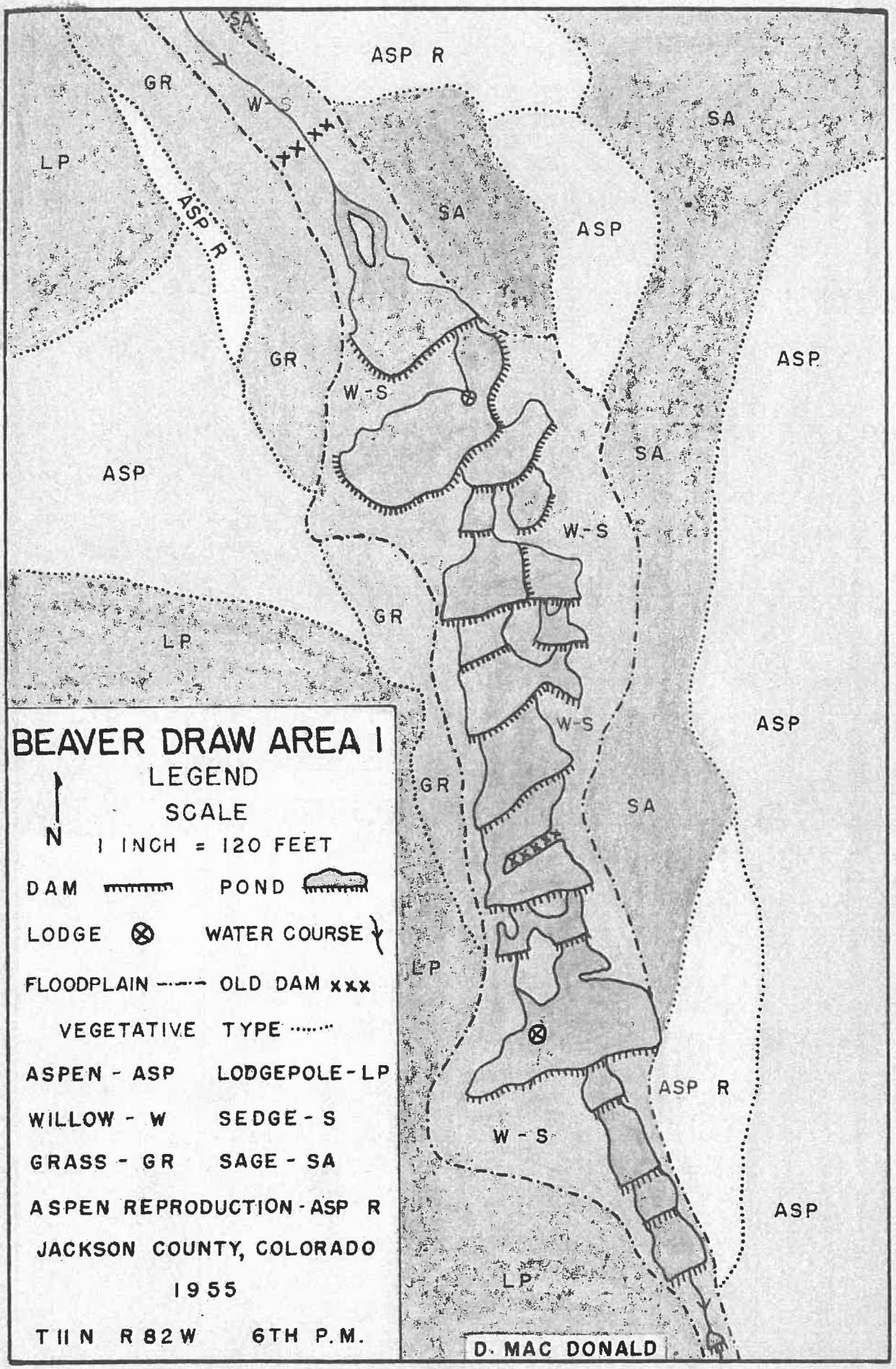
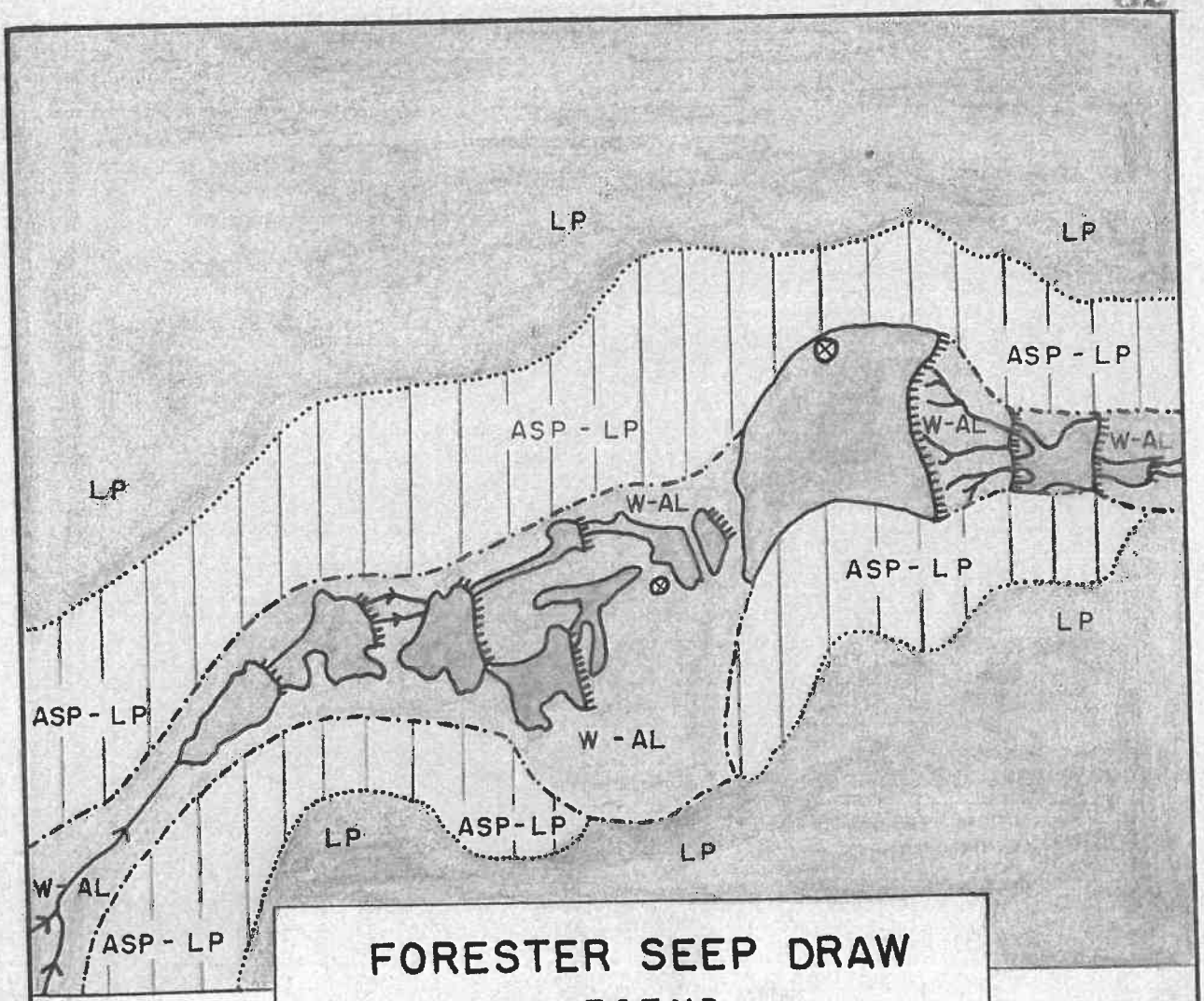

BEAVER DRAW AREA I
LEGEND
SCALE
N
1 INCH = 120 FEET
DAM
POND
LODGE
WATER COURSE
FLOODPLAIN
OLD DAM xxx
VEGETATIVE TYPE
ASPEN - ASP
LODGEPOLE - LP
WILLOW - W
SEDGE - S
GRASS - GR
SAGE - SA
ASPEN REPRODUCTION - ASP R
JACKSON COUNTY, COLORADO
1955
T 11 N R 82 W 6TH P.M.
D. MAC DONALD
ASP R
SA
GR
W-S
LP
ASP
xxx

Figure 3



FOREST SEEP DRAW

LEGEND

SCALE

N

1 INCH = 60 FEET

DAM

POND

LODGE

WATER COURSE

FLOODPLAIN

VEGETATIVE TYPE

ASPEN - ASP

LODGEPOLE - LP

WILLOW - W

ALDER - AL

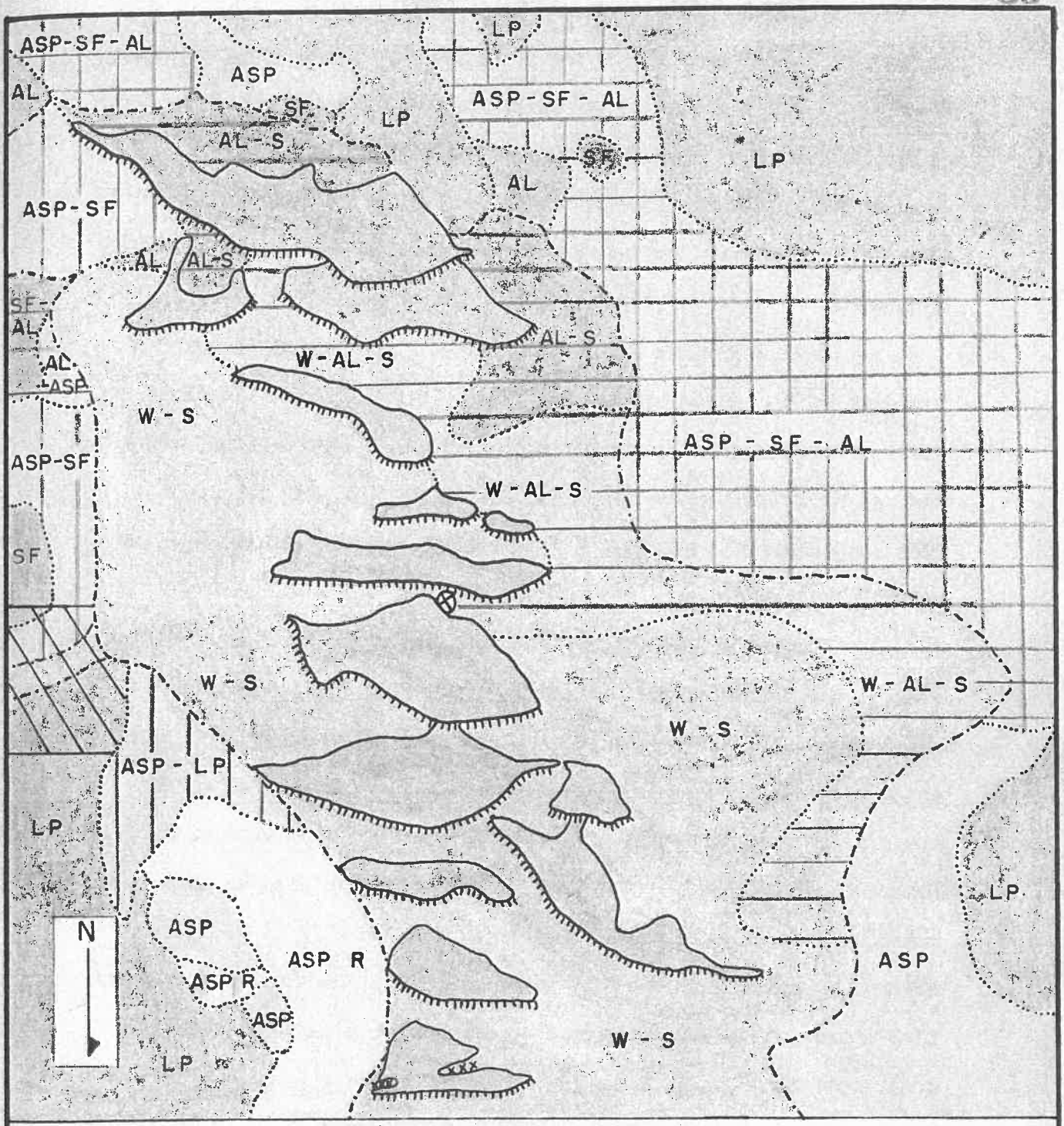
JACKSON COUNTY, COLORADO

1955

T 11 N R 82 W 6TH P. M.

D. MAC DONALD

Figure 4



FORESTER SEEP

LEGEND

SCALE - 1 INCH = 120 FEET

DAM POND LODGE OLD DAM xxxx FLOODPLAIN

VEGETATIVE TYPE ASPEN - ASP ALDER - AL WILLOW - W
SEDGE - S LODGEPOLE - LP SPRUCE-FIR - SF ASPEN REPRO.-ASP R

JACKSON COUNTY, COLORADO - 1955
T 11 N R 82 W 6TH P.M. D. MAC DONALD

Figure 5

section of stream with a very narrow valley and a relatively steep gradient, which contains no beaver activity. Stream flow in the late summer is very low. Seepage from the Pleasant Valley Ditch, which crosses the upper end of Beaver Draw, maintains a fairly constant flow into the stream until irrigation is discontinued about the first of August.

Area 2 appears to have contained a population of beavers for many years. A beaver-scarred stump was found which showed 27 years of callus growth over the scar. Area 1 likewise showed indications of several years of beaver activity. The rock type on this area is generally granitic, and the valley shows little evidence of recent glaciation.

Forester Seep flows north into the North Fork, and originates only a few yards from Forester Creek. Apparently it is fed mainly by seepage from this stream. It is a relatively broad, marshy area, generally convex in surface aspect. It, too, has contained beavers for many years, as indicated by numerous old beaver-cut stumps in the vicinity. The water supply for this area appears to be relatively constant through the summer, but there is no definite stream channel. The rock type is glacial till, and the area is situated approximately 600 feet up from the end of a terminal moraine which runs east and west.

Forester Seep Draw is a side drainage which flows east from Forester Seep and eventually enters the North Fork. The flow is very small but apparently constant, as ponds remained full of water throughout the summer and fall. The colony was new, believed to have been

first occupied during the early summer of 1953. This valley bisects the above mentioned terminal moraine, the rock type again being glacial till.

Forester Creek is one of the major tributaries of the North Fork. It is a typical precipitous mountain stream, with a fairly small and relatively constant flow of water. This area is on two sections of stream which have a relatively low gradient, and which are separated by a short section of stream with a much steeper gradient. Beavers moved into this area during the first week of August, 1954. The valley slopes are very steep (up to 150 percent), and the stream bottom is decidedly narrow. The stream cuts deeply through the terminal moraine previously mentioned.

Vegetation

On Beaver Draw, Area 2, the entire flood plain, except where flooded by beaver dams, was covered with willows, sedges, and a small amount of birch interspersed at the upper end. Immediately adjacent to the flood plain was a strip of sage (Artemesia tridentata)1/ of varying width running the full length of the valley. This area was covered with numerous old beaver-cut aspen stumps in many stages of decomposition, which indicated that the stands had been invaded by sage after being cut off by the beavers. Above the sage, the slopes are covered with mature aspen for a distance of several hundred feet. At the junction of the sage and aspen are several

1/ See Appendix A for a complete list of common and scientific names used in this dissertation.

fairly small areas of aspen reproduction of different ages. A few small alpine fire (Abies lasiocarpa) and Engelmann spruces (Picea Engelmanni) are present in the understory of the mature aspens (Figure 2).

The valley bottom of Beaver Draw, Area 1, was very similar to that of Area 2, except that somewhat less willow was present. Sedges were more dominant. The eastern slope of the valley was similar to that of Area 2, with sage forming a fairly wide strip between the flood plain and an extensive stand of mature aspen. Here also were scattered areas of aspen reproduction between the sage and mature aspen. A few small Engelmann spruces were found in the understory of the aspen stand.

The western slope of the valley presented a somewhat different vegetational picture. Here, adjacent to the flood plain, grasses replaced sage. A narrow area of mature aspen extended up the slope for a few hundred feet, but the dominant tree here was lodgepole pine (Pinus contorta), which extended to the edge of the flood plain over most of the lower half of the study area (Figure 3).

The flood plain of Forester Seep Draw was covered with sedges and an almost equal proportion of alder and willow. Above this, on the slopes, was a fairly narrow strip of mature aspen mixed with some lodgepole pine, Engelmann spruce, and alpine fir. Beyond this strip was an almost pure stand of lodgepole pine (Figure 4).

On Forester Seep, the entire flood plain was covered with various mixtures of sedge, willow, and alder. Willow and sedge were the dominant species, with several species of grasses and forbs inter-

spersed in small amounts. Most of the willow growth was shrubby, with few clumps standing higher than two feet. The southwestern edge of the flood plain was bordered by a fairly wide area of mixed aspen, Engelmann spruce, alpine fir, and alder, whereas the northwest part was bordered by a relatively small aspen stand. Beyond these strips pure lodgepole pine predominated. The southern border of the area contained differing combinations of aspen, lodgepole pine, alder, and spruce-fir; mixed aspen and spruce-fir constituted the main growth along the southeast edge. A considerable area of aspen reproduction covered the northeast border of the flood plain. Some mature aspen stood beyond this area, and beyond that was a pure lodgepole pine stand (Figure 5).

A great percentage of the narrow flood plain of the Forester Creek colony was inundated by beaver dams. The remaining areas contained a few willow and alder clumps and some herbaceous growth, mostly several species of grass. The upstream area possessed a fairly wide band of mature aspen on both sides of the stream; downstream, it was heavily interspersed with lodgepole pine. Pure stands of lodgepole pine covered the area beyond the aspen. A few small alpine firs were scattered over the wetter area (Figure 6).

General land use

Grazing.--The area under consideration was grazed by cattle on an allotment administered by the U. S. Forest Service. Cattle, owned by the Big Horn Cattle Company, were put on the area July 1 and ranged freely over it until September 15. Some attempt was made to concentrate the stock on certain areas by use of salt blocks. The

main concentration was usually found in the valley of the North Fork. Several animals were usually to be found on Beaver Draw. Grazing on the other areas was sporadic through the summer.

Hunting.--This part of the North Platte drainage has some of the better mule-deer (Odocoileus hemionus) range in Colorado. Hunting pressure here is considered moderate. There is a fairly sizeable elk (Cervus canadensis) herd in the vicinity, and a small herd of big-horn sheep (Ovis canadensis) occurs a few miles to the west along the Continental Divide. There is a fair population of dusky grouse (Dendrogapus obscurus) throughout, and moderate numbers of snowshoe hares (Lepus americanus) are also present. Hunting, other than for deer, is negligible.

Fishing.--Most of the streams and beaver ponds in the locality contain large populations of small brook trout (Salvelinus fontinalis). Some of the larger ponds hold native cut-throat trout (Salmo clarkii), brown trout (Salmo trutta), and rainbow trout (Salmo gairdnerii) of fair to excellent size. Fishing pressure is fairly heavy, considering the remoteness of the area, especially on holiday weekends during the summer and early fall.

Recreation.--Helena Camp Ground, in the valley of the North Fork, is a regularly maintained Forest Service camp site, with picnic tables and fireplaces. This camp ground receives moderate use through the summer and early fall.

Chapter IV

METHODS AND MATERIALS

In this chapter the methods, techniques, and materials used in gathering data are discussed. The same techniques were employed in studying each of the five areas, except that total counts of stems cut by beavers, rather than samples, were taken on the smaller tracts where it was physically possible to give complete coverage.

Establishment of the study areas

The first step in initiating this investigation was the location of a suitable forested and watered area, where a number of relatively undisturbed beaver colonies were to be found. The western side of North Park, Colorado, was finally selected as containing a large number and variety of such beaver habitations. Personnel familiar with this locality were consulted, resulting in the suggestion of several specific drainages which were later surveyed, both on foot and from the air. Ultimately selected, as previously stated, was the drainage of the North Fork of the North Platte River, in the northwest quarter of the Park.

The base camp, from which field studies were conducted, was on Forester Creek, within easy walking distance of all of the individual study sites. Subsequent to initiation of the investigation, an indeterminate number of beavers was dead-trapped on Beaver Draw, Area 2, necessitating the abandonment of this site for carrying

capacity studies. Some of the data collected there, however, were utilized in other aspects of the investigation.

Mapping

Early in the summer of 1954 a survey line was run parallel to each drainage being studied by use of a pocket compass, chain, and Abney level. Stakes were placed at measured intervals along this line. Detailed maps were drawn during the summer of 1955 showing location of various beaver structures, width of the flood plain, and the several vegetative cover types. Fill-in data were obtained by pacing from the established survey line. Later the maps were planimetered to determine the acreages of the various types involved.

Stream gradients

All stream sections on the areas under investigation were measured for gradient with an Abney level. Sections of stream between colony areas, which contained no beaver activity, were measured in like manner. Measurements were taken by standing immediately above the uppermost pond on a colony area and sighting on an individual standing just below the lowermost dam. Wherever possible, sightings were taken over the entire colony area. Elsewhere, two or more measurements were made and the average computed.

Stream flow

Stream flow on all of the areas fluctuated to such an extent that actual measurements were considered to be of little value. Rough estimates were recorded, however, of the maximum and minimum stream flow during the period of the study. Of necessity, these

estimates were limited to the period of about June 15 to September 30 for each of the two years. Thus, maximum stream flows, occurring in early spring, were never determined or recorded.

Measurements of beaver food present

Stand tables were prepared for each area showing the amount and composition of all woody plant species present. Transects 6.6 feet wide were run across each tract, measured by carrying a pole of this length. They were oriented at right angles to the stream channel, were located with reference to the survey line along each area, and were long enough to include all food species considered to be within foraging range of the beavers. Data were recorded on a field form entitled "Stand Composition" (Appendix B). All woody plant species except willow were tallied by diameter classes; willows were recorded by clump size (number of stems). Willow stems were separated into three size classes based on diameter: Class I stems were under 1/4 inch, Class II stems between 1/4 and 1/2 inch, and Class III stems were over 1/2 inch. The proportion of willow stems of each class present on sample plots was used to determine size composition for the total area. Sample plots were established as a basis for determining willow utilization.

Transects were located on the cover maps, and the area of each cover type sampled was determined. Total area of each type was determined by planimetering of maps. The percent of sample was thus established, and the data were then projected to give the total amount, by size classes, of each woody species present on each tract under consideration.

It was necessary to equate aspen trees of various sizes as to relative amounts of beaver food contained in order to obtain a figure for making comparisons. Data from O'Brien (1938) (Table 3, REVIEW OF LITERATURE), gave total amounts of beaver food yielded by different sizes of aspen. As these data extended only through trees seven inches in diameter, and since many trees of considerably larger diameters were present on the study areas, it was necessary to project O'Brien's values to trees of larger diameters by use of a multiple regression curve. Since O'Brien's data came from a different region of the country, it was believed that the use of actual pounds of beaver food, as determined by him, could not be justified. It was believed, however, that the proportion of food contained in different sizes of trees would remain relatively constant. Thus, it was decided that a standard unit be selected, with which all trees could be equated. The two-inch aspen tree was thus chosen, and was called the beaver food unit. The numbers of such tree-units in all aspen stands involved were then calculated.

Finally, it became necessary to determine the relative amounts of beaver food present in willow stems of the three size classes, and it was further required that these quantities be equated with the previously determined beaver food unit, based on aspen. Since no data to this end were available from the literature, a peeling and weighing study was set up to determine the amount of beaver food present in willow stems. Twenty-five willow stems of various sizes were collected, peeled, and weighed. Similar to O'Brien's work in 1938, the bark and cambium layer were removed to a diameter

of one-eighth inch, and the twigs below this diameter were weighed without removing the bark. The total weight of beaver food present on the average willow stem of each size class was compared with that in a two-inch aspen (as determined by O'Brien), thus providing a figure for determining the number of beaver food units contained in varying sizes of willow stems.

Alder was known to be of minor importance as a beaver food on the areas studied. The amount of beaver food represented by alders of various sizes was estimated to be approximately one-half of that contained in aspen trees of the same size. This figure was based on careful observation of the relative thickness of the bark of the two species, and was intended to be used only as a rough estimate of the beaver food present in the form of alder on the several areas.

Having determined the amount of beaver food, expressed in beaver food units, for all woody food species of various sizes, the total number of units present on each area was then calculated. The resultant values not only made possible direct comparisons between the several areas, but also permitted determination of the percent of the standing food supply utilized over the period of study.

Determination of numbers of beaver present

The number of beavers present on each of the study areas was determined by exhaustive dead-trapping in the fall of 1955. This was accomplished by Keith G. Hay (1955), in connection with a companion study on beaver census techniques. Mr. Hay was assisted in this project by Jack D. Remington and William H. Rutherford of the

Colorado Game and Fish Department.

Determination of beaver food utilization

Aspen.--The chief beaver food present on all of the areas studied was aspen. Utilization of this species was determined by tallying all trees cut on each of the sites, recorded on a field form entitled "Aspen Food Utilization" (Appendix C). This form included date, diameter at stump height, degree of utilization expressed in percent (determined by ocular estimation), and percent of slope (measured with an Abney level). All stumps were painted with canned spray paint when tallied, a different color for each monthly tally. These markings were clearly visible 15 months after the original count was completed.

The first tally on each area necessarily required the recording of trees cut within the past year, as determined by stump condition. Subsequent observations of stumps from known-aged cuttings indicated that the original estimations were relatively accurate. Further accuracy was indicated by the fact that the winter period of beaver inactivity left a fairly sharp distinction as to condition between one-year old and two-year old stumps.

One month after the original count, a second tally was made on each area. Three additional monthly tallies were taken on Forester Seep Draw during the first summer. In these monthly tallies, note was made of all partially used trees which had been counted before. Thus, any further utilization subsequent to the first tallying of a partially used tree was estimated and recorded. Only those trees felled immediately prior to any one tally appeared to be further

utilized, except on Forester Creek where several large trees which had been only slightly used in 1954 were stripped of additional bark during the summer of 1955. This area contained a very limited supply of aspen, and was relatively dark, damp, and cool -- conditions that may account for the preservation, in useable condition, of the felled-tree bark.

The most important tally of food utilization was the one made one year from the date of the original tally. This gave the total of aspen used for a one-year period. Monthly tallies made in 1954, and three additional monthly tallies on each area in 1955, gave an indication of seasonal use of various foods.

Willow.--Willow utilization was determined by the use of sample plots. Fifteen one-milacre plots were established on Forester Seep Draw; 25 four-milacre plots were set up on Beaver Draw, Area 2; 10 four-milacre plots were established on Beaver Draw Area 1; and 15 four-milacre plots were used on Forester Seep. Total counts of willow stems utilized were made on Forester Creek. Sketch maps for each area permitted randomized location of samples and adequate coverage of each area. The plots were then located in the field. They were oriented so as to include the greatest amount of willow on or immediately adjacent to the mapped sites. Thus, the sample was not strictly randomized. Total counts of stems present on the sample plots were compared with the total present on the area involved (as determined from the transect data), and the proportion thus established was used to project utilization data from the plots.

Utilization data were recorded on a field form entitled "Willow Food Utilization" (Appendix D), which included date, plot number, number of live stems present in each size class, number of beaver-cut stems in each size class, and information for stems taken by livestock and/or big game.

The first tally recorded the size and number of willow stems cut by beavers on each of the plots. Subsequent monthly tallies again recorded the number of beaver-cut stems. This total, compared with the number of cut stems recorded for the previous tally, gave the number of stems utilized during the intervening period. Thus, individual marking of cut stems was made unnecessary. One monthly tally was taken for all areas in 1954, with three additional counts being made on Forester Seep Draw. In 1955, three monthly tallies were taken on all areas. As in the aspen counts, the anniversary count gave utilization for one year, and monthly tallies indicated seasonal use of willow.

Alder.--Considerable amounts of alder were present on three of the study areas: Forester Seep, Forester Seep Draw, and Forester Creek. No alder was observed to have been cut on Forester Seep. A total count of all alder stems cut on Forester Seep Draw was made in the late summer of 1955, and this figure was projected over the entire period of beaver occupancy. Alder utilized on Forester Creek was likewise determined. Few instances were noted where this material was taken as food, but considerable use was made of alder in construction on the two areas indicated above.

Herbaceous material.--No actual measurements of herbaceous material utilized as food were made. The difficulty in taking data of this nature is such as to render them beyond the scope of the problem. Nash (1951) believed that herbaceous material, though of considerable importance as beaver food, should not be considered a limiting factor as it is usually present in abundant supply wherever the other requirements of beaver occupancy exist (REVIEW OF LITERATURE, p. 25).

An attempt was made to determine, by rough estimate, the percentage of herbaceous material used by beavers during the various seasons of the year. To this end, the winter food supply (i.e. the total of woody material cut during the fall and placed in the food cache) was projected over the entire winter, and the average required per month was thus determined. The food of the beavers during this period was considered to be made up entirely of woody material. Whenever the use of such food fell below this figure during the spring and summer months (before young of the year influence the volume used), the difference was presumed to have been made up by the use of herbaceous growth. Observations of feeding beavers during the summer months, together with the cutting of small amounts of woody material during this season, indicated that herbaceous plants constitute the major food source during the warmer months of the year.

Growth and reproduction

Aspen.--Reproduction of aspen was determined, in general terms, by measurements made of the total area on which reproduction

of this species was present. Area was determined by planimetering the cover maps.

Growth of aspen presented a more difficult problem. It was found necessary to determine the actual growth rate on a representative sample of aspen trees. Eighty cross-sections of beaver-cut stumps were collected, 20 selected randomly from each of four study areas. These were chosen to include an equal representation of the various size classes. Information was recorded in the field as to diameter at stump height, distance from the water, and percent of slope. The latter two factors showed no correlation with growth, probably as a result of the masking effect of several other factors not recorded, such as site, exposure, and position of dominance in the stand.

Stump sections were dried for approximately one month, smoothed with a disc sander, and then studied under a binocular microscope. Annual growth rings were counted and measured along the average radius of the section. Measurements were made with an etched steel millimeter rule. In order to facilitate the reading of annual rings, a groove was cut along the average radius. This groove was then flooded with clear machine oil which showed differential penetration, making the growth rings more clearly visible. From the data gathered, the average diameter growth rate for aspen in the North Park region was determined. Growth rates for the four areas were compared, and no significant difference was noted.

Willow.--In the original tallies on the willow plots for each area, counts were made by size class of all live stems present

on each plot. In the anniversary tallies, one year from the original, all live stems were again counted. The resultant figures, when compared with the number of stems cut by the beavers, gave an indication of the growth and reproductive potential of this species.

Chapter V

ANALYSIS OF DATA

In this chapter, data collected during the summer and fall seasons of 1954 and 1955 on beaver carrying capacity are presented. Statistical analyses are made where applicable. Discussion and application of the findings are given in Chapter VI.

Physical factors

Cover types.--Areas represented by the several vegetative types were determined by planimetering cover maps based on field surveys. Boundaries were determined by using the arbitrary limit of 100 yards for food availability based on reports in the literature. Results are given in Table 8.

Stream gradients.--Stream gradients on all areas studied were measured with an Abney level. Figures are based on a single sight taken, wherever possible, over the entire area. In other cases the average of several sights is used. Measurements are given below:

Stream Section	Percent
Beaver Draw, Area 1	7
Beaver Draw, Area 2	3
Section between Areas 1 and 2	8
Forester Seep	6
Forester Seep Draw	4
Forester Creek, occupied sections	5
Area between occupied sections	15

Table 8.—ACREAGE BY COVER TYPES ON BEAVER STUDY AREAS

Beaver Draw, Area 1		Acres
Flood plain		3.79
Open water	1.69	
Willow & sedge	2.10	
Sage		2.91
Grass		1.06
Aspen		6.71
Aspen reprod.		1.25
Total		15.72

Forester Seep	Acres
Open water	1.89
Aspen	1.38
Aspen reprod.	0.57
Aspen & reprod.	0.05
Aspen & spruce	0.56
Aspen & lodgepole	0.30
Aspen & alder	0.04
Aspen, alder & spruce	3.01
Willow & sedge	4.08
Alder	0.16
Alder & sedge	0.66
Alder & spruce	0.12
Willow, alder & sedge	1.47
Total	14.29

Beaver Draw, Area 2		Acres
Flood plain		8.08
Open water	3.98	
Willow & sedge	4.10	
Sage		9.48
Aspen		22.76
Aspen reprod.		1.95
Total		42.27

Forester Seep Draw		Acres
Flood plain		0.511
Open water	0.178	
Willow & alder	0.333	
Aspen & lodgepole		0.760
Total		1.271

Forester Creek		Acres
Flood plain		0.550
Open water	0.359	
Willow & herb.	0.176	
Alder	0.015	
Aspen		1.283
Aspen & lodgepole		0.568
Total		2.401

Stream flow.—Estimates of maximum and minimum stream flow on three areas, June 1 to September 30, are recorded as follows:

Area	Maximum	Minimum
Beaver Draw	0.5 cu. ft./sec.	0.1 cu. ft./sec.
Forester Seep Draw	0.3 " "	0.2 " "
Forester Creek	7 " "	3 " "

No estimates could be made on Forester Seep, as no stream channel was evident on this study area.

Determination of stand composition

Stand tables were constructed for each area showing total amounts and sizes of each woody plant species present. In addition to the total number of stems in each size class, by species, the number of beaver food units, the number of stems per acre, and the number of beaver food units per acre are shown. The total number of beaver food units for the entire area is given at the bottom of each stand table, 9 through 13.

The beaver food unit was determined from data given by O'Brien (1938), as shown in Table 3. These data were projected for trees of larger diameter than studied by O'Brien by use of the multiple regression equation shown below

$$\hat{Y} = 38.6 - 2.19 X_1 + 1.48 X_2$$

Results are presented as Table 14, and the resulting curve is shown as Figure 7.

A series of typical willow stems of varied sizes were collected, peeled, and weighed to determine the amount of beaver food yielded by this species. Results were compared with the data for aspen, shown above, in order to determine the number of beaver food units in each size class of willow. Results are given in Table 15.

It can be seen from Table 15 that considerable variation was demonstrated in the amount of beaver food present in the willow stems peeled. It is believed, however, that the calculated averages provide usable, if not completely accurate, figures with which comparisons can be made.

Table 9.--STAND TABLE AND BEAVER FOOD UNITS FOR WOODY PLANTS, TOTAL AND PER ACRE: FORESTER CREEK[1/].

Aspen

Size	Total	Total B. F. U.	No. Per Acre	B.F.U. Per Acre
0-1"	4,092	1,146	2,465	690
1-3	350	350	211	211
3-5	306	1,065	184	642
5-7	175	1,426	105	859
7-up	88	1,695	53	1,021
		5,682		3,423

Willow

Class	Total	Total B. F. U.	No. Per Acre	B.F.U. Per Acre
I	533	1.65	3,028	9.38
II	140	1.90	795	10.81
III	125	4.27	710	25.99
		7.75		46.18

Alder

Size	Total	No. Per Acre
0-1"	168	2,024
1-2	68	819
2-	121	1,458

Alpine Fir

Size	Total
0-3"	79

Total B.F.U. for Forester Creek Area -- 5,690

1/ Due to the small number of conifers on the study areas, data relative to number per acre and B.F.U. are not given for this group in table.

Table 10.—STAND TABLE AND BEAVER FOOD UNITS FOR WOODY PLANTS, TOTAL AND PER ACRE: BEAVER DRAW, AREA 1 1/.

Aspen

Size	Total	Total B. F. U.	No. Per Acre	B.F.U. Per Acre
0-1"	28,592	8,006	3,572	1,006
1-3	2,113	2,113	265	265
3-5	2,465	8,578	310	1,078
5-7	986	8,036	124	1,010
7-up	211	4,064		511
		30,797		3,869

Willow

Class	Total	Total B. F. U.	No. Per Acre	B.F.U. Per Acre
I	128,850	399.44	61,357	190.21
II	19,377	263.53	9,227	125.49
III	1,633	59.77	778	28.46
		722.74		344.16

Eng. Spruce

Size	Total
0-3	161

Total B.F.U. for Beaver Draw, Area 1 — 31,520

1/ Due to the small number of conifers on the study areas, data relative to number per acre and B.F.U. are not given for this group in table.

Table 11.—STAND TABLE AND BEAVER FOOD UNITS FOR WOODY PLANTS, TOTAL AND PER ACRE: BEAVER DRAW, AREA 2 1/.

Aspen

Size	Total	Total B. F. U.	No. Per Acre	B.F.U. Per Acre
0-1"	53,136	14,878	2,150	602
1-3	9,831	9,831	398	398
3-5	7,373	25,658	298	1,038
5-7	3,220	26,243	130	1,062
7-up	847	16,313	34	660
		92,923		3,761

Willow

Class	Total	Total B. F. U.	No. Per Acre	B.F.U. Per Acre
I	181,694	561.39	44,169	136.92
II	84,300	1146.48	20,561	279.63
III	14,115	516.61	3,443	126.00
		2224.48		542.55

Alpine Fir

Size	Total
0-3	635
3-6	79

Eng. Spruce

Size	Total
0-3	159

Birch

Size	Total
0-3	6,825

Total B.F.U. for Beaver Draw, Area 2 — 95,147

1/ Due to the small number of conifers and birch on the study areas, data relative to number per acre and B.F.U. are not given for this group in table.

Table 12.—STAND TABLE AND BEAVER FOOD UNITS FOR WOODY PLANTS, TOTAL AND PER ACRE: FORESTER SEEP DRAW 1/.

Aspen

Size	Total	Total B. F. U.	No. Per Acre	B. F. U. Per Acre
0-1"	1,663	457	2,149	601
1-3	313	313	412	412
3-5	313	1,089	412	1,433
5-7	112	913	147	1,201
7-up	45	867	59	1,141
		3,639		4,788

Willow

Class	Total	Total B. F. U.	No. Per Acre	B.F.U. Per Acre
I	5,814	16.02	17,618	54.61
II	2,895	39.37	8,773	119.30
III	680	24.89	2,061	75.42
		82.28		249.33

Alder

Size	Total	No. Per Acre
0-1"	4,333	13,130
1-2	2,289	6,936
2-	622	1,885

Alpine Fir

Size	Total
0-3	66

Eng. Spruce

Size	Total
0-3	426
3-6	98

Total B.F.U. for Forester Seep Draw Area — 3,721

1/ Due to the small number of conifers on the study areas, data relative to number per acre and B.F.U. are not given for this group in table.

Table 13.--STAND TABLE AND BEAVER FOOD UNITS FOR WOODY PLANTS, TOTAL AND PER ACRE: FORESTER SEEP 1/.

Aspen

Size	Total	Total B. F. U.	No. Per Acre	B.F.U. Per Acre
0-1"	11,253	3,151	1,904	533
1-3	716	716	121	121
3-5	985	3,428	167	580
5-7	567	4,621	96	782
7-up	358	6,859	61	1,161
		18,775		3,177

Willow

Class	Total	Total B. F. U.	No. Per Acre	B.F.U. Per Acre
I	248,155	769.28	44,713	138.61
II	8,338	113.40	1,502	20.43
III	78	2.85	14	.51
		885.53		159.55

Alder

Size	Total	No. Per Acre
0-1	15,731	2,881
1-2	4,064	744
2-	2,135	391

Alpine Fir

Size	Total
0-3	772
3-6	140

Eng. Spruce

Size	Total
0-3	1,754
3-6	596

Total B.F.U. for Forester Seep Area -- 19,661

1/ Due to the small number of conifers on the study areas, data relative to number per acre and B.F.U. are not given for this group in table.

Table 14.--BEAVER FOOD UNITS IN ASPENS OF VARIOUS DIAMETERS

Diameter at Stump Height (inches)	Weight (pounds)	Beaver Food Units 1/
1/4	0.75	0.14
1/2	1.50	0.28
1	3.15	0.58
2	5.40	1.00
3	10.61	1.96
4	18.78	3.48
5	29.91	5.54
6	44.00	8.15
7	61.05	11.31
8	81.06	15.01
9	104.03	19.26
10	129.96	24.07
11	158.85	29.42
12	190.70	35.31
13	225.51	41.76
14	263.28	48.76
15	304.01	56.30
16	347.70	64.39

1/ One two-inch tree equals one beaver food unit.

In this instance the relationship of food contained to total weight of stems, expressed in percentage, was determined. These figures show much more consistency, as would be expected, since variation within size classes is not a factor. Results are as follows:

Percent of Beaver Food to Total Weight of Willow Stems

Class	Mean	Standard Deviation
Class I	53.76 percent	4.95 percent
Class II	44.25 percent	5.06 percent
Class III	42.68 percent	3.51 percent

This information may be used as a basis for determining the beaver food present simply by weighing willow stems without peeling.

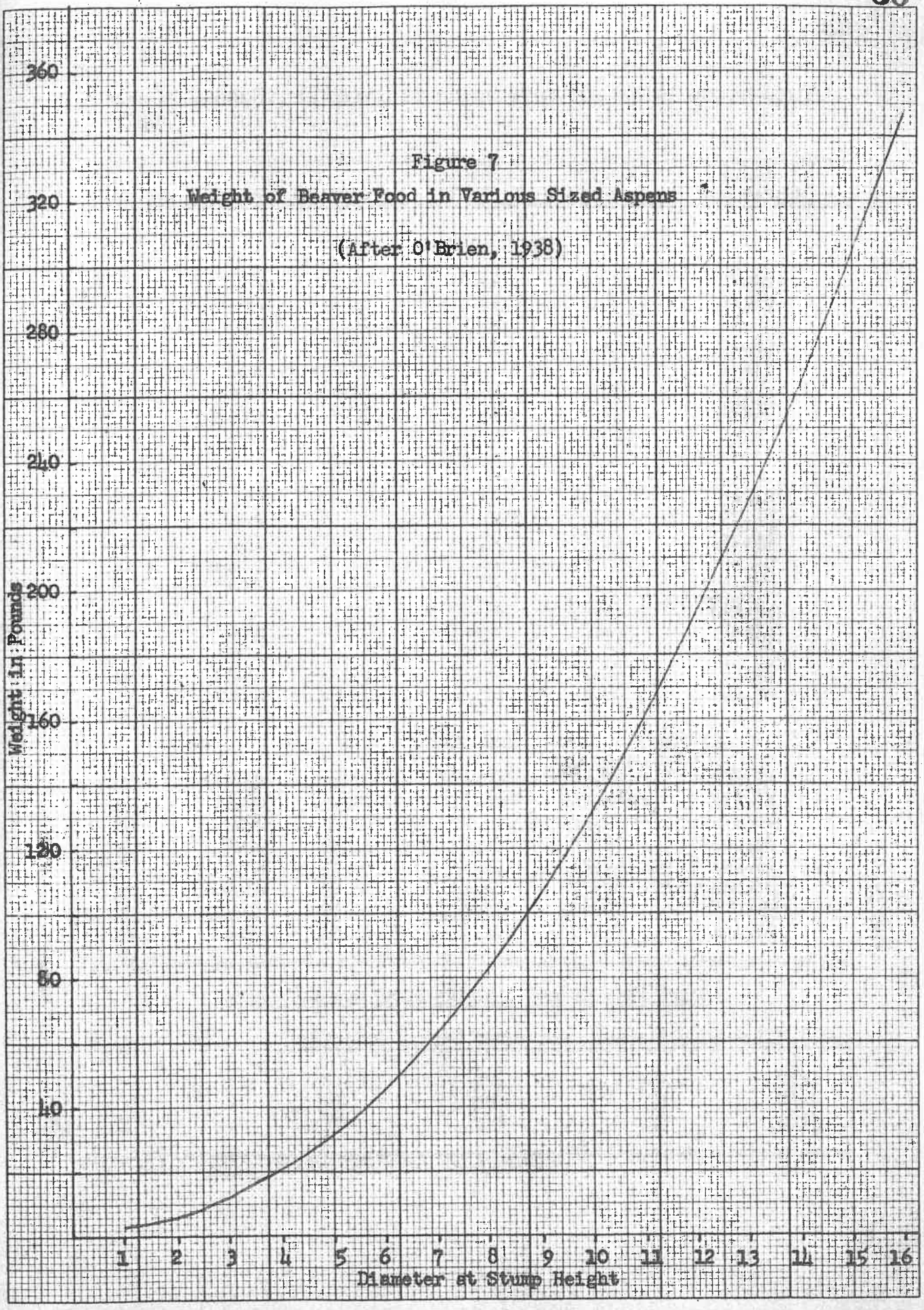


Figure 7

Weight of Beaver Food in Various Sized Aspens

(After O'Brien, 1938)

Table 15.—WEIGHT, IN GRAMS, OF BEAVER FOOD YIELDED BY PEELED WILLOW STEMS.

Stem No.	Twigs[1]	Bark	Total Food	Peeled Stems	Total Stem Weight
			Class I		
1	4.23	6.37	10.60	8.09	19.69
2	2.93	4.19	7.12	4.75	11.87
3	0.97	2.62	3.59	2.65	6.24
4	2.00	7.15	9.15	7.42	16.57
5	2.12	6.62	8.74	10.43	19.17
6	2.03	4.88	6.91	7.68	14.59
7	1.93	5.25	7.18	6.14	13.32
			Class II		
8	3.57	16.57	20.04	31.14	51.18
9	4.57	20.27	24.84	42.53	67.37
10	18.31	29.90	48.21	56.05	104.26
11	12.65	22.82	35.47	43.00	78.47
12	7.53	15.18	22.71	19.03	41.74
13	12.27	35.94	48.21	69.02	117.23
14	4.94	23.15	28.09	43.28	71.37
15	6.67	10.27	16.94	17.20	34.14
16	12.21	21.71	33.92	39.11	73.03
17	17.12	37.80	54.92	69.84	124.76
			Class III		
18	33.43	93.50	126.93	174.18	301.11
19	29.00	110.26	139.26	209.88	349.14
20	17.55	61.87	79.42	132.22	211.64
21	17.04	55.45	72.49	82.99	155.48
22	9.52	33.88	43.40	63.73	107.13
23	20.48	45.86	66.34	75.72	142.06
24	33.91	99.30	133.21	145.02	278.23
25	15.03	41.13	56.16	78.37	134.54

Average Weight in Pounds and Beaver Food Units

Class	Mean	Standard Deviation	Stems/B.F.U.	B.F.U./stem
I	.0168	.0046	321	.0031
II	.0735	.0276	73	.0136
III	.1977	.0778	27	.0366

[1] Twigs under one-eighth inch in diameter.

It will be noted from the stand tables that, although a tremendous variation exists in total beaver food units present on the several areas, the number of food units per acre of aspen was relatively consistent. The average per acre for the five areas was 3,800. In effect, the figures for the five areas represent five separate population parameters. Thus, no confidence intervals can be placed on the average figure. The differences appear to be partially explained by the percent of the total stand in the one- to three-inch and three- to five-inch size classes. For aspen, Forester Seep Draw showed nearly 13 percent of the total stand in the three- to five-inch class, the same amount in the one- to three-inch class, and contained the greatest number of beaver food units per acre. For the same species, Forester Seep contained the lowest number of beaver food units per acre, and had only five percent in the one- to three-inch class and sever percent in the three- to five-inch class. This would indicate that the greatest amount of beaver food is to be found in aspen stands with a high percentage of the total stand in one- to five-inch trees.

Willow stands showed no such consistency in beaver food units per acre. The average number per acre, not including the Forester Creek colony, which had very small amounts of willow, was approximately 325 beaver food units. The figures for individual colonies ranged from 160 on Forester Seep, which supported mostly small, shrubby willow growth, to 543 on Beaver Draw, Area 2, which contained a large amount of dense willow of the larger sizes. With this species, the average figure of 325 beaver food units per acre is of necessity of

less value than the average figure for aspen. In broad terms, it can be stated that dense stands of large willows would yield approximately 550 beaver food units per acre, average densities of medium sized willows about 300 beaver food units per acre, and relatively sparse willows would yield approximately 100 beaver food units per acre, Table 16. Relative stocking for heavy, medium, and sparse willow stands is likewise indicated in this table.

Size composition may vary considerably from these figures, of course, since the basic criterion considered in this evaluation was the beaver food unit.

Table 16.--STEMS PER ACRE IN WILLOW STANDS OF DIFFERENT DENSITIES, NORTH PARK, COLORADO.

	Heavy	Medium	Sparse
Class I	50,000 and up	25,000 - 50,000	15,000 - 25,000
Class II	20,000 and up	2,000 - 20,000	1,000 - 2,000
Class III	3,000 and up	0 - 3,000	0 +

Number of beavers present

Dead-trapping by Hay (1955) resulted in determination of the number of beavers present on each area in the fall of 1955. Results are shown below:

Forester Seep Draw - 2 adults, 2 kits

Forester Seep - 6 adults, 1 yearling

Forester Creek - 2 adults, 1 kit

Beaver Draw, Area 1 - 2 adults, 3 yearlings, 3 kits

An indeterminate number of beavers was taken from Beaver Draw, Area 2, in the spring of 1955. Animals from this area are not used in carrying capacity calculations.

Determination of food availability

Measurements were made of the distance from the water and percent of slope for each aspen cut by beavers on the several study areas. Results are summarized in Tables 17 and 18.

Maximum distances travelled for food, and the effect of slope on these distances, were noted for the five study areas. On two areas, however, all aspens were within easy reach of the beavers. On the other three areas there was enough aspen within relatively easy reach so that maximums recorded here probably do not represent the ultimate distance, correlated with slope, that beavers would forage under conditions of extreme food scarcity. Most references in the literature give approximately 100 yards as the distance beavers normally travel for food (Hodgdon and Hunt, 1953; Bailey, 1927; Lawrence, 1954). This figure, thus, was arbitrarily chosen in this investigation as a measure for determining aspen availability. Maximum distance travelled for food and the corresponding slopes for the five study areas are listed below:

Forester Seep Draw:	(All aspen within reach)
Forester Creek:	(All aspen within reach)
Beaver Draw, Area 1:	60 yards, 40% slope
Beaver Draw, Area 2:	60 yards, 30% slope 40 yards, 41% slope 35 yards, 55% slope

Table 17.—DISTANCE FROM WATER OF ASPENS CUT BY BEAVERS ON STUDY AREAS.

Forester Seep Draw

1953-1954

	Yards
Range	0 to 15
Mean	6.4
Standard Deviation	3.77

Total, 1953-1955

Range	0 to 25
Mean	6.51
Standard Deviation	4.74

Beaver Draw, Area 1

1953-1954

	Yards
Range	3 to 40
Mean	19.78
Standard Deviation.	8.61

Total, 1953-1955

Range	0 to 60
Mean	25.31
Standard Deviation.	14.92

Forester Seep

1953-1954

	Yards
Range	3 to 70
Mean	34.29
Standard Deviation	15.08

Total, 1953-1955

Range	0 to 70
Mean	26.85
Standard Deviation	17.06

Beaver Draw, Area 2

1953-1954

	Yards
Range	4 to 60
Mean	25.55
Standard Deviation.	12.62

Total, 1953-1955

Range	0 to 60
Mean	23.99
Standard Deviation.	12.08

Forester Creek

Total, 1954-1955

	Yards
Range	0 to 30
Mean	8.71
Standard Deviation	8.33

Table 18.--PERCENT OF SLOPE FOR ASPENS CUT BY BEAVERS ON STUDY AREAS.

	Percent
Forester Seep Draw	
1953-1954	
Range	0 to 5
Mean	1.4
Standard Deviation	1.05
Total, 1953-1955	
Range	0 to 50
Mean	3.72
Standard Deviation	6.75
Forester Seep	
1953-1954	
Range	-10 to 17
Mean	2.08
Standard Deviation	2.71
Total, 1953-1955	
Range	-10 to 30
Mean	3.58
Standard Deviation	6.15

	Percent
Beaver Draw, Area 1	
1953-1954	
Range	0 to 50
Mean	21.04
Standard Deviation	12.34
Total, 1953-1955	
Range	0 to 50
Mean	25.86
Standard Deviation	14.44
Beaver Draw, Area 2	
1953-1954	
Range	2 to 45
Mean	24.09
Standard Deviation	6.40
Total, 1953-1955	
Range	0 to 50
Mean	19.82
Standard Deviation	9.92

	Percent
Forester Creek	
Total, 1954-1955	
Range	0 to 150
Mean	30.27
Standard Deviation	27.67

Forester Seep: 70 yards, 4% slope
55 yards, 20% slope
50 yards, 30% slope

More than one measurement is recorded for those areas where slopes varied considerably, in order to give a picture of the effect of steep slopes on the distance foraged.

Coefficients of correlation were determined for each area comparing: (1) slope with distance, and (2) size of tree cut with distance from open water. Results from the original field tally and for the total of all trees cut are given below:

Distance vs. Slope

	1954	Total
Forester Seep Draw	.0093	.321
Forester Seep	.149	.144
Beaver Draw, Area 1	.279	.336
Beaver Draw, Area 2	.121	.375
Forester Creek.		.464

Distance vs. Size

	1954	Total
Forester Seep Draw.	.090	.091
Forester Seep	.285	.414
Beaver Draw, Area 1	.375	.336
Beaver Draw, Area 2	.441	.375
Forester Creek.		.171

It will be noted that, in most cases, the mean distance of cut aspens from water and the mean slope increased from the first tally. This is as would be expected, indicating that in general the beavers cut first the closest and most available food trees.

Coefficients of correlation for distance vs. slope and distance vs. size were, with three exceptions, statistically non-significant. There are indications, however, that these factors are correlated with food availability. It may be seen that there is some-

what more correlation demonstrated between distance and slope as the mean distance increases. Distance vs. size, however, does not show this increase in correlation. It is believed that the factor of size would be of more importance as distance increased toward the maximum.

A multiple regression was calculated on the factors of size of aspens cut, distance from the water, and percent of slope. The regression proved to be non-significant (R = .0058). The figure for significance at the five-percent confidence level with 2390 degrees of freedom is approximately R = .0300. Thus, it can be seen that no correlation was demonstrated between the above factors. As in the case of the coefficients of correlation, observations on the extreme distances present on the several study areas indicate that these factors are probably correlated to some extent as distances and slopes become extreme. Thus, beyond a certain distance beavers will probably tend to take smaller trees, due to transportation difficulties. Likewise, although moderate slopes increase the beaver's foraging range, slopes steeper than given percentages will tend to reduce it. It is believed that an extensive study of numerous beaver colonies, recording the extremes of distance and slope, would show a much more significant correlation between these factors and size of aspens cut.

Competition with livestock and big game

The entire area contains a fairly large population of mule deer, and it is moderately grazed by cattle from July 1 to September 30. Data collected on sample plots of willow, however, indicate that neither big game nor livestock offers serious competition to beavers

as regards browse on this particular area. In addition to the fact that very little willow was taken by grazing in the locality, that which was taken was principally the top 20 percent or less of each willow stem browsed, leaving a considerable amount still available for beaver use. For aspen, careful note was likewise taken of all use by competitors, and although some young saplings were utilized by cattle and big game, there appeared to be no major interference with aspen reproduction from this source. Other workers (Yeager and Hill, 1954; Neff, 1956) have, however, reported serious competition from livestock and big game on various Colorado watersheds.

Determination of beaver food utilization

Aspen utilization was determined by total counts of all trees cut by beavers on the several areas. The original tally for all areas provided an estimate of the number of trees cut during the previous year. In all utilization aspects of this study, Beaver Draw, Area 2, was eliminated from consideration due to the indeterminate number of animals present. Table 19 presents a summary of aspen utilization data, showing the number of trees cut, the number of beaver food units cutsand utilized, and the percentage of use.

No aspen or other utilization figures were available for 1954 on Forester Creek, as this colony was begun in the late summer of 1954. Figures for 1955, however, include all cuttings for one year following the establishment of the colony. Thus, the figures given include all construction needs for the establishment of a new colony.

Table 19.—ANNUAL ASPEN UTILIZATION BY BEAVERS ON STUDY AREAS, 1953-1954, 1954-1955.

Area	Year	Mean Inches	No.	Std. Dev. Inches	Med., Inches	Mode Inches	Total B.F.U.	Used B.F.U.	Percent Used
Forester Seep Draw	1954	2.52	288	1.84	2.15	1	666.64	585.68	87.86
Forester Seep Draw	1955	2.65	190	2.28	1.60	1	552.06	395.19	71.58
Beaver Draw, Area 1	1954	4.05	123	1.81	3.90	3	549.18	527.22	96.00
Beaver Draw, Area 1	1955	3.75	250	2.25	3.76	4	1,054.50	991.15	93.99
Forester Seep	1954	2.56	208	2.36	1.80	1	610.65	519.78	85.12
Forester Seep	1955	3.83	204	3.00	3.36	1	1,117.36	992.49	88.82
Forester Creek	1955	3.11	348	3.13	2.01	1	1,636.56	883.48	53.98

Willow utilization was obtained by projecting data from sample plots. Table 20 summarizes the willow stems cut by size class and total beaver food units. No attempt was made to estimate willow use for the year of 1953-54 (one year prior to the original tally), since aging of willow stumps proved to be much less certain than in the case of aspen. Thus, the original tally consisted of the total of all cut stems on the plots at that time, and was useful mostly in the determination of future use.

Table 20.--WILLOW UTILIZATION (NUMBER OF STEMS CUT) ON STUDY AREAS, JUNE, 1954 TO JUNE, 1955.

Area	Class I	Class II	Class III	B. F. U.
Forester Seep Draw	767	1,221	274	29.02
Beaver Drew, Area 1	6,977	2,093	872	82.01
Forester Seep	3,544	253	0	14.43
Forester Creek	38	23	52	2.33

Table 21 presents total food use for one year, expressed in beaver food units, including aspen, willow, and alder. Alder is considered to yield approximately one-half of the beaver food supplied by aspen of equivalent size.

In most cases, the use of alder was probably more for construction than for food; but its use does reduce the amounts of the more palatable beaver food species required for construction. It should be noted that only small quantities of alder were observed to have been utilized as food.

Table 21.—TOTAL ANNUAL FOOD USE BY BEAVERS, IN BEAVER FOOD UNITS, ON STUDY AREAS, 1954-1955.

Area	Aspen		Willow,	Alder,	
	Total Cut	Used	Total Used	Total Used	Total Used
Forester Seep Draw	552.06	395.19	29.02	102.40	526.61
Forester Seep	1,117.36	992.49	14.43	....	1,006.92
Forester Creek	1,636.56	883.48	2.33	100.31	986.12
Beaver Draw, Area 1	1,054.90	991.15	82.01	....	1,073.16

Table 22.—AVERAGE NUMBER OF BEAVER FOOD UNITS CUT AND USED PER BEAVER ON STUDY AREAS, 1954-1955.

Area	No. of Beavers	Total Cut	Total Used	Cut/beaver	Used/beaver
Forester Seep Draw	2 ad., 2 kits	683.48	526.61	170.87	131.65
Forester Seep	6 ad., 1 yrl.	1,131.79	1,006.92	161.68	143.85
Forester Creek	2 ad., 1 kit	1,739.20	986.12	546.40	325.37
Beaver Draw, Area 1	2 ad., 3 yrl., 3 kits	1,136.51	1,073.16	142.06	134.15

Table 22 gives the number of beavers present on each area, the amount of food cut per animal, and the amount of food, including waste, utilized on each area.

As already noted, the Forester Creek colony was established during the period of study. Colony structures consisted of eight rather high dams and a lodge, all built during the period covered by this report, a circumstance that serves to explain the high use of woody material at this site.

The average annual utilization of food per beaver on the three areas, excluding Forester Creek (considered atypical), was 136.55 beaver food units. The average number of units cut (including waste) was 158.17 per year. The latter figure will be used in carrying capacity calculations. Allowance must be made, however, for increased cutting during the first year of occupancy of a new colony site.

No attempt was made to determine the amounts of cut materials used separately for food and construction. It was noted, however, that at the older colonies nearly all of the material used in construction had been previously used as food. Very few unpeeled stems were found on dams or lodges. On the contrary, most of the material used in construction at the new colony site (Forester Creek) was unpeeled. The Forester Seep Draw colony was also new, as it was begun approximately one year before the inception of this study. Unpeeled material was also noted in the dams of this colony, but such material was almost without exception cut prior to the original tally, i.e., during the first year of establishment. The use of additional

material for original construction can be noted in the higher total of cut stems shown by the original tally. It is of interest, also, that this greater quantity was cut by a smaller total of animals, probably a pair of two-year-olds.

The percent of waste in aspen, as shown in Table 19, was relatively low for the older colonies, and relatively constant for the two years recorded. Forester Seep Draw showed the greatest waste among older colonies, and waste here during the second year was somewhat higher than during the first. This can be explained by the use made of somewhat larger than average trees during the second year. As stated, waste by the Forester Creek colony was considerably higher than for any other area. Two factors may be cited to account for this circumstance: first, there were many large aspen trees cut on here, and waste was invariably higher for the larger trees; and second, it was a new colony, requiring building material in quantity greater than that provided in normal food utilization.

Table 23 shows the percentage of aspen, by diameter classes, used on all areas except Forester Creek, which is considered atypical in this respect.

It will be noted that the percentage of utilization increased sharply above the nine-inch diameter class. This apparent inconsistency has been noted in other beaver food-habits studies and is explained by the fact that the larger trees are heavier, and thus less prone to be lodged out of reach of the beavers. The smaller sample size must also be taken into consideration. The larger trees referred to in the previous paragraph are generally smaller than nine

Table 23.—PERCENT OF ASPEN UTILIZATION BY DIAMETER CLASSES ON STUDY AREAS.

D. S. H.[1/]	Number	Percent Used
1/4	24	100.00
1/2	99	100.00
1	448	99.10
2	255	96.79
3	227	95.10
4	205	92.85
5	149	92.00
6	111	83.20
7	69	82.25
8	37	68.95
9	13	60.77
10	16	82.18
11	7	79.29
12	2	89.99
13	1	80.00
14	0	....
15	1	90.00

1/ Diameter stump height in inches.

inches in diameter. Figure 8 is a graphic representation of the above data.

Note was taken of the number and size of all aspens lodged out of reach of the beavers. Table 24 shows the number lodged in each size class on the five study areas.

The number lodged (61) represents 2.6 percent of the total number of trees cut on all areas. It will be seen that the trees from three to seven inches in stump diameter show the greatest tendency to lodge. Smaller trees can be pulled down by the beavers if they lodge, and the larger ones generally are heavy enough to fall through to the ground.

Figure 8

PERCENT OF ASPEN WASTED BY DIAMETER CLASS

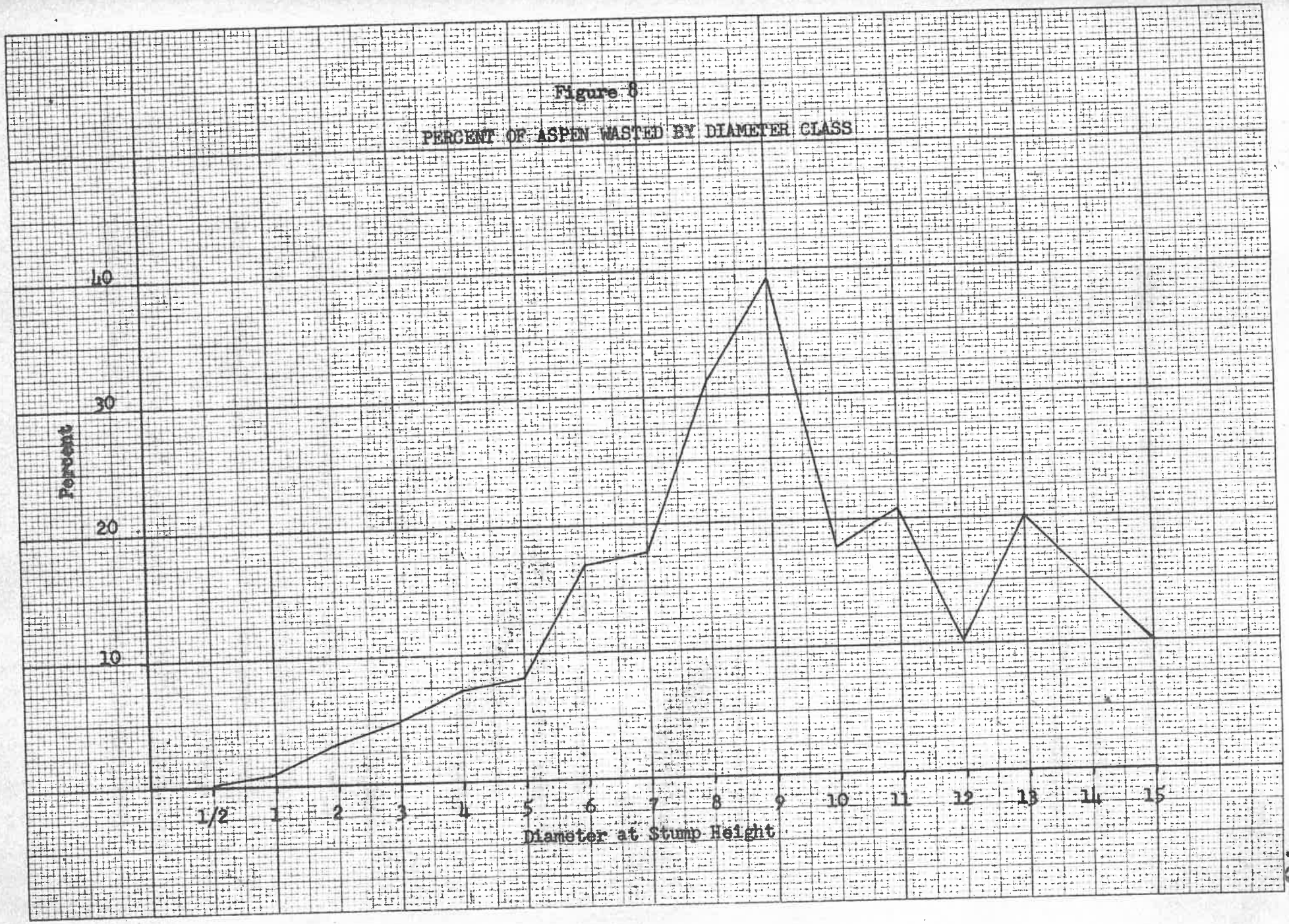


Table 24.—SIZE DISTRIBUTION OF ASPENS LODGED ON STUDY AREAS.

D. S. H. 1/	Number Lodged
1	2
2	2
3	9
4	13
5	7
6	8
7	9
8	4
9	4
10	2
11	1
	61

1/ Diameter stump height in inches.

Table 25 shows the number of aspen trees of each size class present in the stand and the percent of the stand cut of each on the five study areas. Figure 9 gives the percent of the total cut in each size class, contrasted with the percent cut of the total available in the stand in each size class. The latter figures were reduced to a basis of 100 percent so that direct comparisons could be made. Figure 10 shows the average for the five areas.

The high figure for the percentage cut of the one- to three-inch tree class on Forester Creek can be explained best by the relatively low proportion of trees of this size present on the area.

Figure 9 demonstrates certain definite patterns in food preference. Invariably, the three smaller size classes of aspens showed a higher percentage of the total number cut than the percentage cut in relation to the total available in the stand. Likewise, with

Table 25.—SIZE PREFERENCE FOR ASPEN ON STUDY AREAS.

Area	Size Inches	Number Present	Number Cut	Percent Cut
Forester Seep Draw	0-1	1,633	10	.0061
	1-3	313	111	.3546
	3-5	313	26	.0831
	5-7	112	28	.2500
	7-up	45	15	.3333
Forester Seep	0-1	11,253	18	.0016
	1-3	716	65	.0908
	3-5	985	51	.0518
	5-7	567	31	.0547
	7-up	358	39	.1089
Forester Creek	0-1	4,092	24	.0059
	1-3	350	192	.5486
	3-5	306	67	.2190
	5-7	175	19	.1086
	7-up	88	46	.5227
Beaver Draw, Area 1	0-1	28,592	20	.0007
	1-3	2,113	47	.0222
	3-5	2,465	97	.0394
	5-7	986	68	.0690
	7-up	211	18	.0853
Beaver Draw, Area 2	0-1	53,136	11	.0002
	1-3	9,831	74	.0075
	3-5	7,373	38	.0052
	5-7	3,220	15	.0047
	7-up	847	15	.0177

one exception, the one- to three-inch trees, and those over seven inches in diameter, show the highest percentage cut with reference to availability. The high percentage of cut trees over seven inches in diameter, in relation to the total available, may be a reflection of the low total number of this size in the stands. If this is the case, the data would seem to indicate that the preferred size class is the

Figure 9.--Size preference for aspen, each area.

The red columns represent the percent cut in each size class of the total number of trees cut on each area. The black columns represent the percent cut in each size class of the total present in that class in the stands. The latter figures reduced to 100 percent so that direct comparisons can be made.

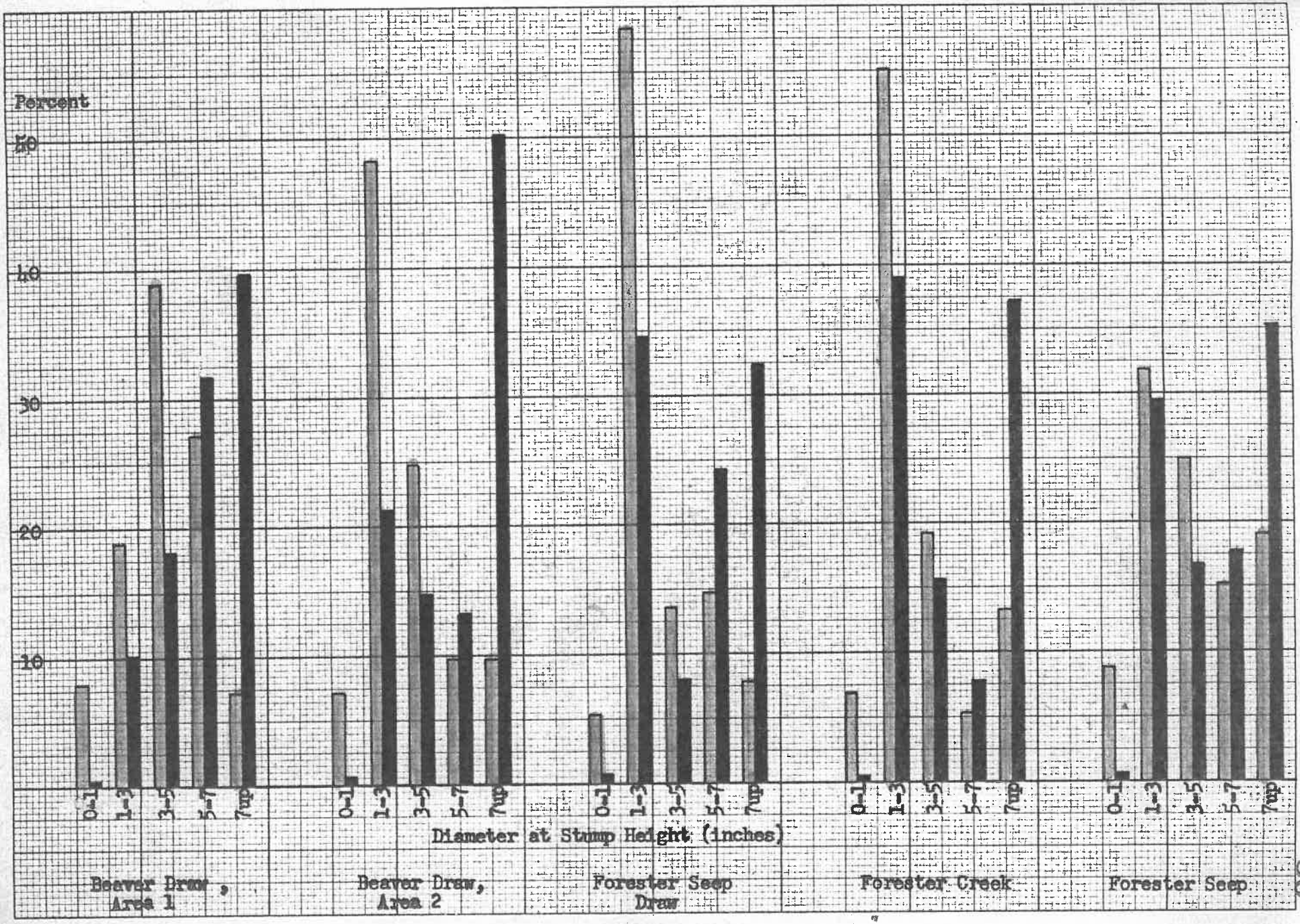
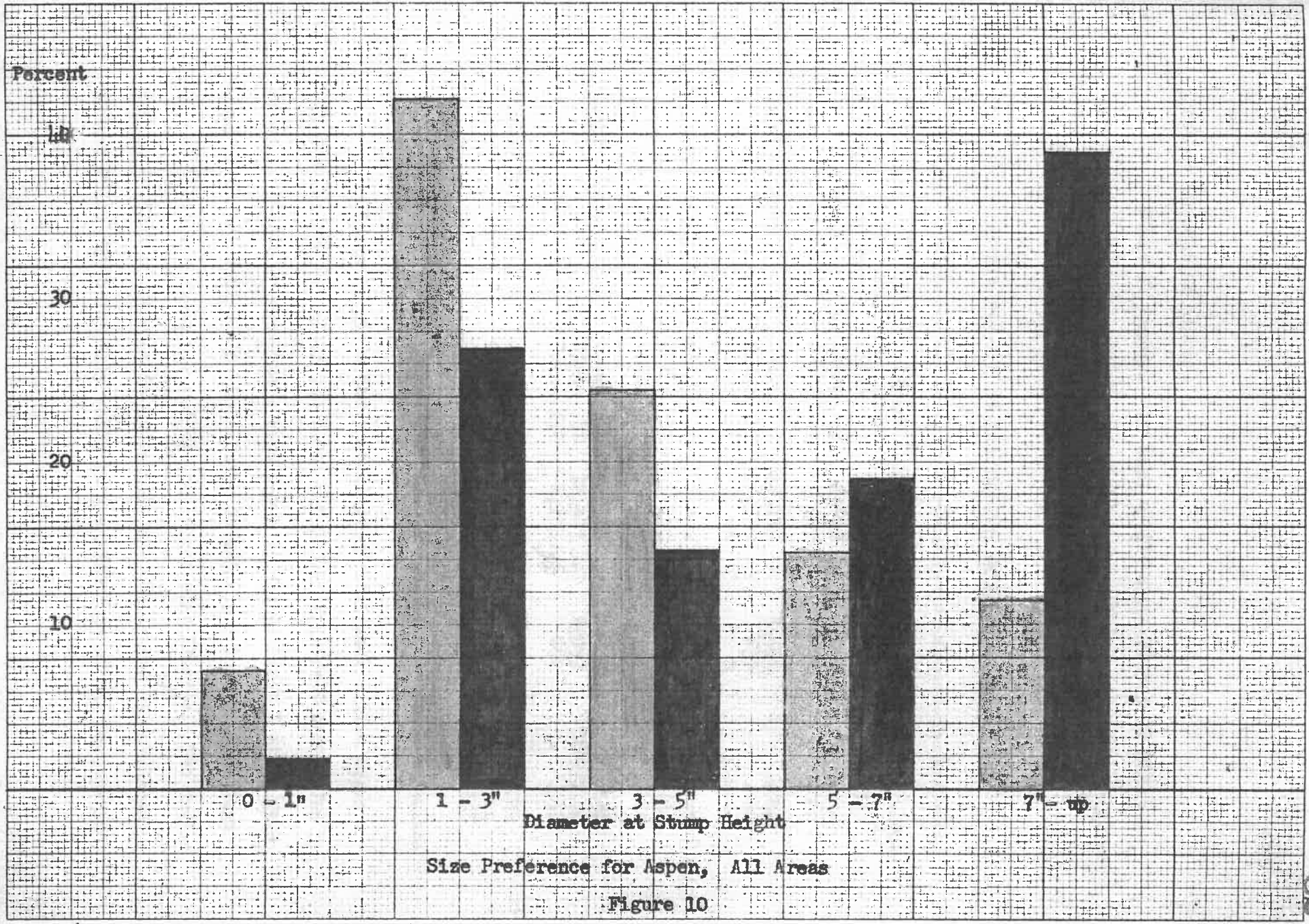

Percent
50
40
30
20
10
0-1
1-3
3-5
5-7
7up
Diameter at Stump Height (inches)
Beaver Draw, Area 1
Beaver Draw, Area 2
Forester Seep Draw
Forester Creek
Forester Seep

Figure 9

Figure 10.--Size preference for aspen, all areas.

This graph represents the average for all areas as shown in Figure 9.



Size Preference for Aspen, All Areas

Figure 10

one- to three-inch aspens.

Table 26 presents for each of the size classes of willows the number of stems present, the number cut, and the percent cut on the several areas.

Table 26.—SIZE PREFERENCE OF BEAVERS FOR WILLOW ON STUDY AREAS.

Area	Number Present		Number Cut	Percent Cut
Forester Seep Draw	Class I	5,614	767	.132
	Class II	2,895	1,221	.442
	Class III	680	274	.403
Forester Seep	Class I	248,155	3,544	.014
	Class II	8,338	253	.030
	Class III	78	0	———
Forester Creek	Class I	533	38	.071
	Class II	140	23	.164
	Class III	125	52	.416
Beaver Draw, Area I	Class I	128,650	6,977	.054
	Class II	19,377	2,093	.108
	Class III	1,633	872	.534
Beaver Draw, Area 2	Class I	181,094	5,759	.032
	Class II	84,300	3,665	.044
	Class III	14,115	2,094	.148

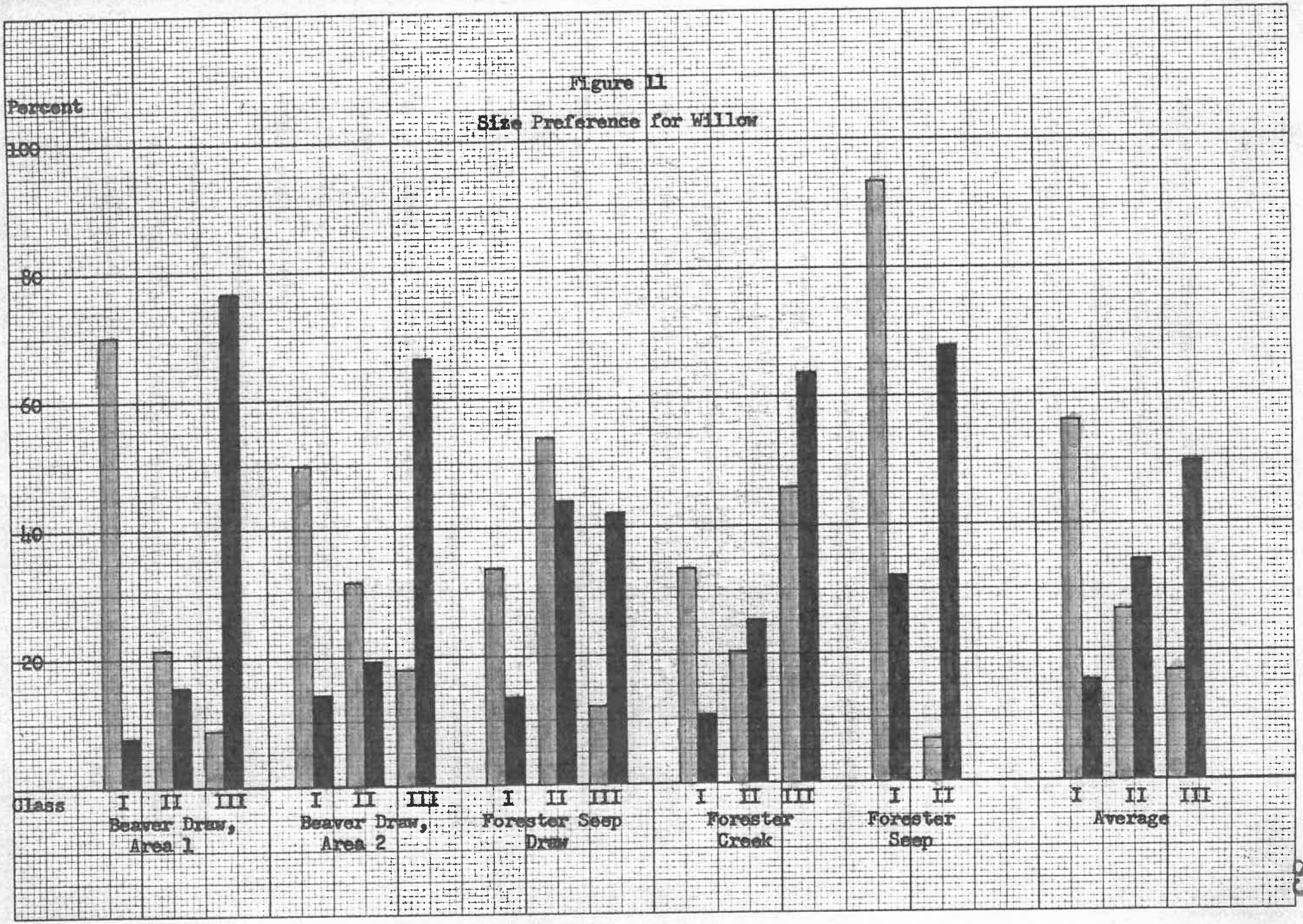
Figure 11 gives the percentage of available willow stems cut and the percentage of the total cut (as in Figures 9 and 10 for aspen). It can be seen that, with two exceptions, Class I stems were used most frequently, but that almost invariably a larger percentage of the total available was cut in the larger size classes. The indication is that preference is definitely for the larger stems (Class II and III). This probably works to the advantage of the beavers in

Figure 11.—Size preference for willow.

The red columns represent the percent cut in each size class of the total stems cut on each area. The black columns represent the percent cut in each size class of the total present in that class in the stands. The latter figures are reduced to 100 percent so that direct comparisons can be made. The series of columns on the right represents the average of all areas combined.

Figure 11

Size Preference for Willow



two ways: first, the larger sizes yield more food per unit of effort; and second, since the larger stems tend to die off naturally and are replaced with sprout growth, the taking of larger stems would be advantageous from the replacement factor.

In considering carrying capacity for beavers, it is necessary to know the number of animals present, the amount of food on the area, the amount required per year per beaver, and something of the replacement factors of the food supply. Once a tree has been cut it is removed from the potential food supply regardless of the degree of utilization. Thus, if the percentage of waste is relatively constant, the total amount of food removed is of much more importance in determining carrying capacity than the amount actually used. For this reason, the figure of 158 beaver food units (see page 73 above) will be used in determining the animal's annual food requirements. The amount of food present on a given area is, of course, a dynamic rather than a static situation. Further consideration of the replacement factors will be given below under Growth and reproduction.

Table 27 indicates the total amount of beaver food present on each area, and the length of time that an average colony of six beavers could exist on this static supply. These figures assume a sufficient supply of herbaceous material for sustenance during the three summer months.

It should be noted that Beaver Draw, Area 1, was supporting ten beavers as of October, 1955. That area probably is large enough to support two normal colonies. Beaver Draw, Area 2, is much larger still, and could be expected to support several full-sized colonies.

Table 27.--BEAVER FOOD UNITS, BY STUDY AREAS, AND CARRYING CAPACITY FOR STATIC FOOD SUPPLY.

Area	Total Food Present (B.F.U.)		Years of Food Supply (6 beavers)
Forester Seep Draw	Aspen	3,639	
	Willow	82	
	Total	3,721	4
Forester Seep	Aspen	18,775	
	Willow	886	
	Total	19,661	21
Forester Creek	Aspen	5,682	
	Willow	8	
	Total	5,690	6
Beaver Draw, Area 1	Aspen	30,797	
	Willow	723	
	Total	31,520	34
Beaver Draw, Area 2	Aspen	92,923	
	Willow	2,224	
	Total	95,147	102

The average number of beaver food units per acre of aspen on five areas was 3,800; for willow, on four areas, it was approximately 325 units. Thus, it can be seen that 0.041 acres of aspen or 0.413 acres of willow, or combinations of lesser amounts of the two, would support one beaver for one year.

The presence of appreciable amounts of alder on an area would probably reduce somewhat the amounts of willow or aspen required. However, reduction would appear to be negligible on areas with an abundant supply of aspen or willow, as alder is seldom cut under such circumstances.

An attempt was made to determine, in general terms, the seasonal use of various foods by the beavers. Monthly tallies of aspen are summarized in Table 28.

Table 28.—MONTHLY TALLIES OF ASPEN CUT BY BEAVERS ON STUDY AREAS.

Forester Seep Draw

Date	No. Cut	Mean Size Inches	B.F.U.
7/10/54	288	2.52	667
8/10/54	9	1.39	10
9/8/54	29	1.98	46
10/10/54	71	2.86	203
11/20/54	41	4.26	254
7/12/55	40	1.35	36
8/12/55	43	2.23	126
9/12/55	32	1.89	46
10/7/55	109	3.11	358

Forester Seep

Date	No. Cut	Mean Size Inches	B.F.U.
8/7/54	208	2.56	611
9/9/54	51	1.63	74
8/9/55	153	4.57	1,043
9/8/55	58	1.28	85
10/9/55	75	3.48	310

Beaver Draw, Area 1

Date	No. Cut	Mean Size Inches	B.F.U.
7/21/54	123	4.05	529
8/24/54	5	3.60	22
7/21/55	245	3.75	1,033
8/23/55	20	2.80	69
10/7/55	22	5.45	194

Beaver Draw, Area 2

Date	No. Cut	Mean Size Inches	B.F.U.
7/20/54	248	2.52	723
8/21/54	25	1.06	15

(1955 biased; not included)

It can be seen from this table that the average size and total number of aspens cut increased with the approach of fall.

Although no actual measurements were obtained for the utilization of herbaceous plants, an attempt was made to determine the relative amounts taken during various periods of the year. Thus, it was assumed that the food consumed during the winter months was 100

percent woody material.[1] By calculating the average consumption of bark per month during the winter, it was possible to estimate the monthly food requirements. Thus, when consumption of bark fell below this average figure, during the summer months, the difference was presumed to be made up by herbaceous material. Only three of the study areas were used for this determination, since Beaver Draw, Area 2, was not applicable due to trapping of an unknown number of animals in the spring of 1955, and Forester Creek had only a very small growth of sedges and similar plants. It must be emphasized that the figures derived are only a general estimate of the actual situation, since a high degree of accuracy would be difficult to obtain. Table 29 summarizes the seasonal use of the various foods involved.

It is apparent that herbaceous materials make up nearly three-fourths of the food consumed from about mid-spring until the middle of August. This was borne out by observations of beavers feeding during this period. Figure 12 is a graphic representation of these generalized data.

Growth and reproduction of beaver food species.

Aspen.--The growth rate of aspen was studied, using cross-sections of 80 beaver-cut trees. The average diameter growth rate

[1] It is known that beavers wintering in ponds containing water lilies or similar vegetation make use of such food during the winter. None of the ponds studied contained herbaceous plants of this nature.

Table 29.--SEASONAL USE OF VARIOUS FOODS BY BEAVERS ON STUDY AREAS, EXPRESSED IN PERCENT.

Forester Seep

	Sept 9-May 9	May 10-July 9	July 10-Aug 9	Aug 10-Sept 8
Aspen	99.36	30.82	16.84	62.28
Willow	0.64	1.17	2.59	2.09
Herbaceous	0.00	68.01	80.57	35.63

Beaver Draw, Area 1

	Sept 24-May 9	May 10-July 20	July 21-Aug 23	Aug 24-Sept 23
Aspen	97.31	24.92	18.28	71.01
Willow	2.69	3.51	10.17	28.99
Herbaceous	0.00	71.57	71.55	0.00

Forester Seep Draw

	Sept 9-May 9	May 10-July 9	July 10-Aug 10	Aug 11-Sept 8
Aspen	97.17	30.77	16.79	77.58
Willow	2.83	4.96	11.36	5.42
Herbaceous	0.00	64.27	71.85	17.00

Average

	Sept 14-May 9	May 10-July 12	July 13-Aug 14	Aug 15-Sept 13
Aspen	97.95	28.94	17.30	70.29
Willow	2.05	3.21	8.04	12.17
Herbaceous	0.00	67.95	74.66	17.54

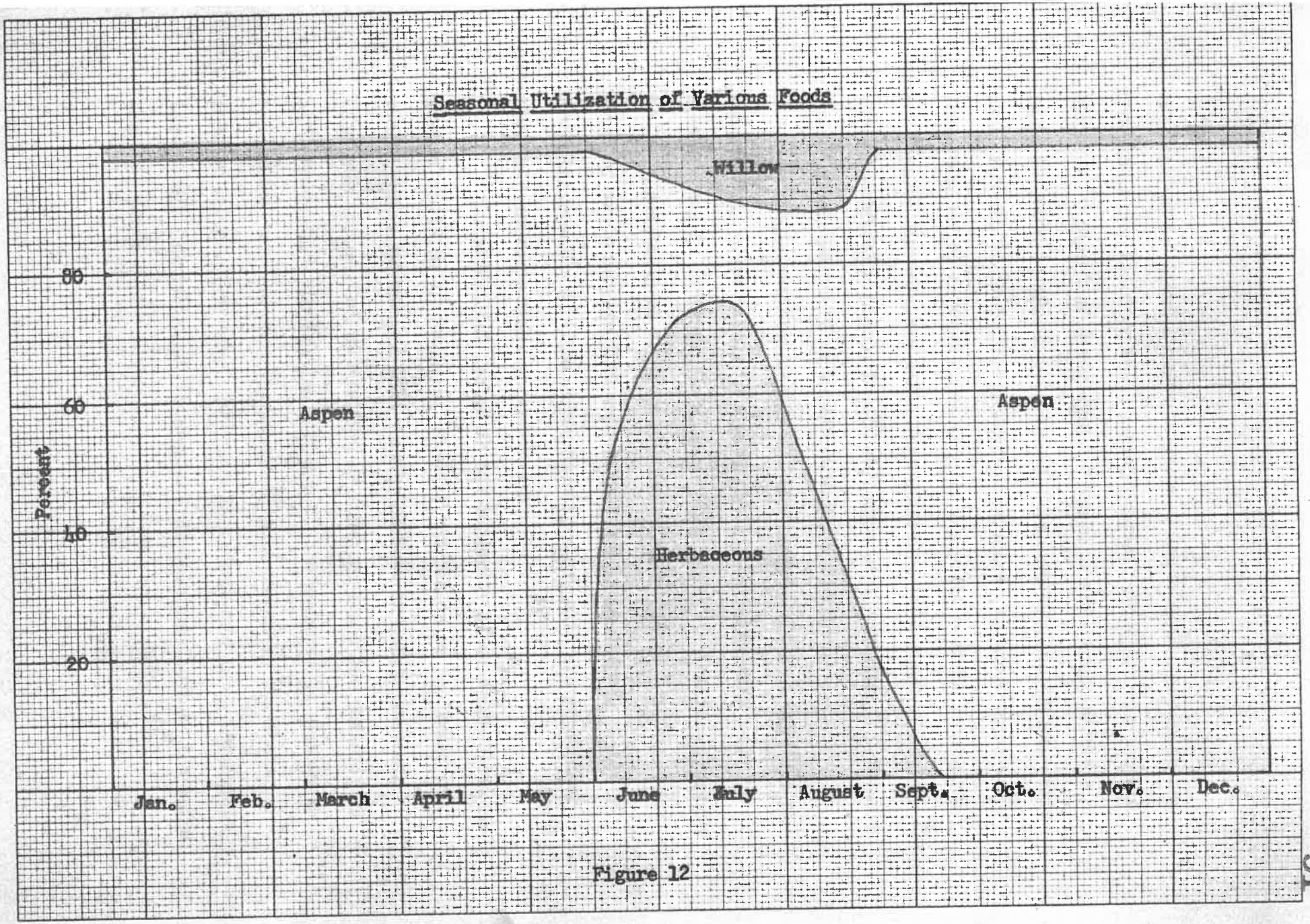

Seasonal Utilization of Various Foods
Willow
Aspen
Aspen
Herbaceous
Percent
80
60
40
20
Jan.
Feb.
March
April
May
June
July
August
Sept.
Oct.
Nov.
Dec.

Figure 12

was found to be 0.064 inches per year. Figure 13 is a multiple regression curve based on these growth studies, and shows the average diameter of aspens at given ages. Several of the stumps showed a rapid increase in growth rate for the last two or three years. This would seem to indicate that foreging operations by the beavers may tend to serve as a "release cutting". Thus, the beavers themselves may tend to increase the basic food potential of a stand of aspen through activities which, in effect, serve as silvicultural practices. Such a situation would be termed ecological cosation.

It is obvious that if all the increase in food were put on the standing trees (i.e., no reproduction), this increase would be of little value in prolonging a food supply. Thus, it becomes necessary to learn something of the reproduction of the species. To this end, areas of aspen reproduction were mapped and planimetered. Table 30 gives the results of these measurements, along with the percent of the total aspen acreage in reproduction.

An additional factor in the longevity of an aspen stand is that of invasion by conifers. Most of the stands on the areas involved were interspersed with varying amounts of lodgepole pine, Engelmann spruce, and alpine fir, as shown in the stand tables. It is possible that the cutting activity of the beavers, by opening up the stands, may increase the length of time necessary for these species to take over completely; but it is believed that, eventually, the process of ecological succession will eliminate most of the aspen from the area.

Figure 13

SIZE VS. AGE OF ASPEN

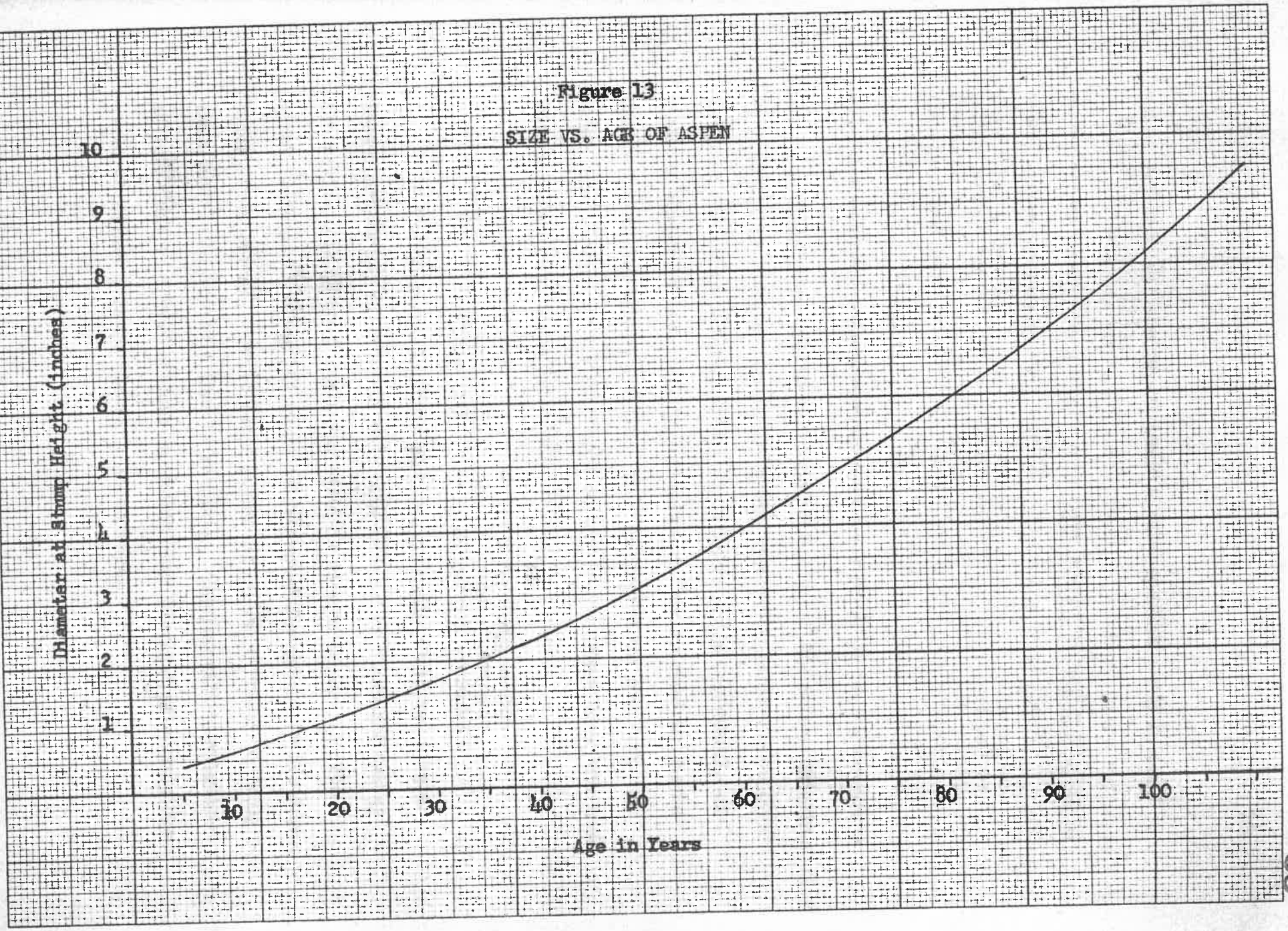


Table 30.--AREA AND PERCENT OF ASPEN STANDS ON STUDY AREAS IN ASPEN IN REPRODUCTION, 1955.

Area	Acres	Percent of Aspen in Reproduction
Beaver Draw, Area 1	1.25	16 percent
Beaver Draw, Area 2	1.95	9 percent
Forester Seep	0.62	10 percent
Forester Seep Draw	0+	0+ percent
Forester Creek	0+	0+ percent

Willow.--Comparative counts were made of the number and size of live willow stems on the sample plots from the time of the original tally to the tally one year later. This information was correlated with the number of stems cut to determine the growth rate and reproductive potential of the species. For the five areas combined, the three size classes of willow showed the following change over the one-year interval (cut stems included):

Class	I	-	3 percent increase
Class	II	-	1 percent decrease
Class	III	-	22 percent increase

The decrease in Class II stems probably indicates that a larger proportion of stems of this size changed to Class III during the period than Class I stems increased in size to Class II. The great increase in Class III stems is accounted for mostly by the Forester Creek colony, where a large number of stems in the first tally were just below one-half inch in diameter. The generally low number of half-inch or larger willows in stands thus permit a relatively few stems to effect a large change in percentage.

Table 31 shows the change, natural increase, and number of stems cut on each area.

Table 31.--REPRODUCTION AND GROWTH OF WILLOW ON STUDY AREAS, 1954-1955

Area	Number Present (sample plots) 1954	Number Present (sample plots) 1955	Number Cut (sample plots)	Percent Increase
Forester Seep Draw				
Class I	631	599	98	10
Class II	350	164	156	(-) 9
Class III	54	45	35	2
Forester Seep				
Class I	3,948	4,301	56	10
Class II	154	108	4	(-) 27
Class III	0	1	0	...
Beaver Draw, Area 1				
Class I	1,924	1,840	120	2
Class II	377	227	36	(-) 30
Class III	37	9	15	(-) 35
Beaver Draw, Area 2				
Class I	3,520	3,193	110	(-) 6
Class II	1,596	1,465	70	(-) 4
Class III	257	223	40	2
Forester Creek				
Class I	533	488	38	(-) 1
Class II	140	205	23	63
Class III	125	164	52	73

It can be seen from the above tabulation that factors other than use by beavers tend to reduce a stand of willow. The reduction on Forester Seep Draw was due in great part to flooding by beaver impoundments. Two plots were inundated during the study. It was noted that willows appear to die faster after flooding than do alders. Observation indicates die-off in older willow stems from loss of vigor,

and reduction in numbers of sprouts through competition for available light and nutrients. Cutting by beavers appears to stimulate sprouting.

On the basis of these comparisons, it would appear that beavers could harvest approximately 20 percent of a stand of willow annually without reducing the basic stand.

Annual increament in total food.--Using the average figure of 3,800 beaver food units of aspen per acre, and 325 beaver food units of willow per acre, it is clear that, for the area studied, the average increase in aspen would be equivalent to 243 beaver food units per acre per year; and the increase in willow would be 76 beaver food units per acre per year.

The above figures relative to reproduction and growth rates indicate that approximately two-thirds of an acre of aspen would support one beaver in perpetuity. Likewise, approximately two acres of willow would be required to support one beaver. Thus, four acres of aspen, twelve acres of willow, or combinations of lesser amounts of the two, would support a colony of six animals on a sustained yield basis. These figures assume adequate reproduction of aspen.

Chapter VI

DISCUSSION

In this chapter, the findings presented in Chapter V are discussed. Reference is made to studies reported in the literature when pertinent. In addition, applications to beaver management in Colorado and needs for further study to this end, are suggested.

Physical factors

Cover types.—Table 8 indicates the wide variety of colony types included in the study. Area variation ranged from just over one acre on Forester Seep Draw to 42 acres on Beaver Draw, Area 2. Nearly four surface acres of water were impounded on the latter colony, as compared with less than 0.2 acre at the former site. On all areas, aspen was the major food source. Willow was the only other important food source (excluding herbaceous plants), and was likewise present on all areas. However, the proportion of willow to aspen varied from one to 2.6 on Forester Seep Draw to one to 10 on Forester Creek. Obviously, therefore, the results of this study are most applicable to colonies containing a mixture of aspen and willow, with aspen predominant. This is believed to be a relatively common situation on beaver colonies throughout Colorado, but many situations exist where colonies are supported exclusively on willow growth (Neff, 1956; Hay, 1955).

Stream gradients.--Stream gradient appears to be a definite limiting factor to beaver occupancy (Retzer, 1955). None of the occupied areas studied were on stream sections with a gradient steeper than seven percent. All but one would be classified as Excellent, and that one would be classified Good, in this regard by Retzer (loc. cit.). Two unoccupied sections of stream, both between occupied areas, were somewhat steeper. The section between Area 1 and Area 2 on Beaver Draw would be classified Good (i.e., 8 percent) and the section between occupied areas of Forester Creek would be Unsuitable (i.e., 15 percent).

Stream flow.--It seems apparent from the results of this study that only a very small minimum stream flow is required by beavers. The major concern appears to be constancy of flow rather than amount. Data show that a flow of 0.2 cubic feet per second was completely adequate to maintain the maximum water storage capacity on Forester Seep Draw. On Beaver Draw, Area 2, where the flow was less constant and the storage capacity was much greater, many of the ponds were lowered about one foot during the period of lowest stream flow (approximately 0.1 cubic feet per second). This lowering of pond levels appeared to have no adverse effect on the beaver population, occurring as it did in late summer. A slight increase in stream flow during the early fall served to fill ponds to capacity during the period of preparation for winter season.

Determination of stand composition

Determination of the amount of beaver food provided by

aspens and willows of various diameters, and the choosing of a standard unit (beaver food unit) with which both size and species can be equated, are considered essential to the present study. With this determination, the total food present in a stand, the annual food requirements, food present per acre, etc., can be presented as a single figure. Calculation of the beaver food unit was based on original data from Maine (O'Brien, 1938), and it is realized that there may be variations in form, height growth, etc., between aspens in Maine and Colorado. It is believed, however, that, by using only the proportions established, not actual weights, any inherent bias in the data becomes negligible. Error may also be present in the projection of Maine data to trees of greater diameter than used in the original study. The significance of the regression equation, however, indicates that such error was slight.

The average number of beaver food units per acre of aspen (3,800) provides a figure with which carrying capacity can be determined on an area basis. Stand tables show that the greatest amount of beaver food per acre is found where one-inch to five-inch aspens predominate. Variation between areas was small enough that use of the average figure is believed to be acceptable for intensive carrying-capacity determinations. The stocking density of aspen on the several areas investigated was considered to be average for mountain range in Colorado.

Willow densities varied considerably among the several areas. Table 16 presents the average number of beaver food units per acre in heavy, medium, and sparse stands of willow. These data are

considerably more generalized than in the case of aspen. They provide, however, a figure with which area determinations of carrying capacity can be made.

Food availability

Two factors were measured which affect the availability of aspen for beaver utilization. These were distance from the water and percent of slope. Coefficients of correlation were calculated relating size of tree cut with distance from water, and distance from the water with percent of slope. In addition, a multiple regression was calculated comparing the interaction effect of all of these factors. None of the correlations demonstrated any significance. The main reason for no significance is believed to be the lack of extreme conditions in availability. Most of the aspen was easily accessible, making it unnecessary for the beavers to forage great distances or up particularly steep slopes. Maximum travel distances and corresponding slopes indicate, however, that an increase in slope beyond 15 or 20 percent seemed to limit the distance beavers will forage for food. It is also indicated that a somewhat lower gradient is beneficial in aiding beavers in transporting materials. Thus, it would appear that a moderate slope would extend the foraging range, while a very steep slope would limit it.

Aspens cut at the greatest distances from water were invariably smaller than the average size taken, indicating that extremes of distance tend to limit the size of aspens cut.

It is suggested that extensive studies, measuring the extremes of distance and slope on a large number of colony areas, would

provide more accurate determinations of the limits of availability of a beaver food supply than obtained in the present investigation.

Reports from the literature (Hodgdon and Hunt, 1953; Bailey, 1927; Lawrence, 1954) were relied upon to provide the average figure of 100 yards for the normal limit of availability used in this study.

Competition with livestock and big game

Food competition between beavers and livestock and big game was studied in general terms. It was indicated that the moderate stocking of cattle and the fairly large mule-deer population on the study areas offered no serious competition in this respect. It has been noted by other workers (Yeager and Hill, 1954; Neff, 1956) that heavy grazing, especially by sheep, may retard willow stands materially, and is effective in limiting aspen reproduction.

Beaver food utilization

Aspen.--Aspen utilization, determined by total counts of all trees cut by beavers, Table 19, shows that, with the exception of Forester Seep Draw, the annual food use increased in 1954-55 over that for 1953-54. This is undoubtedly due to increase in the number of animals present. The decrease on Forester Seep Draw can be explained by construction needs during 1953-54, the first year of occupancy. It will be noted that the number of trees cut decreased in 1954-55 on Forester Seep, while the number of beaver food units cut was nearly doubled. This was due to the larger size of trees cut.

Willow.--The number of willow stems cut varied greatly between areas, and was directly correlated with the amount of willow

available, except on Forester Seep Draw where the aspen supply was limited.

Total food use.--It should be noted that no alder was used on Forester Seep, although it was present in considerable amounts. Alder was used by the colonies on Forester Seep Draw and Forester Creek. Construction needs were high on the latter two areas, and practically non-existent on Forester Seep. This would seem to indicate that use of alder, where other foods are available, is generally limited to construction.

The number of beaver food units used per beaver on the several areas, excluding Forester Creek (considered atypical), was decidedly constant, and the total cut was only slightly less so. Thus, the average number of food units cut and used are thought to provide reliable figures with which to make carrying-capacity determinations. The average number cut per animal (158) is considered the more important figure, since wasted food is lost to future use by the colony. It must be noted that more material is required per colony during the first year of occupancy than in subsequent years.

Waste of aspen.--The percent of aspen waste on all areas except Forester Creek averaged about 13 percent. This is close to the average found in several studies in the literature (O'Brien, 1938; Aldous, 1938; Stegeman, 1954; Gese and Shadle, 1943). Waste would probably be somewhat higher where extremely dense aspen stands are harvested, since more trees would be likely to lodge out of reach of the beavers.

Size preference for aspen.—The data in Table 25 and Figures 9 and 10 indicate that the one-inch to three-inch size class in aspen was cut most frequently. Likewise, a greater proportion of the trees in this size class was taken. It would thus appear that the beavers exhibited a distinct preference for one-inch to three-inch trees. All aspen stands on the several areas contained trees of every age and size up to the maximum present. Thus, although the preferred size class seems likely to be taken first, the over-all carrying-capacity aspects of an aspen stand would not be materially effected by this preference. However, an even-aged aspen stand, with most trees in the one-inch to three-inch class, would probably constitute some advantage to the animals. Such a stand would likely be more densely stocked than an all-age stand, waste would be considerably less than for larger trees, and sprouting (reproduction) would probably occur at the maximum rate.

Size preference for willow.—Table 26 and Figure 11 demonstrate a distinct preference by beavers for larger willow stems (classes II and III). This being the case, beavers tend to remove more of the larger stems in a willow stand. This serves not only to stimulate sprout growth, but also results in faster growth of the remaining stems in a clump due to less competition for space, light, and available nutrients.

Seasonal use of various foods.—Herbaceous plants constitute a considerable proportion of the food consumed by beavers. The difficulties involved in actual measurement of herbaceous food use are extensive, and were considered beyond the scope of this problem. By

determining the average use of woody material during months when such food was used exclusively, it was possible to obtain an average figure, in beaver food units, for the total monthly food requirement. Thus, when use of woody material was below the average monthly needs (found to occur only in summer), the remainder of the food was assumed to be made up of herbaceous plants. Table 9 and Figure 12 show the results of this procedure on the three areas used in this determination. It can be seen that nearly three-fourths of the total food consumed from mid-spring to the middle of August is herbaceous. It is also noted that the use of willow increased in the late summer. Herbaceous food, although of considerable importance in the beaver diet, is considered to be of little importance in carrying-capacity determinations, since such types are generally present in abundance wherever suitable conditions for beaver habitation exist. In addition, herbaceous plants reproduce rapidly and usually annually, so that use by beavers in one year will not likely affect the amount present in the next. If such plants are entirely lacking from a colony area, the requirement for woody plants would undoubtedly be considerably above average. This factor may partially account for the high food use of aspen and willow on Forester Creek, which possessed only small growths of herbaceous material.

Growth and reproduction of beaver foods

Aspen.--Growth studies indicated that the average annual diameter increment for aspen on the study areas was 0.064 inches. Of the three study areas with any appreciable amounts of aspen reproduc-

tion, the acreage of reproduction was approximately 10 percent of the total aspen stand. In order for a colony subsisting mostly on aspen to maintain itself indefinitely, the growth rate of the trees must equal the amount taken by the beavers, and the cut trees must be replaced by reproduction. With the very slow rate of growth evidenced by aspen in North Park, and with the relatively small amount of reproduction present, it would appear that aspen stands here are generally unable to perpetuate themselves in the face of unlimited beaver numbers, at least on a colony-site basis. Invasion by conifers also tends to shorten the life of the aspen stands.

Willow.--The data on willow growth and reproduction indicate that approximately 20 percent of the stand could be harvested annually without reducing the volume present. It appears, therefore, that a beaver colony subsisting mainly on willows could be kept within limits, through systematic harvest, which would allow for continuous occupation of any given willow site, provided the area was large enough to yield the basic food requirements.

Carrying capacity

The definition of carrying capacity, as used in this study, is the number of beavers which can exist indefinitely on a section of stream without depleting its food supply. This definition implies an area larger than the immediate colony site, and is meant to include all of the actual or potential range available for beaver occupancy on a continuous stream section. Thus, carrying capacity, by this definition, is based not on the individual colony site, but

rather on an entire stream section, which might include potential range for several separate colonies.

It was determined that four acres of aspen, twelve acres of willow, or combinations of lesser amounts of the two, would support an average colony of six animals on a sustained-yield basis. In the case of aspen, this could only be true where reproduction (sucker growth) kept pace with beaver-cutting activity.

It must be realized, of course, that many beaver colonies in Colorado mountain range presently exist on much less than four acres of aspen. It was in connection with over-stocking of this sort that Yeager and Hill (1954) and Neff (1956) reported on colony areas that had been completely "eaten out" and abandoned. Sustained yield in food production in all cases requires that beaver populations be kept to carrying-capacity numbers.

Another major problem in using the individual colony site as a unit of carrying capacity is the difficulty in delimiting colony areas on streams with a continuous series of dams. Hay (1955) found that distinct colonial limits were present on such streams, but that they were difficult to determine. Beaver colonies commonly move short distances up or down stream to a new food supply when that adjacent to the old colony site is exhausted (Hodgdon and Hunt, 1953).

Stream areas suitable for beaver habitation are of two general types. The first is the short, isolated, stretch of stream large enough to support but one colony, limited by a localized food supply or delimited by physical features precluding beaver occupancy. The carrying capacity of this type must be based on a single colony.

Generally, colonies of this type are of relatively short duration unless beaver numbers are kept within the carrying capacity of the area.

The second type is the section with suitable food and physical factors extending over a considerable distance along the stream. In this case it is logical to make carrying-capacity determinations for the whole section. Thus, the area involved would support a certain number of individual colonies, which might be allowed to exhaust the food supply at a particular site provided unoccupied sites were nearby to which the beavers could move.

It is generally believed that young beavers move out of the parent colony during the spring of their second year. If the animals are allowed to increase progressively, the new colonies established by these two-year-olds will soon occupy all suitable areas within the vicinity of the parent colony. Thus, carrying-capacity determinations must be coordinated with some form of harvest if habitat stability is to be maintained.

It is probable that, over a long period of years, conifers would invade aspen stands and materially reduce the carrying capacity of such sections of stream. Periodic inventory of the aspen food supply would permit modification in carrying capacity, and thus periodic adjustment of beaver numbers to meet environmental limitations.

Management applications

Beaver numbers in Colorado have reached a point where some form of management is essential (Annual Report, 1953-54, Colorado Game and Fish Department). The population dispersion, wherein two-

year-old animals emigrate from the parent colony (Cook, 1943; Townsend, 1953), is such that beavers are now present on nearly 100 percent of the suitable range on public land in Colorado. Population pressure and lack of available colony sites force many beavers off public lands onto farm and ranch land, where they do much damage by flooding pastures and undermining irrigation structures. Surplus beavers are not only creating serious control problems, but are also depleting the available food supply. If population numbers continue to go unchecked, it is conceivable that most of the aspen stands on suitable range throughout the state will be eliminated, and that much of the willow growth in the valleys will be killed by flooding.

The first step in a beaver-management plan is some form of enumeration of the animals present. The aerial census technique described by Hay (1955), in which food caches are counted in the fall, should provide an excellent appraisal of the total number of animals present. In the present study, determinations have been made of the total food requirements of an average colony in terms of beaver food units, and of carrying capacity in terms of area, for aspen and willow stands or combinations of the two. Correlation of this information with beaver numbers would supply the basis for making carrying-capacity determinations for any area.

In formulating management plans involving carrying capacity, it is believed that aerial photographs of streams suitable for beaver occupancy would supply most advantageously the required information. Such photographs, if taken during the fall, would show clearly the number of food caches present, and hence provide a close approxima-

tion of the number of beavers. Likewise, the total acreage of aspen and willow on each section of stream could be determined. It would also be possible to appraise from photographs the physical factors of suitability, such as valley grade and valley width (Retzer, 1955). Rock type could be determined from geological maps.

Study of suitable photographs would show, for each stream section, the number of beavers present as well as the total available food, permitting ready calculation of carrying capacity, as stated. Where beaver numbers exceed the calculated carrying capacity, a designated number of animals should be trapped from that section. Where numbers were below carrying capacity, they should be allowed to increase. Since the reproductive potential of this species is fairly well understood, one set of photographs would probably suffice for a period of at least ten years of beaver management. More frequent enumerations of population numbers could be made by aerial observations, without photographs.

The main advantage of such a plan is that harvest of beavers could be controlled by sections of stream, based on relatively accurate determinations of carrying capacity. Photographs could be taken over inaccessible terrain at a cost much lower than that of an intensive ground survey.

In a general open season, it is inevitable that the easily accessible beaver colonies would be trapped to extirpation, and that colonies in less accessible areas would be allowed to build up to the point of exhausting their food supply. Aerial reconnaissances would readily detect localities in greatest need of beaver harvest.

Recommendations for further study

It is recognized that the present study covered a limited area, and that it extended only over a short period of time. Several phases of the investigation itself were limited in application. For these reasons the following additional studies are considered to be in order:

1. Since only aspen-dependent colonies were studied, it is recommended that similar coverage be given to beavers living mainly on willow range.

2. Determine extreme distances to which beavers will forage for aspen or other food. It is recommended that many measurements be taken of extreme distance and slope involving cut aspens, and that these data be used in modifying the availability limits reported in this study.

3. Determine through more detailed studies the factors governing growth and reproduction of aspen and willow as beaver-food species.

Chapter VII

SUMMARY

This investigation was designed for the purpose of obtaining beaver management information based on the food requirements of beaver colonies for continuous occupancy on streams in the mountain areas of Colorado. Five colony sites, all in the drainage of the North Fork of the North Platte River, in Jackson County, were studied. All areas were on the Routt National Forest at elevations between 8,600 and 9,500 feet. Field investigations were conducted from June to November, 1954, and from June to October, 1955.

Physical factors

1. Total acreages in all cover types were determined for each area. Colony areas varied from one to 42 acres. Aspen was the major food source in all cases, and willow was second in importance. Study areas represented exclusively the mixed aspen-willow food type.

2. Stream gradients represented by the several areas fell within limits considered by Retzer (1955) to be excellent or good for beaver occupancy.

3. Stream flow on the several areas varied from a minimum of 0.1 cubic foot to three cubic feet per second. It was determined that very small stream flows were sufficient for occupancy of sites provided flows were relatively constant through the year, particularly through the drier seasons.

Determination of stand composition

1. A standard beaver food unit was calculated in order to facilitate the equating of various-sized aspens, and to compare willow with aspen in determining the amount of beaver food contained in given stands. This unit is equivalent to a two-inch aspen.

2. Stand tables were prepared, showing the total number and size of all woody plant species present on each area. These data were reduced to a single figure representing the total number of beaver food units present on each area.

3. Determinations were made of the average number of beaver food units per acre of aspen and willow. The average figure for aspen was 3,800; for willow, in dense stands, 550 units, in medium-sized stands, 300 units, and for sparse stands, 100 units.

Number of beavers present

1. Beaver numbers were determined by dead-trapping in the fall of 1955. An average of 5.5 beavers was found on the several study areas.

Determination of food availability

1. Measurements were made of distance from water and percent of slope for all aspens cut by the beavers. These data failed to demonstrate significant correlation.

2. Maximum distances from the water and percentages of slope were noted for aspens cut at all colonies. The findings indi-

cated that increases in slope beyond 15 or 20 percent would limit the distance beavers would travel for food.

Competition with livestock and big game

1. No significant competition for food was noted on the study areas between beavers and livestock or big game.

2. Reports from the literature indicate that heavy grazing by cattle or sheep may seriously limit a beaver food supply.

Determination of beaver food utilization

1. Aspen utilization was determined by total counts of all trees cut by beavers on the several study areas. The total number of beaver food units of aspen cut, as well as used, was noted for each area. Aspen use increased in 1954-55 over 1953-54, on all except one study area, probably due to increase in beaver numbers. The decrease in aspen use at Forester Seep Draw was explained by construction needs during the first year of occupancy.

2. Willow utilization was determined by counts of stems cut on sample plots. Variation in willow use on the study areas was directly proportional to the amount of willow present.

3. Total food use was determined for each colony. Alder was used on two of the study areas, but almost exclusively for construction purposes. Food use was related to the number of beavers present on each colony area, and the annual food requirement per beaver was determined. The averages were remarkably constant except for one new colony, where construction needs introduced a bias. The

average number of beaver food units felled per beaver (excluding the new colony) was 158. This figure was used in carrying-capacity determinations.

4. Percent of waste was determined for aspens on the several areas. The average waste, not including the newest colony, was approximately 13 percent. The greatest waste was in six- to nine-inch aspens. Three- to seven-inch aspens showed the greatest tendency to lodge out of reach of the animals.

5. By comparing the number of aspens cut in each size class to the number of trees of comparable size present in the stand, it was determined that a distinct preference was demonstrated by the beavers for the one-inch to three-inch trees. This demonstrated size preference is believed to be of little importance in determining carrying capacity.

6. It was also demonstrated that beavers prefer the two larger size classes of willow stems (over 1/4 inch in diameter). This preference is thought to benefit beavers by stimulating sprout growth, and by expediting the harvesting of stems that are likely to die off naturally and become lost as beaver food.

7. It was estimated that herbaceous material makes up nearly three-fourths of the beavers' diet during the early summer. This type of food, however, is believed to be of little importance in carrying-capacity determinations since it is almost universally present in abundance wherever conditions suitable for beaver occupancy exist.

Growth and reproduction of beaver food species

1. Growth studies indicated that the average annual diameter increment in aspen was 0.064 inches. Aspen reproduction made up approximately 10 percent of the total aspen stand on the three colony sites where it was found. Two of the study areas contained no appreciable amounts of aspen reproduction.

2. Data on willow growth and reproduction indicate that approximately 20 percent of a willow stand is replaced each year.

Carrying capacity

1. Carrying capacity is defined, for purposes of this study, as the number of beavers which can exist indefinitely on a section of stream without depleting its food supply. It was determined that four acres of aspen, twelve acres of willow, or combinations of lesser amounts of the two, would support an average colony of six animals on a sustained-yield basis.

2. Habitable sections of stream may be of two types: (1) a small section of suitable stream large enough to contain but one individual colony; and (2) a continuous section at least several hundred feet long, or large enough for more than one individual colony. The former type would require management on an individual colony basis.

3. The basis for carrying-capacity determinations is considered to consist of habitable sections of stream rather than individual colony sites. Thus, carrying capacity would be determined

on the basis of the total amount of available food on an entire stream section, in terms of numbers of animals or number of colonies, whichever appears most appropriate for the particular situation.

Management applications

1. The first step in any beaver management plan is enumeration of the animals present. This may be accomplished by the method outlined by Hay (1955), in which food caches are used as an indication of active colonies.

2. The second basic step in management of the beaver is a knowledge of the amount of food required per beaver and the amount available on any given area.

3. The recommended form of management is procurement of aerial strip photographs of all mountain streams in Colorado having suitable beaver range. These records, if obtained in the fall, would supply information both on the acreage of aspen and/or willow present and the number of active colonies, thus providing the basis for determining carrying capacity for any particular section of stream. The same information, permitting comparison of the beaver population with the food supply, would provide a simple means for determining the number of beavers which should be harvested. Adjustment of beaver populations to food supply is considered to be the only feasible means of obtaining sustained yield in beaver production and stability of beaver-inhabited range.

APPENDICES

APPENDIX A

LIST OF COMMON AND SCIENTIFIC NAMES OF PLANTS AND ANIMALS USED IN THIS DISSERTATION

Flora (nomenclature based on Harrington, 1954)

Aspen - *Populus tremuloides* Michx.
Willow - *Salix* spp.
Alder - *Alnus tenufolia* Nutt.
Birch - *Betula glandulosa* Michx.
Sedge - *Carex* spp.
Sage - *Artemesia tridentata* Nutt.
Alpine fir - *Abies lasiocarpa* (Hook) Nutt.
Engelmann spruce - *Picea Engelmanni* Parry in Engelm.
Lodgepole pine - *Pinus contorta* Engelm.

Fauna

Class *Mammalia* (nomenclature based on Hamilton, 1939)

Beaver - *Castor canadensis* Kuhl
Mule deer - *Odocoileus hemionus*
Elk - *Cervus canadensis*
Big-horn sheep - *Ovis canadensis*
Snowshoe Hare - *Lepus Americanus*

Class *Aves* (nomenclature based on Peterson, 1941)

Dusky Grouse - *Dendrogapus obscurus*

Class *Osteichthyes* (nomenclature based on Hubbs and Lagler, 1947)

Cutthroat trout - *Salmo clarkii*
Rainbow trout - *Salmo gairdneri*
Brown trout - *Salmo trutta*
Brook trout - *Salvelinus fontinalis*

Game and Fish Department
Denver, Colorado

STAND COMPOSITION

Colony No. _____ Drainage _____ Date _____

Transect No. _____ Width _____ Length _____

Species	Class	Tally	Total
Aspen	0-1"		
	1-3"		
	3-5"		
	5-7"		
	7" →		
Willow	0-10		
	10-25		
	25-100		
	100-200		
	200 →		
Lodgepole Pine	0-3"		
	3-6"		
	6" →		
Alder	0-1"		
	1-2"		
	2" →		
Other			

Appendix B

Original data are on file

in the archives of the

Colorado Cooperative Wildlife Research Unit

BIBLIOGRAPHY

BIBLIOGRAPHY

Aldous, Shaler E. 1938. Beaver food utilization studies. Jour. Wildl. Mgt. 2(4):215-222.

Aldous, Shaler E. 1942. Wyoming beaver population trends. Wyo. Wildl. 7(5):1-4.

Aldous, Shaler E. 1947. Beaver survey for 1947. Wyo. Wildl. 11(11):8-11.

Atwater, M. M. 1940. South Fork (Montana) beaver survey: 1939. Jour. Wildl. Mgt. 4(1):100-103.

Atwood, Earl L. Jr. 1938. Some observations on adaptability of Michigan beavers released in Missouri. Jour. Wildl. Mgt. 2(3):165-166.

Bagley, Lester. 1941. Wyoming's beaver problem. Wyo. Wildl. 6(1):9-13.

Bailey, R. Wayne. 1954. Status of beaver in West Virginia. Jour. Wildl. Mgt. 18(2):184-190.

Bailey, R. Wayne and R. F. Stephens. 1951. Effects of beavers on fish. W. Va. Cons. 15(6):11-16, 26.

Bailey, Vernon. 1926. How beavers build their houses. Jour. Mamm. 7(1):41-44.

Bailey, Vernon. 1927. Beaver habits and experiments in beaver culture. USDA Tech. Bull. No. 21.

Baillie-Grohman, Wm. A. 1882. Camps in the Rockies. Chas. Scribner's Sons, N. Y.

Beard, Elizabeth B. 1953. The importance of beaver in waterfowl management at the Seney National Wildlife Refuge. Jour. Wildl. Mgt. 17(4):398-436.

Berry, S. Stillman. 1923. Observations on a Montana beaver canal. Jour. Mamm. 4(2):92-103.

Bradt, Glenn W. 1938. A study of beaver colonies in Michigan. Jour. Mamm. 19(2):139-162.

BIBLIOGRAPHY--Continued

Bradt, Glenn W. 1939. Breeding habits of beaver. Jour. Mamm. 20:486-489.

Bradt, Glenn W. 1947. Michigan beaver management. Mich. Dept. Cons.

Bralchage, George K. and F. W. Sampson. 1952. Rabies in beaver. Jour. Wildl. Mgt. 16(2):226.

Cook, A. H. 1940. Screwworms infect beaver in Texas. Jour. Mamm. 21(1):93.

Cook, David B. 1940. Beaver-trout relations. Jour. Mamm. 21(4): 397-401.

Cook, David B. 1943. History of a beaver colony. Jour. Mamm. 24(1):12-18.

Couch, Leo K. 1937. Trapping and transplanting live beavers. USDA Farmer's Bull. No. 1768.

Dalke, Paul D. 1947. The beaver in Missouri. Mo. Cons. 8(6):1-3.

Denney, Richard N. 1952. A summary of North American beaver management; 1946-1948. Colo. G & F Dept., Denver. Current Rept. No. 28.

Dugmore, A. Radclyffe. 1854. The romance of the beaver. J. B. Lippincott & Co., Philadelphia.

Erickson, Arnold B. 1939. Beaver populations in Pine County, Minnesota. Jour. Mamm. 20(2):195-201.

Erickson, Arnold B. 1949. The fungus (Haplosporangium parvum) in the lungs of the beaver (Castor canadensis). Jour. Wildl. Mgt. 13(4):419-421.

Finley, Wm. L. 1937. The beaver - conserver of soil and water. Trans. 2nd N. A. Wildl. Conf. 2:295-297.

Friley, Charles E. Jr. 1949. Use of the baculum in age determination of Michigan beaver. Jour. Mamm. 30(3):261-267.

Gaffney, Wm. S. 1941. The effects of winter elk browsing, South Fork of Flathead River, Montana. Jour. Wildl. Mgt. 5(4):427-453.

Gese, Edward C. and Albert R. Shadle. 1943. Reforestation of aspen after complete cutting by beavers. Jour. Wildl. Mgt. 7(2):223-228.

BIBLIOGRAPHY--Continued

Grange, Wallace B. 1928. A beaver's fearlessness. Jour. Mamm. 9(1):66-67.

Grasse, J. E. 1948. Wyoming beaver survey. Wyo. Wildl. 12(9): 4-14.

Grasse, J. E. 1949. Beaver and trout. Wyo. Wildl. 13(11):4-13, 34.

Grasse, J. E. 1951a. Beaver ecology and management in the Rockies. Jour. For. 49(1):3-6.

Grasse, J. E. 1951b. Survey of furbearer populations and their present and potential habitat. Wyo. Wildl. 15(8): 10-11, 37.

Grasse, J. E. and E. F. Putnam. 1950. Beaver management and ecology in Wyoming. Wyo. G. & F. Comm. Bull. 6.

Grater, R. K. 1936. An unusual beaver habitat. Jour. Mamm. 17(1):66.

Grinnell, J. B., J. S. Dixon and J. M. Linsdale. 1937. Furbearing mammals of California. V. II. Univ. of Cal. Press, Berkeley.

Gunderson, Harvey L. and James R. Beer. 1953. The mammals of Minnesota. U. of Minn. Press, Minneapolis.

Hamilton, W. J. Jr. 1939. American Mammals. McGraw-Hill Book Co., Inc., New York.

Hamilton, W. J. Jr. 1943. The mammals of Eastern United States. Comstock Pub. Co., Inc., Ithaca, New York.

Hammond, M. C. 1943. Beaver in the Lower Souris Refuge. Jour. Wildl. Mgt. 7(3):316-321.

Harrington, H. D. 1954. Manual of the plants of Colorado. Sage Books, Denver.

Harris, Dave and Shaler E. Aldous. 1946. Beaver management in the northern Black Hills of South Dakota. Jour. Wildl. Mgt. 10(4):348-353.

Hatt, R. T. 1944. A large beaver-felled tree. Jour. Mamm. 25(3): 313.

BIBLIOGRAPHY --Continued

Hay, Keith G. 1955. Development of a beaver census method applicable to mountain terrain in Colorado. M.S. thesis, unpub. Colo. A & M College.

Hazeltine, F. T. 1850. A study of beaver-colony composition and woody plant utilization on two streams in Penobscot County, Maine. M.S. thesis, U. of Maine, Orono. Unpub.

Hensley, A. L. and B. C. Fox. 1948. Experiments on the management of Colorado River beaver. Cal. Fish and Game 34(3): 115-131.

Heter, Elmo W. 1950. Transplanting beavers by airplane and parachute. Jour. Wildl. Mgt. 14(2):143-147.

Hiner, L. E. 1938. Observations on the foraging habits of beavers. Jour. Mamm. 19(3):317-319.

Hodgdon, Kenneth W. and John H. Hunt. 1953. Beaver management in Maine. Dept. of Inland Fish and Game. Augusta, Me. Game Div. Bull. 3.

Hoover, R. L. 1952a. Some effects of beavers upon big game forage production. Colo. Coop. Wildl. Res. Unit Quart. 5(3): 58-68.

Hoover, R. L. 1952b. Beaver relationships to muskrat and waterfowl. Estes Park region, Colo. Colo. Coop. Wildl. Res. Unit Quart. 5(4):12-16.

Hoover, R. L. 1952c. Beaver-wildlife relationships on a small watershed in the Estes Park region. Colo. Coop. Wildl. Res. Unit Quart. 6(1):15-22.

Houk, Ivan E. 1924. When beaver aid irrigation. Sci. Am. March 130(3):161.

Hubbs, Carl L. and Karl F. Lagler. 1947. Fishes of the Great Lakes region. Cranbrook Inst. of Science, Bloomfield Hills, Mich.

Jahoda, Wm. J. 1946. Use of oaks by beavers in New Hampshire. Jour. Wildl. Mgt. 10(4):366-367.

Johnson, C. E. 1922. An investigation of the beaver in Herkimer and Hamilton Counties of the Adirondacks. Roos. Wildl. Bull. 1(2):117-186.

BIBLIOGRAPHY--Continued

Johnson, C. E. 1927. The beaver in the Adirondacks: its economics and natural history. Roos. Wildl. Bull. 4(4):501-611.

Lawrence, Wm. H. 1952. Evidence of the age of beaver ponds. Jour. Wildl. Mgt. 16(1):69-79.

Lawrence, Wm. H. 1954. Michigan beaver populations as influenced by fire and logging. Ph. D. thesis, U. of Mich., Ann Arbor.

MacNamara, Chas. 1929. Beavers resume earlier work. Jour. Mamm. 10(3):255-256.

Martin, A. C., H. S. Zim, and A. L. Nelson. 1951. American wildlife and plants. McGraw-Hill Book Co., Inc., New York.

Martin, Horace T. 1892. Castorologia: or the history and traditions of the Canadian beaver. Wm. Drysdale & Co., London.

Martin, Kenneth W. 1947. A note on the beaver. Wyo. Wildl. 11(9):31-34.

Mills, Enos A. 1913. In beaver world. Houghton-Mifflin Co., Boston, Mass.

Moore, George C. and Ernest C. Martin. 1949. Status of beaver in Alabama. Ala. Dept. Cons., Montgomery, Ala. 30 pp. illus.

Morgan, L. H. 1868. The American beaver and his works. J. B. Lippincott & Co., Philadelphia.

Nagel, W. O. 1946. The beaver...history maker...is coming back. Mo. Cons. 7(9):6-7, 16.

Nash, John B. 1951. An investigation of some problems of ecology of the beaver in northern Manitoba. Dept. of Mines and Nat. Res. G. & F. Branch, Manitoba.

Neff, Don J. 1954. A review of literature on North American beaver with special reference to environmental relationships. Unpub. manuscript. Colo. A & M.

Neff, Don J. 1956. Ecological effects of habitat abandonment by beavers on a high mountain valley in Colorado. M. S. thesis, Unpub., Colo. A & M.

O'Brien, D. F. 1936. A qualitative and quantitative food habit study of beavers in Maine. M. S. thesis, U. of Maine, Orono, Unpub.

BIBLIOGRAPHY--Continued

Olive, John R. 1951. Beaver-trout relationships in West Rainbow Lake. Colo. A & M. (Unpubl. manuscript).

Osborn, Dale J. 1953. Age classes, reproduction, and sex ratios of Wyoming beaver. Jour. Mamm. 34 (1):27-44.

Packard, Fred N. 1940. Beaver killed by coyotes. Jour. Mamm. 21(3):359-360.

Packard, Fred N. 1947. Survey of beaver population of Rocky Mtn. Nat. Park, Colorado. Jour. Mamm. 28(3):219-227.

Parker, R. R., Edw. Steinhaus, Glen Kohls, and Wm. Jellison. 1950. Tularemia in beavers and muskrats of the N. W. Nat. Inst. of Health Bull. No. 193, USGPO.

Perry, Clay. 1948. Beaver crisis in the North East. Am. For. 51(2):72-73, 92-95.

Phares, John H. 1952. Mississippi beaver harvest. Miss. Game & Fish, 16(12):3.

Retzer, John L. 1955. Physical environmental effects on beavers in The Colorado Rockies. Rocky Mtn. For. and Range Exp. Station,(Unpub. manuscript).

Riley, S. 1921. Some observations on beaver culture with reference to the National Forests. Jour. Mamm. 2(4):197-206.

Rutherford, William H. 1954. Interrelationships of beavers and other wildlife on a high altitude stream in Colorado. M. S. thesis, Colo. A & M, Unpub.

Salvesen, Sigvald. 1928. The beaver in Norway. Jour. Mamm. 9(12): 99-104.

Scheffer, Victor B. 1941. Management studies of transplanted beavers in the Pacific Northwest. Trans. N. A. Wildl. Conf. 6:320-326.

Scott, J. W. 1940. Winter kill in beaver. Jour. Mamm. 21(4):462.

Shadle, A. R. 1930. An unusual case of parturition in beaver. Jour. Mamm. 11(4):483-485.

Shadle, Albert R. and T. S. Austin. 1939. Fifteen months of beaver work at Allegheny State Park, N. Y. Jour. Mamm. 20(3): 299-303.

BIBLIOGRAPHY--Continued

Shadle, Albert R., A. M. Nauth, E. C. Gese, and T. S. Austin. 1943. Comparison of tree cuttings of six beaver colonies in Alleghany State Park, N. Y. Jour. Mamm. 24(1):32-39.

Shaw, Samuel P. 1948. The beaver in Massachusetts. Bull. No. 11, Div. of Res. & Mgt., Mass. Dept. Cons., Boston.

Simon, J. R. and R. C. Brown. 1948. Castors and castoreum. Wyo. Wildl. 12(6):14-16.

Stegeman, Leroy C. 1954. The production of aspen and its utilization by beaver on the Huntington Forest. Jour. Wildl. Mgt. 18(3):348-358.

Svihla, Ruth D. 1931. Mammals of the Uintah Mtn. Region. Jour. Mamm. 12(3):262.

Swank, Wendell G. 1949. Beaver ecology and management in West Virginia. Cons. Comm. of W. Va., Charleston, W. Va. Bull. 1.

Swank, Wendell G. and F. A. Glover. 1948. Beaver censusing by airplane. Jour. Wildl. Mgt. 12(2):214.

Tappe, Donald T. 1942. The status of beavers in California. Cal. Dept. Nat. Res., Div. Game and Fish. Game Bull. No. 3.

Tevis, Lloyd Jr. 1950. Summer behavior of a family of beavers in N. Y. State. Jour. Mamm. 31(1):40-65.

Thomas, Earl M. 1953. The fur-bearing mammals of Wyoming: the beaver. Wyo. Wildl. 17(9):16-19, 22-25.

Townsend, Joseph E. 1953. Beaver ecology in Western Montana with special reference to movements. Jour. Mamm. 34(4): 459-478.

Trippensee, R. E. 1948. Wildlife management. McGraw-Hill Book Co., Inc., New York.

Warren, E. R. 1926a. The beaver in the Yancey region of Yellowstone National Park. Roosevelt Wildl. Bull. No. 1.

Warren, E. R. 1926b. Notes on the beaver colonies in the Longs Peak region of Estes Park, Colorado. Roosevelt Wildl. Bull. 2.

Warren, E. R. 1927. The beaver, its works and ways. Williams and Wilkins Co., Baltimore.

BIBLIOGRAPHY--Continued

Warren, E. R. 1928a. Cutting of oaks by beavers. Jour. Mamm. 9(3):253-254.

Warren, E. R. 1928b. Beavers in the Elk Mtn. region, Colorado. Jour. Mamm. 9(4):320-334.

Warren, E. R. 1932. The abandonment and reoccupation of pond sites by beavers. Jour. Mamm. 13(4):343-346.

Warren, E. R. 1940. A beaver's food requirements. Jour. Mamm. 21(1):93.

Warren, E. R. and E. Raymond Hall. 1939. A new subspecies of beaver from Colorado. Jour. Mamm. 20(3):358-362.

Whitelaw, C. J. and E. T. Pengelley. 1954. A method for handling live beaver. Jour. Wildl. Mgt. 18(4):533-534.

Wilde, S. A., C. T. Youngberg, and J. H. Hovind. 1950. Changes in composition of ground water, soil fertility, and forest growth produced by the construction and removal of beaver dams. Jour. Wildl. Mgt. 14(2):123-128.

Wing, Leonard W. 1951. Practice of wildlife conservation. John Wiley & Sons, Inc., New York.

Wire, Frank B. and A. B. Hatch. 1943. Administration of beaver in the western United States. Jour. Wildl. Mgt. 7(1):81-92.

Yeager, Lee E. and Ralph R. Hill. 1954. Beaver management problems in western public lands. Trans. 19th N. A. Wildl. Conf. 19:462-480.