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The Beaver in Colorado

ITS BIOLOGY, ECOLOGY, MANAGEMENT AND ECONOMICS

Technical Publication Number 17

Game Research Division

Colorado Game, Fish and Parks Department



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THE BEAVER IN COLORADO

ITS BIOLOGY, ECOLOGY, MANAGEMENT AND ECONOMICS

By WILLIAM H. RUTHERFORD

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Colorado Game, Fish and Parks Department,
Beaver Investigations, Project W-83-R,
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INTRODUCTION

HISTORY AND GENERAL STATUS:

THE HISTORY of the Beaver in North America began long before the coming of the white man. The earliest evidence of the presence of these rodents occurs in the Pleistocene deposits, which were laid down not more than a million years ago (Henderson, 1960). It can logically be assumed that, prior to the coming of the white man, beavers had occupied stream valleys throughout North America for thousands of years and had probably attained a population level which was about maximum for the available habitat. Plant succession, with its attendant influence upon the amount and quality of habitat, had undoubtedly contributed to population fluctuations among beavers for ages.

The Indians killed beavers for food and used their skins for clothing; and were adept at capturing beavers, using their native ingenuity in devising snares, nets, and deadfalls. Such inroads upon the then existing beaver populations were, however, almost insignificant, and can be considered simply a part of the natural environmental pressures against wildlife in general.

The coming of the white man drastically changed the controls which influenced beaver population levels. The invasion of North America by Europeans not only altered the natural conditions, but caused the Indians to modify their own ideas (Presnall, 1943). Beaver pelts became a much sought-after item in the fashion markets of Europe, and the exploitation of this resource to satisfy the demand assumed astonishing proportions. The early fur trade depended almost entirely upon the Indians as producers of the commodity, which was then offered in trade for whatever the white men had to exchange. Gradually the demand for beaver pelts exceeded the ability of this system to supply the required numbers, and thus the era of the white trapper or "mountain man" came into being. Between the years 1800 and 1850, the major explorations beyond the limits of civilization were made solely for the purpose of discovering new beaver trapping areas.

About midway through this 50-year period of time, the steel trap, as we know it today, was invented. This device enabled the trapper to operate with

¹ For scientific names of plants and animals, refer to the list at the end of the text.

much greater efficiency than had been possible before, at a time when the demand for furs was reaching its peak. The extirpation of the beaver from much of its original habitat followed shortly, and by 1850, when the whims of fashion decreed that the silk hat should be the successor to the beaver hat, the scarcity of beavers had become noticeable. Trappers were going further into the headwater areas of stream drainages, were staying longer, and were returning with increasingly fewer pelts.

In what is now Colorado, fur trappers had worked their way up the Platte and Arkansas rivers from the east, and the Colorado River system from the west, prior to 1850. By the time the gold-seekers arrived, during the late 1850's, Colorado's beaver population, in common with that of most of the West, had been severely depleted.

Even the low pelt prices which were common after 1850 did not bring an end to the exploitation of the beaver. Trappers who knew no other way of life continued to eke out a living by selling pelts for whatever the market would bring, and beaver populations continued to dwindle throughout the last half of the 19th century. The low point was reached sometime between 1890 and 1900 (Seton, 1937).

Most western states, Colorado included, gave complete protection to beavers starting some time around 1900, and from this time until the present, beaver populations have experienced a steady growth in numbers (Yeager and Hill, 1954). Man's alteration of much of the original beaver habitat during the late 19th and the 20th centuries has created a situation making it extremely unlikely that beaver numbers will ever again approach the magnitude of the pre-white man era.

From the time that Colorado first afforded legislative protection to beavers up until 1937, a permit system allowing limited trapping of nuisance beavers on private lands was in effect. In 1937, all permits were revoked by the Game and Fish Commission, and nuisance beaver control was restricted to full- or part-time salaried trappers. With the enactment of the Beaver Control Act of 1941, harvest remained restricted to salaried State trappers largely for the relief of damage to private property. The 1941 law provided that landowners would receive one-half of the sale value of pelts taken from their lands, and the Game and Fish Department would retain the other half. Under these various beaver control laws, practically all trapping was done on private property, even though beavers could be taken on public land starting in 1937 (Yeager and Hill, 1954).

As the inevitable result of beaver harvest restricted primarily to private holdings, beaver populations on National Forests and other public lands in the state have increased year after year, except for certain localities where die-offs have occurred. More efficient law enforcement and declining prices for beaver pelts since about 1947 have reduced poaching to a minimum (Yeager and Hill, 1954).

By the early 1950's, it became obvious that beaver populations on public lands in Colorado could no longer be ignored. Many observers, both within and without the Game and Fish Department, had recorded the rapid build-up of beaver populations to levels which, in many cases, far exceeded the carrying capacity of the habitat. Beaver habitat along numerous stream valleys was being depleted, destroyed, and abandoned, with attendant loss of the watershed protection, fishery, wildlife, and recreational values associated with beaver workings.

Largely through the auspices of the Colorado Cooperative Wildlife Research Unit at Colorado State University at Fort Collins, and in cooperation with the Colorado Game and Fish Department, the first studies dealing with evaluations of beaver populations and beaver ecology were initiated in 1951. In 1954, Federal Aid Project W-83-R, Beaver Investigations, was begun. Under this project, work was initiated on studies dealing with beaver-

abandoned streams, beaver productivity, beaver habitat suitability requirements, and beaver harvest.

In 1955, the Legislature of the State of Colorado passed a law which made many changes in the legal status of beavers, and in 1956 the first public trapping season on beavers since the 1890's was opened. The new law allows landowners to trap beavers on their own holdings or to hire licensed trappers to do so, with all proceeds from the sale of pelts to belong to the landowner or trapper. If landowners request the Game and Fish Department to take beavers from private property, the beaver pelts so taken become the sole property of the state. The law further specifies that the Game and Fish Commission is to be given authority to set seasons and establish rules and regulations for the management of beavers on public lands.

With the passage of this favorable legislation, the work of Project W-83-R took on added significance, since it was now imperative that a beaver management plan be developed, tested, and put into operation in order to properly care for the populations and habitats of this important animal.

This publication is the culmination of the Beaver Investigations Project. It attempts to answer, insofar as possible, the questions which led to the establishment of the project: Which areas are suitable and which are not for beaver occupancy? How is this determined? What is the annual rate of increase of beaver populations? Does this vary according to habitat type and quality? What are the positive values of beaver occupancy of stream valleys? What are the negative values of unmanaged beaver populations? What is the best census method? How is habitat carrying capacity determined? The objectives implied in the answers to these questions have, for the most part, been attained.

ORGANIZATION OF BULLETIN:

IN DEALING with an animal whose biological and ecological characteristics are as complex and closely interwoven as those of the beaver, a complete separation of the two for purposes of discussion is neither practical nor desirable. In the following text, the broad aspects of environment are consigned to the section dealing with ecology; and specific references to the beaver's way of life will be found in the section on biology. Thus, the biology section unavoidably contains much material on ecology, but in a specific rather than a general sense.

In certain instances, the converse is also true. For example, the discussion of beaver food habits (really a part of biology) is included in the discussion on characteristics of Colorado beaver habitat, under ecology. This is done to avoid repetition, since the food species which beavers use are a part of the environmental complex of the habitat.



BIOLOGY

ADAPTATIONS TO HABITAT:

THE BEAVER is generally regarded as being the only mammal, other than man, capable of altering the habitat to suit its own needs and requirements. Because the beaver has adapted itself to an aquatic existence, water in considerable volume is a major requirement for the survival of the species. In some cases, beavers are found to inhabit natural ponds and lakes, or deep holes in river bends, where the amount of naturally impounded water is sufficient for living, provided that a source of food is available. In most cases, however, the limitations of food availability dictate that beavers must provide their own impoundments in order to have water in sufficient quantity.

To meet this need, the expedient of dam-building has been evolved. The dam is built of sticks and mud and any other available material, including rocks, sod, and discards from the civilization of man such as bottles and tin cans. There is a considerable amount of engineering ingenuity manifested in the choice of locations for dams. Usually only one dam is built to provide the impoundment for the main lodge. This can be considered the primary or "home" dam. According to the availability of food, the soil type, and the terrain, secondary dams of any number or size may be built. These function mainly as transportation aids.

Governed by the same conditions which allow the construction of secondary dams, beavers may also build canals to aid in transporting food to the home pond. Under the most favorable of conditions, elaborate networks of canals may be developed over a long period of beaver occupancy of a colony site. The author has seen canals built on at least three different levels, with "locks" to control the water at each level. These allowed the beavers to cut trees for food a considerable distance from the home pond, with a minimum of dragging over dry ground.

To serve the needs of shelter and protection in the beaver's aquatic existence, a lodge or house is commonly constructed by the animals. Typically, this takes the form of a dome shaped structure built of sticks and mud, and having an interior chamber for living quarters. It is usually built so that it is completely surrounded by water, but may also be built with one side against the bank. The entrances are under water and are commonly two or more

in number. Beavers occupying new colony sites often build simple bank dens or burrows to serve as living quarters during the first year.

FAMILY AND COLONY ORGANIZATION:

THE BEAVER colony is defined as a group of beavers occupying in common a pond, ponds, or a stretch of stream, utilizing the same food cache, and maintaining communal dams (Hay, 1955). Typically, this colony is a family unit, and usually consists of the parent male and female plus their progeny of the previous year and the current year. Yearling animals are allowed to remain in the colony with the young of the year until they reach the age of two years, whereupon they are driven from the parent colony by the adults (Bradt, 1947; Gregg, 1948; Grasse and Putnam, 1955). It has been affirmed that two-year olds may be killed by the parents if they refuse to leave (Thomas, 1954). Upon departure, these young beavers locate living sites as close to the family lodge as possible and, presumably, the colonial association is fostered and maintained through the combination of proximity and kinship.

Studies aimed at developing an applicable census method for beavers, carried out under the direction of the Beaver Investigations Project and reported by Hay (1955), showed that in the establishment of colony boundaries, topographical features unfavorable to the beaver are usually the limiting criteria. For example, stream gradient may be too steep or the valley width too narrow to permit occupancy. Absence of food, due to depletion by previous generations of beavers, was another delineating factor. Thus, it is seen that the family and colony organization of beavers is frequently limited by physical features of the habitat, and dispersal of young beavers from the parent colony may in a short time use up all of the habitat within the physical boundaries of the colony site. Members of a colony apparently confine themselves to their colonial boundaries except when habitat saturation forces certain beavers to migrate elsewhere.

SOCIAL WORK CYCLE:

HAY (1955) found that the number of lodges in beaver colonies is not consistent and that during the summer, members of the same colony might occupy several lodges and bank dens. The parent male often takes up quarters away from the home lodge, in a bank den or another lodge, at the time the young are born, and does a considerable amount of moving around through the summer. The yearlings extend their range but continue to use the home lodge and pond, although they may be found quartered in other lodges or dens through the summer months. With the advent of autumn, these summer quarters are abandoned and the entire colony moves into one main lodge in the home pond.

The concentration of beavers at the home pond occurs sometime during September in Colorado. Immediately, the animals set to work repairing and strengthening the dam and lodge, and begin the prodigious task of laying in the winter food supply. In the mountainous regions of the state, where winter comes early and the snow lays deep, the food "cache" is the only means of subsistence for the wintering beaver colony. The cache is placed in water as deep as possible and as near to the lodge as possible. Various wild theories have been advanced as to how the beaver is able to keep sticks of aspen and willow down on the pond bottom. The cache is simply a huge pile of sticks anchored into the mud of the bottom, and its own weight is sufficient to keep it in place.

MOVEMENTS AND DISPERSAL:

THE DAILY movement pattern of the beaver centers, for the most part, around the lodge and pond. Activity is primarily nocturnal, and most of the feeding and construction is done during dusk and after dark. Movement



Beavers built this canal, on the upper Williams Fork River in Grand County, to float aspen sticks approximately 100 yards to the pond.

outside the lodge is much greater just before dark than in the early morning hours after daybreak.

Seasonal movement of beavers varies greatly by sex and age class. As long as a colony site is occupied, the parent female is almost sedentary the year around, being occupied with the care of the young throughout the summer. Little, if any, movement by beavers occurs during late fall, winter, and early spring. With the coming of spring high water and the birth of the new litter, the two-year old beavers are forced to leave the home colony, as previously mentioned. These animals spend the entire summer drifting and roaming about, and make no attempt to settle at any given place until about September, when mates have been acquired. The place finally chosen for setting up winter quarters may be adjacent to the parent colony or it may even be on a different stream drainage, depending on habitat conditions and the selection of mates. Many experienced trappers have expressed the belief that inbreeding is the rule rather than the exception among beavers.

The normal seasonal movements of beavers can be, and often are, changed by conditions which force entire colonies or even the entire population of a stream drainage to migrate elsewhere. Such things as complete habitat disruption by spring flood waters, or depletion of the food supply along a stream, are the most common of these conditions.

REPRODUCTION:

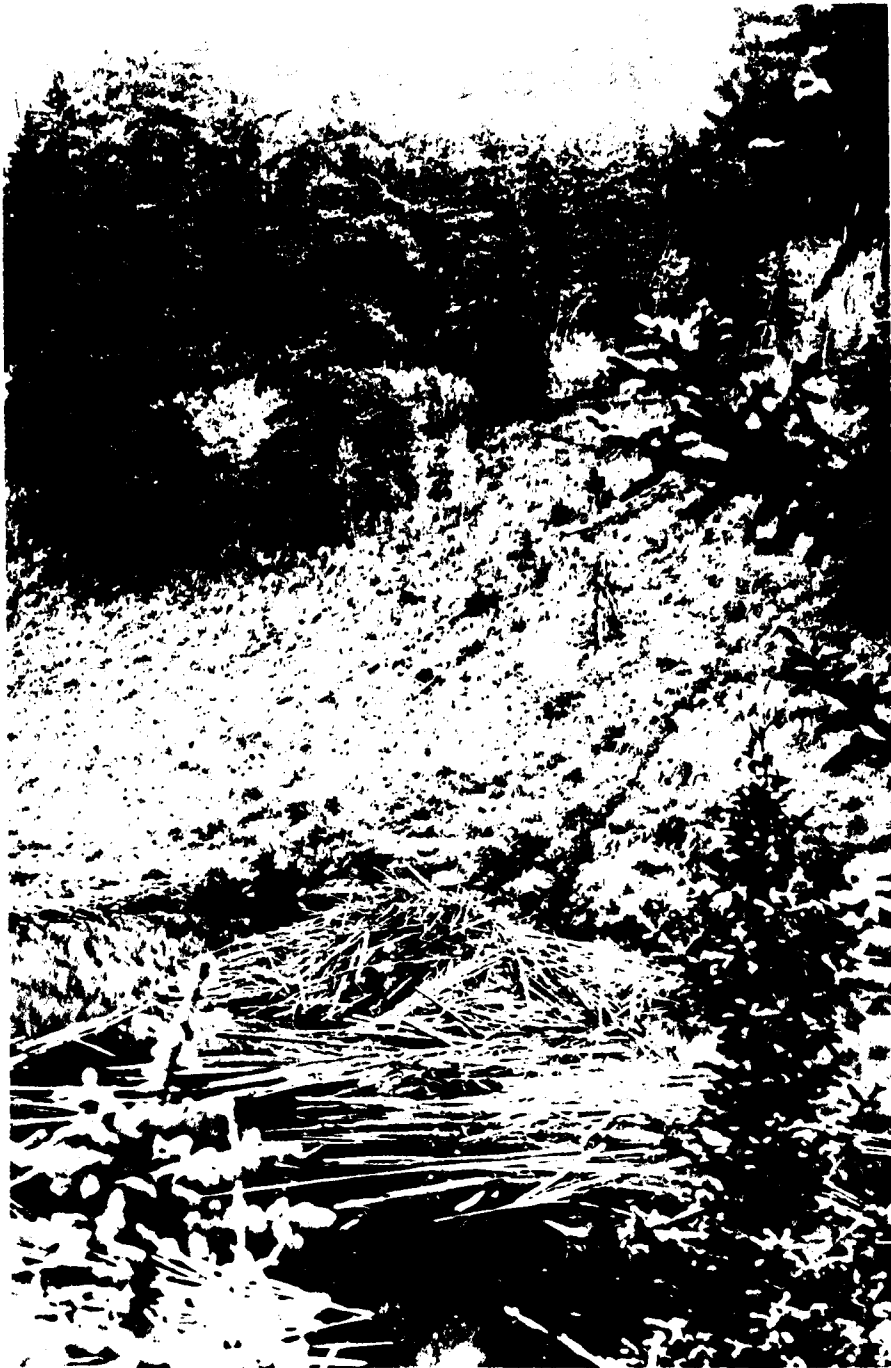
RECORDED information as to the precise duration of the gestation period in beavers seems to be non-existent. Various investigators (Seton, 1937; Bradt, 1947; Hodgdon and Hunt, 1953) have placed this period at from 90 to 120 days, based on knowledge of dates of follicle development and parturition dates. It seems probable that the period is at least 100 days. Mating occurs during the time when the animals are confined to winter quarters.

Personnel of the Beaver Investigations Project have dissected and examined the carcasses of 504 female beavers taken during statewide spring trapping operations. In this sample, the earliest date on which a female was trapped which had already given birth was May 12. Through the latter half of May, the incidence of post-partum females continues to increase, and by the end of May, when spring control trapping normally ceases, more than half of the breeding females are post-partum. During years when it was necessary to extend control trapping operations into June, it was noted that practically all of the breeding female beavers had given birth by June 10. Since the peak in birth dates appears to occur about June 1, and assuming a gestation period of 100 days, it is believed that the peak in breeding activity occurs about the middle of February. Occasionally, kits weighing no more than four pounds are taken during fall control trapping in October and November. These small beavers are almost certainly members of late litters born sometime during July.

PRODUCTIVITY:

IN THE management of any species of wildlife, beaver included, a means of determining the expected rate of annual population increase is necessary. The major objective, therefore, in the dissection and examination of the 504 spring-caught female beavers was to collect data on the number of pregnant females, the number of embryos carried, the number of resorbed embryos, and the breeding condition of females.

It was recognized early in the study that it would not be possible to control experimental beaver populations to the extent that post-natal mortality could be calculated. Figures derived for the rate of population increase are necessarily based on the number of live embryos carried by female beavers, and possibly indicate a rate slightly higher than actually exists. Certainly



Typical location of the food "cache." Note the skid trail on the opposite slope, the lodge, and the cache in the foreground.

some post-natal and juvenile mortality occurs, but it is believed that this will rarely exceed 10 percent of the total number of young born. The belief has been expressed by several experienced trappers in the Game and Fish Department that, regardless of the number of young born, a female beaver will never raise more than four. This belief is apparently based on the fact that the female has only four nipples on the mammae. Project personnel were unable to collect enough data to test the validity of this belief. It can be said, however, that although unborn litters numbering five or six individuals were common enough to be considered not unusual, at no time during autumn population studies were more than four kits trapped from a colony.

A summary of data collected from spring-caught beavers, organized by elevation and habitat type, is presented in Table 1.

The ovaries of each pregnant female beaver were sectioned so that the corpora lutea of pregnancy could be easily seen and counted. One corpus luteum is formed in the ovary for each fertilized ovum. Any difference which occurs between the number of corpora lutea and the number of young produced is the number of fertilized ova which did not develop into full term embryos. Resorption of embryos can occur at any stage of development; the author has seen cases where nearly full term fetuses were dead and in the process of resorption, and others where the uterus showed no indication that an embryo had ever developed, but a corpus luteum of pregnancy was present in the ovary. Embryo resorption, of course, is caused by the female being unable to provide enough nutrition for a large number of developing embryos. Presumably, the rate of embryo resorption is a reflection of the relative habitat quality.

Table 1 shows that the sample of beavers from the plains riverbottom

Table 1. — Productivity in Colorado Beavers as Determined from 504 Females in Late Winter and Spring Populations, 1954-1959.

	Plains Riverbottom Cottonwood- willow	Mountainous Country Aspen-willow	
		NORTHWEST	SOUTHWEST
	So. Platte River elev. below 5000'	North Park, Middle Park, Yampa Valley Elevation above 6000'	Gunnison River and San Luis Valley elev. above 8000'
Total number of females	113	280	111
Number of mature females	56	116	58
Number of 2-year old females	38	116	29
Number of 1-year old females	19	48	24
Number of pregnant females	40	87	49
Pregnancy percentages ¹			
All females	37%	31%	44%
Mature females	75%	75%	84%
Total number of embryos	183	235	113
Average number of embryos per pregnant female	4.4	2.7	2.3
Total number of corpora lutea	202	271	151
Percentage of resorbed embryos	9%	13%	25%
Rate of population increase ²	71%	32%	41%

¹ Includes females which had already given birth.

² Assuming 100:100 sex ratio in population, and allowing 10% juvenile mortality.

habitat (elevation below 5,000 feet) had the highest average number of embryos, the lowest embryo resorption rate, and the highest rate of productivity of any of the population samples. The sample from the southern part of the state (elevation above 8,000 feet) had the lowest average number of embryos and the highest embryo resorption rate, but because the pregnancy rate was the highest of the three samples, the rate of productivity was higher than that for the northern Colorado sample (elevation above 6,000 feet). Data on the number of embryos per pregnant female and the number of resorbed embryos from the three habitat samples were found to be significantly different at the .05 level of probability.

A clear-cut distinction between aspen and willow habitat in both the southern and northern Colorado samples cannot be made, because all areas sampled contained varying mixtures of these two food species. However, the southern Colorado samples were taken from areas of generally higher elevation and poorer quality of aspen and willow stands. It is believed that this accounts for the low average number of embryos and the high resorption rate.

It is apparent that differences in productivity between the two samples from the mountainous sections of the state are not as great as the differences between the mountain and plains samples. This is attributable to food quality and availability. On the higher range, beavers must depend in winter on cached food, whether aspen or willow, since ponds are then solidly frozen over. In the lower zones, streams rarely become heavily ice covered, and then only for a few days at a time. Beavers living on lower elevation streams in Colorado do not regularly cache food but, instead continue to cut fresh trees through the winter. Less rigorous winters, greater food availability, and presumably higher food quality at the lower elevations are reflected in higher productivity (Yeager and Rutherford, 1957).

The high rate of productivity in beaver populations living in the plains cottonwood riverbottom type is in contrast to the findings of Huey (1956) in New Mexico, who determined that the average number of embryos per pregnant female was 4.2 in aspen habitat and 2.75 in cottonwood habitat. He considered cottonwood to be inferior to aspen, which is undoubtedly true in New Mexico; but the studies in Colorado indicate that the cottonwood type is high quality beaver habitat.

These factors of habitat quality are also believed to be responsible for a generally significant difference in weights of beavers among the three habitat samples. Table 2 presents data on the average carcass weights of female beavers, according to age, breeding condition, and habitat type. All weights recorded were those of the skinned carcass with feet removed, since this was the condition in which the greatest number of beavers were available for study.

The carcass weight data for the two classes of mature animals were found to be significantly different according to habitat type, with a probability of less than .001 that the difference was due to chance. The data for the immature females do not follow the same pattern and were found to be

Table 2—Average Carcass Weights of 386 Female Beavers, Spring Trapping Seasons, 1954-1959.

	Mature pregnant		Mature non-pregnant		Immature	
	Number in sample	Average wt. in pounds	Number in sample	Average wt. in pounds	Number in sample	Average wt. in pounds
Plains riverbottom	39	41.9	13	39.4	56	21.5
Northern Colo. Mtns.	53	37.8	30	33.0	107	21.7
Southern Colo. Mtns.	24	34.7	12	32.8	52	19.4



An abandoned beaver colony site on Nutras Creek, Saguache County. Depletion of the food supply was the reason for the migration of beavers from this site; a few hundred yards downstream, food is plentiful and colony sites are occupied.

Table 3.—Sex and Age Distribution of 471 Beavers, Spring Trapping Seasons, 1954-1959.

	Number of Beavers		
	Plains riverbottom habitat; elev. below 5000 feet	Northern Colorado mountains; elev. above 6000 feet	Southern Colorado mountains; elev. above 8000 feet
Males:			
Mature	22	34	64
2 years old	7	14	28
1 year old	16	13	31
Totals	45	61	123
Females:			
Mature	27	35	58
2 years old	11	30	29
1 year old	14	14	24
Totals	52	79	111
Sex ratio; males per 100 females	86.5	77.2	110.8

not significantly different, probably because of the extreme variations in the samples. One- and two-year old animals were combined in the immature class because there is no reliable method for exact age determinations. Approximations can be made on the basis of size and weight, but considerable overlapping occurs.

In an attempt to find whether beaver productivity is influenced by the food species most available, the number of beavers per colony was used as an index of productivity. Where possible, during beaver control operations in the fall trapping season, colonies were trapped to extirpation by project personnel. A sample of 19 colonies situated where aspen was the principal food, and a sample of 20 colonies where willow was the mainstay of the diet, were collected. The samples are necessarily small, partly because beaver control operations seldom require the removal of entire colonies and partly because of the difficulty encountered in making sure that all members of a colony have been taken.

The data collected show means of 5.1 beavers per colony in aspen habitat and 4.5 beavers per colony in willow habitat. It is commonly accepted that aspen is of higher quality than willow as a beaver food, and that this is reflected in the number of beavers per colony. Analysis of the data failed to show a significant difference between the two food types, probably because of the small samples involved. However, a trend in this direction is indicated.

AGE AND SEX RATIOS:

WHEREVER possible, the sex and estimated age of each beaver in the total daily catch were recorded. In many cases the males in the daily catch were not recorded, and although many females were saved for examination of the reproductive tracts, they could not be included in the sex-age data because of the lack of comparable data on males. Thus, the sample of females in Table 3, which summarizes the sex-age data, is considerably smaller than the number shown in Table 1.

The estimated ages of the beavers in Table 3 are based partly on the condition of the reproductive system in the case of females, and partly on an arbitrary weight classification of 10 to 18 pounds for one-year olds, 19 to 29 pounds for two-year olds, and 30 pounds and over for mature beavers. There are no other suitable criteria for classifying beavers according to age. It is recognized that considerable overlapping of weights between different age classes occurs. It is also known that trapping does not provide a true random sample of a beaver population, because some sex and age classes are more susceptible than others to traps. For these reasons, Table 3 is presented simply as incidental information, with no attempt at analysis.

MORTALITY FACTORS (Natural Enemies, Parasites, Diseases, and Floods):

BECAUSE of the protection afforded by the lodge and the aquatic habitat in general, the beaver has few natural enemies. Packard (1940) reported predation by coyotes on beavers, and possibly some predation on small beavers by bobcats occurs where a bobcat is able to corner a beaver on land and prevent escape toward the water. The author has seen one instance of a bear dragging a beaver out of the water and eating it, but it is doubtful that the beaver was killed by the bear. Large pieces of hide and fur left hanging on twigs along the path where the beaver was dragged indicated that the beaver was dead and beginning to decompose. Certainly a bear is capable of killing a beaver, but it is believed that this occurrence is extremely rare.

Personnel of the Beaver Investigations Project did not carry out studies of beaver parasitology. It is known that parasites are of very minor importance in the biology of beavers. Hodgdon and Hunt (1953) reported the occurrence of stomach nematodes and intestinal flukes in Maine beavers, and it is reasonable to assume that beavers elsewhere are also hosts to these or other endoparasites. In Colorado, Olson (1949) found the helminth parasites *Stichorchus subtriquetrus*, *Travassosius americanus*, and *Castorstrongylus castorius* in beavers from the South Platte River, and Choquette and Pimlott (1956) found beavers in Newfoundland to be infected by these same three helminths.

Literature on the subject generally mentions the common occurrence of an ectoparasite, the beaver beetle. These beetles (usually called "lice" by trappers) occur on beavers in Colorado, in varying degree. It has been noted that beavers living in clear, cold, high-altitude streams harbor relatively few of these beetles, and that the incidence increases in warmer and slower moving waters. The presence of this beetle on beavers has not been associated with any damage to the hide or fur.

Epidemics of tularemia among beavers have been reported from various locations in the western United States and Canada (Green, 1937; Scott, 1940; Jellison et al, 1942; Parker et al, 1950; Langford, 1954); and the disease has recently occurred in epidemic proportions in Colorado. In the spring of 1957, trappers began to find unusual numbers of dead beavers in ponds following the melting of the ice cover. Dead beavers continued to occur throughout the summer, mostly in the northern part of the state. In August of 1957, the author, in company with Wildlife Conservation Officers in North Park, found a specimen sufficiently fresh to be autopsied. The carcass was taken to the College of Veterinary Medicine, Colorado State University, where a positive diagnosis of tularemia was made. Subsequently, other specimens were found and autopsied, with the same results. The effects of the disease became apparent during the 1957 fall census, when a drastic statewide reduction in beaver populations was noted. The disease was still present in 1958, but some areas were beginning to recover. By 1959 the disease had run its course, and beaver populations began to increase to their former level. Conversations with "old-timers" in the Game and Fish Department revealed that such epidemics have occurred from time to time in the past. So far as is known, this is the only disease affecting beavers in Colorado.

The effect on beaver habitat of excessive volumes of water either during spring runoff or summer flash floods has been recognized in Colorado ever since the Game and Fish Department first began dealing with beavers. Complete habitat disruption forcing site abandonment is not uncommon. Less well recognized, perhaps, is the effect such floods may have upon individual beavers, particularly young-of-the-year animals. Floods usually occur at a time of year when the young are quite small and unable to cope with high water volume and velocity. Documentary evidence is lacking, but it is believed that any flood which causes severe habitat disruption also takes its toll of young beavers through drowning.



ECOLOGY

CHARACTERISTICS OF COLORADO BEAVER HABITAT:

TWO VASTLY different beaver habitat types occur in Colorado. These are the plains cottonwood riverbottom and the mountain aspen-willow types, as referred to previously. The former is limited to the bottomlands of the rivers which flow eastward across the plains after emerging from the foothills of the Front Range. The elevation is generally less than 5000 feet, and the land which comprises this habitat is almost entirely in private ownership. Historically, this is original beaver range, but the activities of man have combined to make parts of it untenable to beavers and to make beavers entirely unwelcome in the rest of it. That it continues to support relatively large numbers of beavers attests to its high quality as beaver habitat. However, any ecological analysis of the plains riverbottom type is inextricably tied in with management, and the plain truth is that under present-day conditions, the beaver does not have a place here. The management implications of this approach are recognized, and will be discussed later.

The principal beaver food species of the plains riverbottom habitat is cottonwood. Various species of willow are also present, and constitute an important part of the diet. Less frequently, agricultural crops such as corn, alfalfa, and sugar beets are utilized as food by beavers.

The soil of this type of beaver range is primarily alluvium, and in the riverbottom proper consists almost entirely of sand and gravel. River channel shifting occurs commonly during the time of spring high water, and thus adversely affects the permanency of beaver structures. The water is generally shallow, slow-moving, and polluted in varying degree. The rate of fall is low; the South Platte River between Fort Morgan and Julesburg, for example, has an average rate of fall of less than eight feet per mile.

The mountainous sections of Colorado are considered to be the "beaver country" of the state. It is here that the environmental relationships and interrelationships of beavers, the land ownership status, and the capacity to manage beaver populations on an ecological basis give the animals a unique position in the overall administration of the wildlife resource. The lower reaches of such western Colorado rivers as the Yampa, White, Colorado, San Juan, and Rio Grande have habitat characteristics more nearly approaching



A winter scene of beaver habitat on the South Platte River in Logan County. This is typical of the plains cottonwood riverbottom type.

those of the plains riverbottom habitat, and must be considered in the same category.

The staple food items of beavers on mountain range are aspen and willow. Aspen is limited in its altitudinal range, generally occurring only between 7000 and 9500 feet elevation. It is a sub-climax species, and in most of the Rocky Mountain region its presence is directly the result of forest fires. It may occur either in pure stands or mixed with lodgepole pine, which is another sub-climax species (Clements, 1910; Neff, 1957). Where present and available it is the preferred food of beavers, but it is relatively intolerant to continued utilization. For this reason, aspen stands are rather easily depleted or destroyed by beavers.

Willows, in a variety of species, occur throughout the entire mountainous range of beavers, but of course are limited to watered stream valleys. Above the upper limit of aspen growth, willow is the only staple, year round beaver food available, and in many valleys within the range of aspen, beaver colonies subsist entirely on willows, either because aspen was never present due to lack of forest fire history or because previous generations of beavers have destroyed aspen stands. Well-established willow stands in valleys having a stable water cycle are far more tolerant than aspen to continued utilization by beavers.

Average or better than average beaver habitat in Colorado typically has both aspen and willow present, with the willow stands occupying the valley bottom and aspen occurring on adjacent slopes. Regardless of the area of aspen, however, it is seldom utilized farther than 100 yards from the valley bottom. Thus, the area suitable for beaver food production is limited to watered valleys and immediately adjacent slopes, and seldom exceeds 2.5 percent of the total watershed area.

Beaver food production on this limited area is, of course, influenced by the basic fertility of the soil, the stability of the water table, and various climatic factors. Plant growth at high elevations is very slow, due to an extremely short growing season. MacDonald (1956) determined that the annual increment in three- to eight-inch aspens in North Park was only 0.064 inch, or about four times slower than growth in New York (Stegeman, 1954). Lawrence (1954) noted that aspen in Michigan may attain a diameter of two inches in 10 years.

Beavers exhibit seasonal preferences for food to some degree. During the summer months, a great variety of aquatic and semi-aquatic plants such as sedge and cattail roots, waterlilies, and other emergent aquatics are included in the diet. MacDonald (1956) indicated that in parts of North Park, herbaceous plants may constitute the major food source during summer. Beavers living in certain of the kettle lakes of North Park, which support lush growths of waterlilies, utilize these plants heavily and even include them in the winter food cache.

Limited use of alder, bog birch, and other woody species, including even conifers, is made by beavers. MacDonald (1956) noted few instances where these plants were taken as food, but observed that considerable use of them as construction material was made.

Typically, the land ownership status of mountainous beaver range in Colorado involves a mixture of public and private lands. Headwater tributaries of most watershed systems are located within National Forest boundaries, but often where valleys broaden and gradient decreases, even at elevations of 8000-9000 feet, the valley bottom land is in private ownership. Livestock raising, dependent upon the production of an irrigated hay crop, is the primary use of such lands. The influence of this ownership pattern upon beaver occupancy is readily apparent, since much of the high quality beaver habitat is located on these private lands. Interference by beavers, involving both the damming or undermining of ditches and the flooding of valley bottom land, sometimes results in appreciable crop loss. Thus, throughout the mountainous parts of Colorado, there exist in juxtaposition lands upon which beavers can be managed as a resource, and lands upon which control of nuisance beavers dictates management procedures. To further complicate matters, the same individual animals may, at different times, be residents of both of these areas.

The western two-thirds of the state exhibits a wide variety of topographic features. That part which comprises beaver habitat is largely characterized by small- to medium-sized streams having valley gradients of less than 12 percent, and valley bottoms wider than the stream channel width. Beavers occur over a much wider range of conditions than these, of course; the attempt here is merely to describe typical conditions. With respect to topography, the quality of beaver habitat is higher as valley gradient decreases and valley width increases (Retzer *et al*, 1955). Valleys having beaver habitat present are often characterized by pronounced topographic differences among various sections of the valley. This means that only parts of such valleys actually comprise beaver habitat. The most common geologic features which affect the topography of valley sections are rock dikes, glacial terminal

moraines, and the combination of other features influencing valley gradient and width.

Soils of the mountains of Colorado are derived from many different types of parent rock, with each soil type having its own peculiar characteristics of stability, erodability, and fertility. Generally, soils derived from the hard crystalline (igneous) rocks are the most stable, but are shallower and less fertile than other soils. Of prime importance in the stability of this soil type is the fact that rocks of various sizes are nearly always incorporated in the soil mantle. Nowhere is this more apparent than in glacial till, which is the result of mixing and grinding by ice action. Glacial till is considered to be the least subject to water movement of any of the mountain soils. Soils derived from rhyolitic, basaltic, or other volcanic rocks are in an "in-between" category; more fertile but less stable than soils from crystalline parent material. Beaver habitat in these soils can be considered generally good, assuming that other features comply with high quality habitat standards.

From the standpoint of beaver-habitat quality, the least desirable soil type is that which is derived from shale rock. Regardless of other habitat features, stream valleys located in this soil type are considered to be questionable or unsuitable for beaver occupancy. A well-watered shale soil which remains in place is exceedingly fertile, but such soil rarely remains in place. It is "slippery" and highly subject to faulting or sliding action wherein water acts as a lubricant. Moreover, it erodes into very fine, semi-colloidal particles, nonresistant to water pressure. If food species are present, beavers will readily occupy such valleys, but their occupancy is, in the long run, detrimental to all other watershed values (Retzer et al, 1955).

EFFECT OF PHYSICAL ENVIRONMENT ON BEAVERS:

THAT THE presence or absence of beavers in any valley or valley section is wholly dependent upon environmental factors has already been indicated. The influence of food is, of course, an elementary consideration, and can be dismissed with the observation that beavers can tolerate a surprising scarcity of food for a time, but that a complete lack of food is intolerable. Assuming, then, the presence of food species, many different facets of the makeup of physical environments operate to decree whether beavers can or cannot occupy any given site.

The more prominent features of terrain likely to affect beavers are steepness of the adjacent upland slopes, width of the stream valley or flood plain, valley grade, and the presence of natural obstructions across the valley.

The effect of valley grade on beaver occupancy has been observed by other investigators (Atwater, 1940; Swank, 1949; Smith, 1950), but, except for Smith's study in the Gore Range of Colorado, it has not been expressed in quantitative terms. The Colorado Beaver Investigations Project (Retzer et al, 1955) studied 365 separate units or sections located on 61 different mountain streams in the course of an overall evaluation of the relationship of beavers and physical environment. The data on valley grade and beaver occupancy, collected in this study, are presented in Table 4.

From these data, it is clear that valley grade has an important influence on sites inhabited by beavers. The full influence is slightly obscured in Table 4, because other influences (principally lack of food or permanent water) are responsible for the number of low-gradient sections in group C. The elimination of stream sections without food or permanent water leaves a total of 78 sections which have never been occupied for other reasons. Of these 78, 41 have gradients of 13 percent or greater. The remaining 37 sections, which are within valley grade classes considered suitable for beaver occupancy, are characterized by one or more of the following factors: Steep upland slopes, narrow floodplains, unstable and eroding channels, and evidence of heavy spring floodwaters.

Table 4—Number of Stream Sections in Various Valley Grade and Beaver Occupancy Groups¹ (Retzer et al, 1955).

Percent Grade	A	B	A+B	C	A+B+C
1-3	49	26	75	16	91
4-6	39	23	62	23	85
7-9	26	12	38	24	62
10-12	11	8	19	30	49
13-15	5	3	8	14	22
16-18	—	1	1	13	14
19-21	—	—	—	5	5
21	—	1	1	36	37
Totals	130	74	204	161	365

¹ Occupancy groups: A—now occupied; B—once occupied but now abandoned; C—never occupied

Based on the results of this study, valley grades can be classified in four groups according to frequency of beaver occupation: Excellent—valley grades 0 to 6 percent; Good—valley grades 7 to 12 percent; Questionable—valley grades 12-15 percent; Unsuitable—valley grades greater than 15 percent.

The same study (Retzer et al, 1955) dealt with widths of valleys in regard to influence upon beaver occurrence. Valley width data were grouped for analysis into six classes as follows: 0-30, 31-60, 61-90, 91-120, 121-150, and wider than 150 feet. When the 365 study sections are grouped by occupancy and valley width classes, the results appear as shown in Table 5.

It is clear that beavers occupy valleys of all widths, but of all sections in the A and B groups, only 28 percent are in valleys that are 0-30 feet wide. It appears that suitability of site is related to valley width, and that wider valleys are, in general, more suitable than narrow valleys for beaver occupancy. Floods tend to spread and be less destructive in wide valleys than in narrow ones, and beaver structures as a consequence may be more permanent. Also, wide valleys have large areas favorable for the growth of beaver food species. Perhaps narrow valleys are occupied only as a result of population pressures in adjacent favorable areas. The results of this phase of the study can be summed up with the statement that all valleys that are wider than the width of the channel itself are suitable, and that the wider the valley the more satisfactory it appears to be for beaver habitation.

An understanding of the processes of erosion leads one to suspect an inverse relationship between the steepness of a stream and the width of its valley. Table 6 shows the relationship between valley grade and valley

Table 5—Number of Stream Sections in Various Valley Width and Beaver Occupancy Groups¹

Valley width, feet	A	B	C
0-30	27	27	118
31-60	1	1	2
61-90	4	3	1
91-120	5	4	2
121-150	6	6	3
150	87	33	35
Totals	130	74	161

¹ Occupancy groups: A—now occupied; B—once occupied but now abandoned; C—never occupied.

Table 6.—Number of Stream Sections in Various Valley Width and Grade Classes.

Percent grade	Width Classes		
	0-30 Feet	31-150 Feet	150 Feet
1-3	9	12	70
4-6	26	11	48
7-9	33	8	22
10-12	33	5	11
13-15	18	—	3
16-18	11	—	2
19-21	5	1	—
21	36	1	—
Totals	171	38	156

width, with width classes between 31 and 150 feet combined as one class.

Most wide valley sections have grades below 6 percent, and the proportion of wide valleys decreases progressively with steeper grades until valleys wider than 150 feet do not occur above the 16-18 percent grade class. Actually a valley can be no narrower than the channel, and, conversely, there should be no limit to the width of valleys with decreasing grade, other factors remaining equal.

This association of wide valleys with streams of low gradient is favorable to beaver occupancy. By far the greatest number of beaver colonies occurs on sites having this combination. Beaver ponds flood part of the valley and raise the water table. Floods spread over the wider areas and diminish in velocity on the more gentle gradients, and as a result their destructive powers are much less in comparison with floods in narrow valleys with steep grades.

The origin of wide, low-gradient mountain valleys, or so-called "beaver meadows," has long been a subject of speculation. Warren (1926), Ives (1942), and several other investigators have attributed the creation of such sites entirely to the cumulative effects of beaver occupancy over a period of many hundreds of years.

It must be realized that parks, "beaver meadows," or simply wide valleys, as they may variously be called, must have certain basic geologic controls if they are to have any degree of permanence in mountainous country. It is physically impossible for beavers to change, let us say, a valley with 8 percent gradient to one having a gradient of 2 percent, simply by building dams and letting water-carried sediments accumulate behind the dams. Furthermore, in no instance could a food supply be of such permanent nature as to allow uninterrupted beaver occupancy for such a long period of time.

Two highly important geologic agents responsible for control of valley grades were recognized in this study. The first, and probably more important, is the presence of glacial deposits, rock dikes, or other massive valley obstructions which have successfully resisted the erosive power of moving water. Material eroded from upstream sections of a valley is deposited behind such obstructions to form a permanent low-gradient valley floor. The second important agent is the nature of the materials filling the valleys. During the Pleistocene, tremendous volumes of ice and water filled many valleys with large rocks which are resistant to movement by the decreased volume of present-day streams. The presence of these rocks thus contributes to valley stability.

Modern sediments in beaver-occupied valleys are usually sands, silts, and clays; the proportion of organic materials is large and none of it is consolidated. These sediments move readily in any kind of flowing water.



This area of active beaver workings, on Los Pinos Creek in Saguache County, shows the entire complex of beaver habitat characteristics in the Colorado mountains. Note the lodge and dam, the willow-filled valley bottom, and the area of aspen cutting on the adjacent slope.

Beaver dams are not permanent features of the landscape, because they are built of organic material and fine-textured unconsolidated sediments, and rarely do they function alone as valley obstructions for more than a few years.

In nearly every instance noted during the course of this study, the permanency of "beaver meadows" is directly dependent upon one or more of the geologic features just discussed, and individual dams are permanent only to the extent allowed by the physical environment of the valley. Any realistic appraisal of the role of beavers in valley building must recognize the basic influence of these geologic controls.

EFFECT OF BEAVERS ON PHYSICAL ENVIRONMENT:

THE DISCUSSION in the foregoing paragraphs does not imply that beaver dams and ponds do not collect and hold sediments; it simply questions the permanence of such deposits. Beavers exert an appreciable effect upon the areas they occupy, since their structures often control the rate at which sediments move downstream. The slower the rate of water flow, the lower will be the erosion rate and the higher will be the rate of sediment deposition and water infiltration. The greater the distance a channel travels in passing through its valley section, the slower will be the rate of water flow. In a wide, low-gradient valley, a network of beaver dams has tremendous influence upon the rate of water flow.

Because a beaver dam is not permanent, it may be expected that eventual washout is inevitable. If such failure suddenly releases a large head of water, the resultant erosion may be of far greater magnitude than would occur by stream flow alone. Nearly all erosion resulting from beaver activity occurs in stream channels, and results from breaking of dams, whether currently in use or abandoned.

The influence of rock and soil type upon beaver habitat quality has already been discussed. It can now be incorporated into the discussion of beaver influence on the physical environment, since obviously the degree of such influence varies with the inherent stability of the valley bottom. Beaver dam breakage in valleys with soil derived from shale formations commonly results in severe channel cutting and soil movement. On such sites, the stabilizing influence of heavy vegetative growth is lacking, because soil movement, being a continuing process, precludes the establishment of such growth. As long as a food supply exists, beavers will build new dams to replace those which wash out; subsequently the new dams will also fail, and the whole cycle will be repeated until the ultimate abandonment of the site occurs.

In beaver-occupied streams, it is difficult to separate beaver-induced erosion from normal geologic erosion, and no attempt to do so is made in this study. However, in recommending sites which are safe or unsafe for beaver occupancy, it is recognized that on unstable sites the effects of beaver-induced erosion are added to the effects of geologic erosion. Control of that contributing factor which is capable of being controlled; that is, beaver populations, will improve habitat conditions of even the most unstable of beaver-occupied valleys.

BEAVERS AND THE ANNUAL WATER CYCLE:

IN THE MOUNTAINS of Colorado, the annual precipitation and runoff cycles are characterized by snow accumulation and low stream volume flow in winter, runoff of snow melt in spring, and decreasing volume flow through late summer and fall. Generally, mountain streams assume flood proportions each spring, and breakage of beaver dams, particularly on the more unstable sites, is pronounced. The effect of this annual water cycle on beavers may be summarized by stating that beaver populations are peculiarly subject to the contingencies of high water in spring and often inadequate water in winter (Yeager and Rutherford, 1957).



Waterlilies grow profusely in some of the beaver ponds in North Park, Jackson County.



A classic example of the influence of geology in the formation of a "beaver meadow" is shown in this aerial view taken on the South Fork of Clear Creek, in Clear Creek County. The rock slide in the left foreground forms a massive valley obstruction which has resisted movement and has held stream-flow sediments in place. Beavers occupied the site because it was favorable, but they did not create the meadow.

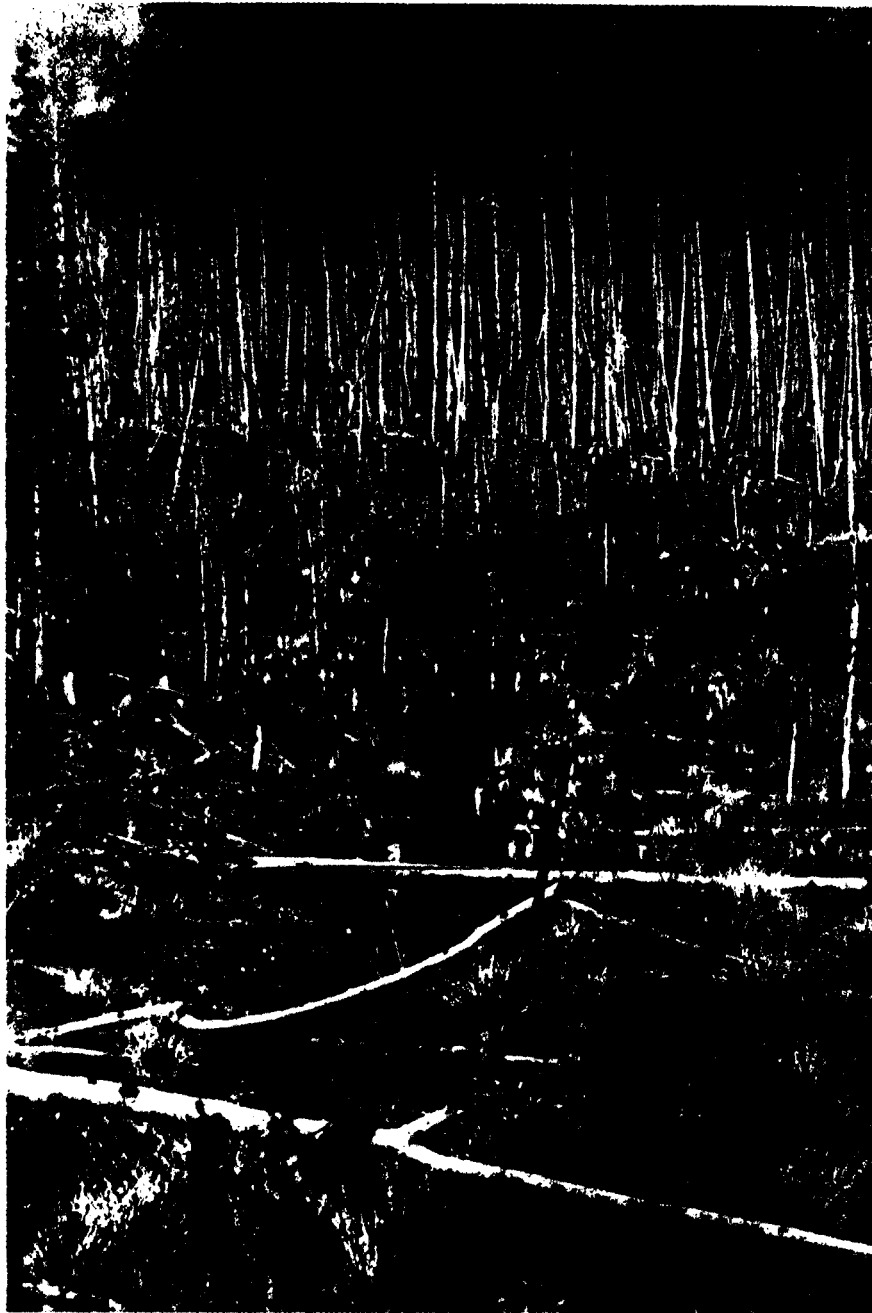
BEAVER INFLUENCE ON PLANT GROWTH AND SUCCESSION:

INITIAL BEAVER occupancy of any valley is, of course, dependent upon already established vegetative types which will provide food for the animals. Once beavers become established, their dam- and pond-building activities become an important factor in local plant succession. Valley bottom areas within the zone of beaver pond influence are converted from mesoserres to hydroseres. Plant species such as conifers, various shrubs, and grasses, which cannot survive flooding, are killed and in their place willows, sedges, and other plants associated with a high water table will take over. This occurrence is not one of normal plant succession, since the entire ecology of the valley is changed. As long as beaver ponds are present to maintain the water table at the increased level, the hydrosere will persist with few changes in plant species composition.

Upland slopes bordering beaver-occupied valleys are outside the zone of direct water table influence, and it is here that plant succession is directly influenced by the activities of beavers. The sub-climax aspen, if not utilized by beavers, will mature, become decadent, and eventually die out to be replaced by conifers. Moderate utilization of aspen stands by beavers encourages root and stump sprouting, and thus keeps a continuous, but steadily declining, stand of young reproduction growing. Such replacement of utilized aspen rarely equals the amount utilized, even under conditions of moderate use, and for this reason aspen cannot be regarded as a "renewable resource" within the probable life of any single beaver colony (Hall, 1960). This type of utilization can be, and sometimes is, responsible for greatly prolonging the life of the sub-climax aspen stage.



Beavers will go just so far and no farther for food. Aspen was heavily utilized on the adjacent slope, and now the plant succession following utilization is apparent. Note the low shrubs on the slope, the sparse willow clumps at the edge of the old pond site, and the grass in the bed of the old pond. This, incidentally, is an extremely stable valley bottom. Los Pinos Creek, Saguache County.



Reproduction of aspen following utilization by beavers prolongs the life of the aspen stand, as long as the reproduction itself is not utilized. Los Pinos Creek, Saguache County.



An aspen stand in the last stages of existence, on Los Pinos Creek in Saguache County. More than half of the arboreal plant cover is now in conifers, the valley bottom is too narrow to support willow growth, and the future of the beaver colony is limited to only another year or two.



The photo on the left was taken in 1955; the one on the right was taken in 1960. This beaver pond site on Nutras Creek in Saguache County was abandoned following food depletion. Heavy watershed runoff has completely silted in the pond in the foreground, but no channel erosion is evident. This site will probably recover in a relatively short time.

More often, however, utilization of aspen on upland slopes is exceedingly heavy at some stage in the beaver occupancy cycle, particularly with unmanaged populations. Aspen reproduction is utilized almost as fast as it appears, and the inevitable result is a complete killing out of that part of the stand which was available and utilized (MacDonald, 1956). Typically, the plant succession on such areas reverts back to a grass-forb type, which was the understory of the aspen stand, and various shrubs such as big sage and cinquefoil will begin to appear.

With the ultimate and inevitable loss of available aspen, the continuation of the beaver colony at any given site is dependent upon terrain. If the valley bottom, which has previously been converted to a hydrosere by the beaver's activities, is wide enough to support a relatively large area of



willow growth, the colony will persist with willow as the mainstay of the diet. If the valley bottom is relatively narrow, with pond surface taking up a large portion of the total flood plain area, the amount of willow present will probably not be enough to sustain the colony.

Depletion of aspen stands by beavers is greatly accelerated by wastage, especially during that part of the occupancy cycle when the beaver population is in the ascendancy and a considerable volume of aspen is readily available. The effects of this can be observed in numerous places throughout the range of aspen in Colorado, where beavers have literally "mowed down" stands in a single season. Trees are felled on top of one another, and only the uppermost branches are utilized. This usually occurs in mature or overmature stands, and is probably done either because the bark on large trunk sections

is less palatable or because these large sections are too heavy for beavers to move. MacDonald (1956) found that beavers exhibited a distinct preference for the one-inch to three-inch size class in aspens, and that overall wastage accounted for 13 percent of the total volume cut. However, these determinations were made in aspen stands which had been logged annually for several years. It is likely that wastage during the first year of heavy cutting will greatly exceed 13 percent.

INTERRELATIONSHIPS WITH OTHER WILDLIFE:

IN THE PRECEDING discussion, the nature and extent of beaver influence upon water flow, erosion, deposition, habitat alteration, plant growth, and plant succession have been pointed out. Since habitat which is occupied and influenced by beavers is also occupied by many other forms of wildlife, it follows that the activities of beavers have a direct bearing upon the occurrence and well-being of wildlife indigenous to valleys and stream courses.

To date, investigators have given more emphasis to studies of these beaver-wildlife interrelationships than perhaps to any other phase of beaver ecology. Seton (1937), Cook (1940), Rasmussen (1940), Bradt (1947), Swank (1949), Hodgdon and Hunt (1953), Grasse and Putnam (1955), Huey (1956), and Knudsen (1962), have discussed this subject from both the eastern and western standpoints; and Frary (1954), Rutherford (1955), Hoover (1955), and Neff (1957) have studied and reported on such interrelationships in several Colorado localities.

In Colorado, with which the present discussion is primarily concerned, the most obvious of these interrelationships involve the aquatic species, principally waterfowl, muskrats, and trout. The aquatic habitat created by beaver impoundments is highly attractive to ducks and muskrats, and except for natural or man-made lakes and ponds, beaver-occupied valleys constitute the only habitat where these species occur in the mountains of Colorado. They are rarely, if ever, found along stream courses lacking some form of impounded water.

Beaver influence upon trout in high-altitude streams of Colorado is generally considered to be entirely beneficial. These waters are cold, they lack pools, and their trout food production is low. Any agent which will slow down and spread out the water in these streams will improve trout habitat by the attendant warming of the water and the increase in biological activity. Beaver ponds serve this purpose remarkably well, and in addition they offer high-quality over-wintering habitat for trout. The belief that beaver dams hinder movement of trout to suitable spawning areas has been found to be not valid in the mountain streams of Colorado. To the contrary, overpopulations of small trout create a constant problem in the management of the beaver pond trout fishery.

Big game activity is difficult to assess in relation to beaver occupancy. It is known that vegetative (forage) production is higher in valley areas within the zone of beaver pond influence, but no clear indication of benefits to big game animals is apparent. The only conclusion is that, on summer ranges at high altitudes, big game animals are too wide-ranging to be influenced by beaver activity on small valley bottom areas.

One little-recognized aspect of beaver-big game interrelationships is that of competition for food. If such competition is present, it invariably operates to the detriment of beaver populations in localized areas. Both deer and elk will browse the tender new shoots of aspen reproduction, and if such browsing is heavy enough, reproduction following beaver utilization of an aspen stand may be kept suppressed to the point that recovery is impossible. Also, the combination of browsing, rubbing, and trampling of willow stands by elk may, in localized instances, adversely affect the beaver's food supply.



Some channel erosion has occurred in this abandoned pond site on Los Pinos Creek in Saguache County, but the rocky substrate will probably prevent serious erosion from occurring.

Domestic livestock on heavily grazed range may be responsible for much the same type of competition (Yeager and Rutherford, 1957).

Such forest-dwelling species as squirrels, dusky grouse, and martens are, of course, influenced to some degree by the activities of beavers, but the areas of influence are so small in comparison with the total forest habitat that the effects are insignificant. On the other hand, snowshoe hares, which are primarily forest-dwellers, appear to benefit from the creation of diversified habitat types characteristic of beaver-occupied valleys.

EFFECTS OF BEAVER HABITAT ABANDONMENT:

BEAVER HABITAT abandonment will occur to some degree under any type of management practice, but is, of course, most pronounced on streams which have had little or no beaver population control. The most common causative agent is depletion of the food supply. Since the ecology of beaver-occupied valley areas adjusts to such occupancy, many of the influences persist long after beavers have left, and in addition, abandonment itself induces certain ecological conditions. Thus, the ecology of beaver-abandoned sites is unique, and is markedly different from that of areas which have never been occupied by beavers.

An evaluation of the effects of beaver habitat abandonment on vegetation and wildlife was conducted by the Beaver Investigations Project, and reported by Neff (1957). The streams which were studied by Neff are extremely stable with respect to features of the physical environment, and it may be assumed that the physical changes which occurred subsequent to abandonment are minimal and that those changes would be correspondingly exaggerated in less stable situations. Other project personnel have made observations of habitat abandonment on less stable sites, and have concluded that the degree of ecological change is primarily dependent upon physical conditions.

Neff (1957) found that abandoned beaver ponds, where physically stable, are quickly invaded by grasses and sedges, and within a few years are valuable as grazing lands for both livestock and wildlife. Production of grasses and sedges was much greater on the abandoned sites. However, the superior growth of willow stands around occupied ponds more than compensated for the loss of willow by flooding, with the result that occupied pond sites produced greater amounts of willow browse than did the abandoned and drained ponds.

Because of the favorable physical conditions on the abandoned streams studied by Neff (1957), channel erosion was limited to the recently deposited pond fills and in no case was a channel cut into the rocky substrate. Water tables remained high, even though drainage of the abandoned ponds had reduced water storage to practically nothing.

In contrast to these findings, it is apparent that beaver habitat abandonment on unstable sites results in a much greater amount of erosion. Soil movement is pronounced, channels are deeply cut, and the water table often goes so low that the site is no longer capable of supporting the existing vegetative growth. Willow clumps die from lack of moisture, herbaceous growth is sparse and slow to develop, and soil continues to be displaced by the erosive power of running water. In time, effects of beaver occupation and abandonment will be obscured by natural plant succession, but such areas may exist for years in a raw, eroding, and unproductive state.

The findings of Neff (1957) indicate that even on the most stable and physically suitable locations, the abandonment of a colony site by beavers means the loss of the aquatic habitat that is necessary for the survival of the trout fishery and the existence of muskrat and waterfowl populations. This effect is also more pronounced on unstable sites, particularly as it applies to the fishery. An eroding, unstable stream channel following beaver abandonment is likely to be entirely devoid of trout populations.



MANAGEMENT

THE PRECEDING sections have presented the information now at hand on beaver populations and habitat. In the aggregate, this information has become the base upon which plans for the proper management of beavers have been derived; indeed, many management implications have already entered into the discussion. The broad objective in the management of beavers, just as with any other wildlife species, is to maintain balance between population and range, in order to utilize the resource to the fullest advantage.

Beaver management must necessarily be more intensive than that of most other wildlife species, because populations are restricted by the peculiar requirements of the animals. Beaver populations may be widely scattered, to be sure, but nevertheless they are limited to a very small portion of the total land area comprising their range. Their capacity for inflicting damage to human values, their effects upon the physical environment, and their ability to influence the occurrence and distribution of other wildlife further decree localized, intensive management. Beaver populations should never be managed for beavers alone.

NECESSITY FOR MANAGEMENT ON ECOLOGICAL BASIS:

THREE SEPARATE and distinct phases of beaver ecology have been recognized in the preceding discussions. These are: (1) the ecology of beaver habitat *per se*; that is, the factors which influence the occurrence, well-being and permanency of the species and of its habitat; (2) the ecology of beavers and other wildlife; that is, the factors which enable beavers to influence the occurrence and well-being of other species; and (3) the ecology of downstream areas which may not be beaver habitat, but which are affected by past or present beaver activity on upstream sites.

A beaver management program must consider these three phases simultaneously, in order to arrive at procedures which will derive the greatest benefits for all concerned. Concessions may have to be made in the management of certain phases, because the overall program should attempt to balance management for the benefit of the beaver and its habitat, management for the benefit of other wildlife, and management for downstream soil and water conservation. Thus, it is seen that ecological considerations become both the primary reason and the primary basis for beaver management.

PROBLEM OF DAMAGE CONTROL:

THE PLAINS riverbottom habitat can in no way be considered suitable for sustained production of beavers as a harvestable resource. Every beaver occurring here is a potential troublemaker. The land is all in private ownership, and crop-raising is dependent upon irrigation insofar as the physical limitations of irrigation systems and the amount of available water will allow. Beaver interference with irrigation systems and crop-raising in general far outweighs any possible economic benefits which might accrue from their presence. The only type of management which is applicable in the low-altitude stream courses of Colorado is that of heavy and continuous trapping. The objective here should be to keep the beaver population as low as possible, and ideally, if not practicably, the goal should be extirpation.

Landowners in the mountains of Colorado are beset with these same problems of beaver depredation, but here management is complicated by the fact that such private lands are often adjacent to National Forest or other public lands where beavers can and should be managed on a sustained yield basis. The passage of the 1955 Beaver Control Act gives landowners the power, through permits, to harvest the beavers on their own lands, and allows them to retain the full pelt price. Thus, a certain measure of responsibility now rests with the landowner, and it is hoped that more of them in the future will take advantage of the existing statutes.

Beavers on public lands may also be in damage status, since it is not uncommon for roads, trails, bridges, culverts, campgrounds, and municipal watersheds to be damaged or jeopardized by beaver impoundments. Under such conditions, proper management practice should depend on the degree of damage, as the beavers may be at the same time both beneficial and detrimental.

In all situations where beavers become nuisances on both private and public lands, the necessity of protecting property outweighs all other considerations in management. Control operations, therefore, are not dependent on conditions of habitat or population density, and removal of the offending animals is the only logical approach to the problem.

PROBLEM OF PELT VALUES:

THE PASSAGE of legislation which allowed landowners to harvest beavers on their own lands, and which authorized the Game and Fish Commission to establish trapping seasons on public lands, was intended to provide the Game and Fish Department with a management tool. That it has not been very effective is a matter of record. It is extremely difficult to develop and encourage any significant degree of trapping pressure when the incentive of high market prices for pelts is lacking.

Colorado beaver pelt prices stayed relatively stable in the \$20-25 average price class during most of the 1940's. In 1949, a trend began which saw pelt prices decline progressively from \$12 to \$8 to a low of about \$5. A slight increase has been noted in the last three years, and beaver pelt prices are currently averaging about \$6-7. If current low prices continue, and there is no reason to believe that they will not, the management of beavers on the basis of trapping economy alone is precarious and highly uncertain. Yet, a regular harvest is absolutely essential if beaver populations are to be managed in keeping with sound ecological principles.

The contingencies of pelt prices require that other measures of the beaver's value be employed. The benefits to be derived from managed beaver populations on most public lands, and the near certainty of the loss of these benefits where populations are not managed, appear to justify substantial subsidization of a beaver management program (Yeager and Hill, 1954). In those cases where an evaluation of the beaver's net worth, both ecologically and economically, indicates the accrual of positive values through manage-

ment, wildlife administrators can justifiably charge the cost of beaver management to any of several habitat improvement programs. To say that beaver management is done at a loss during times of low pelt prices is being, at the very least, unrealistic. As long as the Game and Fish Department is obligated to trap beavers from private lands upon request, there is, of course, no question of economic justification. Continuing encouragement of trapping by landowners and private trappers seems to be the best approach to the problem of private land beaver management.

HABITAT SUITABILITY CLASSIFICATION:

BEFORE PROCEEDING with the description of the beaver management plan which has been developed, it is well to consider the classification of physical environmental factors which influence the suitability of habitat for beaver occupancy. Management on an ecological basis assumes that manageable beaver populations and habitats exist, but first it is necessary to determine to what extent these environmental factors will allow the application of management plans. Since the size, location, and number of beaver colonies must be reconciled with all of the phases of beaver ecology, the development of a habitat suitability classification is based upon an assumed optimum intensity of management.

To use the classification developed here, the land or wildlife manager must understand that every mountain stream varies greatly throughout its course. Some sections of a stream may be highly suitable for beavers, others may be entirely unsuitable, while still others may exhibit any intermediate degree of suitability. The classification as developed is intended to be used as a guide to determine the suitability of stream sections for management of the beaver resource.

Data collected in this study justify the development of four suitability classes, based on factors of valley grade, valley width, and rock type. The classes are defined as follows, both in specific terms for these three factors and in terms of general management requirements (Retzer et al, 1955).

I. **EXCELLENT. Valley grade:** 0-6 percent; improves with decreasing grade. **Valley width:** Wider than channel width and generally wider than 150 feet; improves as width increases. **Rock type:** Glacial till, schist, granite, in that order. **Management requirements:** This classification requires minimum management to maintain stability of site and sustained yield in beaver production, but requires systematic harvest to prevent overpopulations and depletion of food supplies with accompanying abandonment and deterioration of dams. These sites provide the best available habitats for trout, waterfowl, and aquatic fur animals.

II. **GOOD. Valley grade:** 7-12 percent; improves with decreasing grade; 0-12 percent for rhyolite. **Valley width:** Wider than width of channel; improves as width increases. **Rock type:** Glacial till, schist, granite, and rhyolite, in that order. **Management requirements:** Intensive management is required to maintain stable populations in balance with food supply, so as to avoid abandonment followed by dam failures and resultant channel and valley erosion. Provides fair to good habitat for trout and aquatic game.

III. **QUESTIONABLE. Valley grade:** 13-15 percent; 0-15 percent for shale. **Valley width:** Wider than width of channel, but usually narrow. **Rock type:** Glacial till, schist, granite, rhyolite, shale, in that order. **Management requirements:** Constant trapping where beavers occur on Class III sites is required to keep populations low enough to avoid dam breakage and channel erosion. Comparatively few beavers are found naturally on these sites, and establishment of new colonies should be discouraged, especially on shale. May offer fair to good trout habitat, but generally poor for waterfowl and aquatic furbearers.



Beaver management on areas such as these two, on Chavez Creek in Saguache County, is governed entirely by food availability. The last beavers to occupy these sites were reduced to building dams of sod and subsisting on small and scattered willows.



IV. UNSUITABLE. **Valley grade:** Greater than 15 percent. **Valley width:** Seldom wider than channel. **Rock type:** Valley grade and width determine unsuitable class regardless of rock type. **Management requirements:** Beavers seldom occupy and never remain on Class IV sites. Temporary residents should be removed wherever channel instability is evident, but can probably be ignored where the stream bed contains large boulders, since environmental resistance will sooner or later force their departure.

In using this classification, valley grade is the first item considered, and a different grade range occurs in each suitability class. Any valley only channel wide is unsuitable, regardless of grade and rock type. Rock type is limiting only when it is rhyolite or shale. Stream sections in shale rocks are questionable regardless of valley grade as long as the valley is more than channel wide; if only channel wide, they are unsuitable for beaver occupancy.

The field use of the classification will require measurement of valley grades with an Abney level. Average valley width will need to be measured or closely estimated. A limited knowledge of rock types is required. If a local rock cannot be identified, appraisal of valley grade and width will still provide a close approximation of the class of the stream section, but it is well to make positive identification of shales.

BEAVER MANAGEMENT PLAN:

IN ATTAINING management based on the physical suitability of sites and on balance between beaver numbers and range, the field work which is executed must provide information on habitat suitability, carrying capacity, range trend, degree of competition, number of beavers, productivity, and degree of harvest required to maintain stabilized populations and habitat conditions. Techniques for evaluation of habitat suitability have been presented; if stream sections under consideration fall into Classes III or IV, the manager need look no further but can plan management on the basis of habitat suitability alone. Only those stream sections which fall into Classes I or II offer possibilities for sustained yield beaver management where information on populations and range are necessary.

As previously indicated, the beaver's ecologic and behavior patterns decree localized management. Parallel streams only a mile apart or even less may show great variation in food supply, food utilization, or physical features, requiring very different degrees of harvest to effect balance between population and range. The basic beaver management unit, under most conditions, is considered to be the named stream and its unnamed tributaries. In management planning, the combination of a number of streams may be designated as a trapping unit, but plans for the entire area should be the aggregate of those made for each management unit involved (Yeager and Rutherford, 1957).

The first step toward management is the logical one of area survey and appraisal. Reconnaissance may be at any time during the spring, summer or fall. Preferably, it should be an on-the-ground procedure, but for well-

Table 7.—Beaver Carrying Capacity by Food Type and Quality, Expressed as Acres Per Colony.

Food Type	Stand Quality		
	Good	Average	Poor
	Tall, closed stand; Vigorous growth	Medium height, Some Openings; Good growth Rate	Low, open stand; Slow growth or Decadent plants
Aspen	4	6	8
Willow	12	18	25

known range it may be by plane, supplemented by aerial photographs, the latter being highly useful in any case.

The second step is the determination of carrying capacity. MacDonald (1956) established standards for this determination by considering the beaver's requirements on an area basis. He found that, in the absence of competition from livestock and big game, and including wastage, the indicated acreages of aspen and willow of various stand qualities will support one average colony of beavers on a sustained yield basis (Table 7).

The outline of procedures to follow in making carrying capacity determinations is as follows:

1. Measure length of valley section on aerial photograph; or if road parallels valley, measure length by odometer reading. Convert measurement to chains. A section is defined as being a length of valley having more or less homogeneous features. If valley width, gradient, food type, or food quality changes abruptly, record a new section.
2. By pacing or ocular estimate, determine average width of valley bottom willow stand, in chains.
3. By pacing or ocular estimate, determine distance along adjacent slopes, and average width, of aspen stands available within 100 yards of valley bottom, in chains.
4. Multiply length and width of aspen and willow stands to obtain area in square chains, and by marking off one decimal point, convert area to acres.
5. By ocular estimate, determine which of the three quality classes listed in Table 7 best describes the stands of willow and aspen.
6. By dividing acres by the condition class factor (number of acres of a given stand quality required to support one colony of beavers, as shown in Table 7), determine carrying capacity expressed as number of beaver colonies which stream or stream section will support.
7. Deduct the following percentages from the carrying capacity determination to allow for presently existing livestock and/or big game competition:
 - None:** No noticeable browsing on aspen or willow—no deduction.
 - Light:** Browsing only on borders of aspen reproduction or willow stands—10 percent deduction.
 - Medium:** Browsing noticeable throughout stands—25 percent deduction.
 - Heavy:** Light hedging of aspen reproduction and willow stands; stands beginning to open as a result—50 percent deduction.
 - Destructive:** Severe hedging of aspen reproduction and willow stands; stands dying because of overuse—75 to 100 percent deduction, depending on condition.
8. Repeat carrying capacity determination at intervals of 3 to 5 years, depending on degree of change in various site factors.

In all cases, the emphasis is placed on simplicity of operation rather than on a high degree of accuracy. For example, there is no point in taking time to measure distances with tape or chain when pacing or ocular estimate will give figures which, when finally converted to carrying capacity, are accurate to the nearest acre or nearest beaver. Assignment of the condition class factor is of necessity left to the judgment of the individual; some leeway among the three classes can be exercised, but the confusion of using a larger number of classes should be avoided.

Deduction for competition is likewise left to individual judgment. Obviously, only presently occurring competition should be considered here; the effects of past competition will be reflected in the condition class factor which is assigned.

The third step in management is census, which involves the enumeration of beaver colonies and, wherever possible or practicable the enumeration of individual beavers. Hay (1956), after exhaustive studies of all possible census techniques, concluded that the only reliable beaver population index is the fall food cache. Perfect correlation between the number of colonies and food caches exists, in contrast to that between colonies and other structures, such as dams or lodges, which may occur in any number.

The desired level of management intensity will determine the procedure to be used in counting beaver food caches. Enumeration of caches by ground crews is undeniably the most accurate method, but it is time-consuming and, if applied to large areas, it is expensive. Rarely does a statewide beaver management program require such intensive execution.

Personnel of the Beaver Investigations Project have determined that aerial counting of beaver food caches is entirely feasible, economical, and adapted to large areas of beaver habitat. The value of aerial counting lies in the determination of year-to-year trends in beaver populations, rather than in recording absolute numbers. Obviously, every food cache cannot be accounted for by the aerial observer, but if the flights are conducted under the same conditions each year, any annual changes in the number of food caches will almost certainly be a reflection of proportional changes in the beaver population.

As in every other type of aerial wildlife census work, the job of aerial beaver colony counting requires a high-wing monoplane of sufficient horsepower to provide maneuverability and instant response, and a highly skilled pilot. Flying is done as close to the ground as possible, frequently at heights of 300 feet or less, and usually in steep-sided valleys or canyons. Weather conditions must be good enough to permit such flying, and flights should ordinarily be confined to the hours between 9:00 AM and 3:00 PM to take advantage of the best light conditions. Long slanting shadows during hours either earlier or later will seriously impair the observer's ability to distinguish food caches.

The seasonal timing of beaver colony counts is critical. They must be conducted late enough in the fall to insure that all beaver colonies have built food caches, but yet early enough so that the caches will not be obliterated by ice and snow. This, of course, applies to either ground or aerial censusing. In Colorado, six years of aerial beaver colony counting by Beaver Investigations Project personnel have shown that the first two weeks in October is ideal. The seasonal timing is correct, and in addition, good flying weather is usually encountered.

Because carrying capacity determinations are based upon the amount of food consumed by an average colony of beavers, the censusing of beavers by colonies rather than by individuals will usually be all that is required for the needs of management. In some cases, however, it is important to know the approximate number of beavers living in a given stream drainage, and in any event, the wildlife manager should know just what constitutes an average colony of beavers.

To aid in assigning an average number of individual beavers per colony, a sample of colonies trapped to extirpation was collected by project personnel. Nineteen were situated where aspen was the principal food, and 20 where willow made up the greater part of the diet. Means of 5.1 beavers per colony in aspen habitat and 4.5 beavers per colony in willow habitat were established on the basis of these samples, but they were found to be too small



This trapper's expression reflects the old question "Now that I've caught him, what am I going to do with him?"

for statistical treatment. For the most part, these samples were taken from previously untrapped range. Thus far, this is the best information at hand, and using it as a basis, it seems safe to assign an average number of four beavers per colony in willow habitat or where recent control trapping has been done, and an average number of five beavers per colony in high quality aspen habitat or previously untrapped areas.

The fourth and final step in beaver management is that of population control to hold beaver numbers in balance with available range. In the management of a depleted population, this step may involve transplanting, which

will be discussed later, or it may consist simply of allowing an existing population nucleus to increase naturally. More often, the wildlife manager is faced with the necessity for reducing a beaver population which is in excess of the indicated carrying capacity.

Harvest or cropping of surplus beavers in any given stream drainage should be done only upon the specific recommendation of the manager to whom this responsibility is assigned, regardless of the final delegation of authority to do the harvesting. Trapping may be done by public agency or private individual, but it should be clearly understood that a certain measure of control as to the number to be trapped and the specific place of trapping is necessary.

TRANSPLANTING:

THERE IS a school of thought which continues to cling to the somewhat out-dated philosophy that any beaver is more valuable alive than dead. Up to a point this is true; but it has been shown conclusively that unmanaged beavers will rapidly become more detrimental than beneficial. Field studies by the Beaver Investigations Project have proved that in nearly all cases where suitable beaver habitat exists, it is now occupied by beavers. Where beaver populations do not occur naturally, there is usually some ecological factor which prevents or discourages their occupancy. From an intensive management viewpoint, there are very few streams in Colorado which should have beaver transplants made. A surplus beaver is just that, and usually no amount of moving him around will make him otherwise.

The question of what to do with summer-caught, unprime beavers persists. These animals often have to be taken because they are in damage status, and in many cases the procedure has been to live-trap and transplant them in the hope that they will remain at the new site until cold weather brings the fur to prime, then re-trap them for the pelts. There are three major considerations against this policy: First, if they are transplanted to unsuitable habitat they will not stay, but will move elsewhere and continue to be troublesome; second, if the habitat is suitable they may or may not stay, dependent upon populations already present and upon their nature as individuals. If they do stay, they will usually be in competition with an already indigenous population, the carrying capacity will be exceeded, and the principles of ecological management will be defeated; third, it is economically unjustifiable as long as pelt prices remain at their current level. In view of these considerations, it appears that the best management policy for summer nuisance beavers is that of steel-trapping and pelting.

This is not intended as a condemnation of all transplanting. Wherever suitable and unoccupied beaver habitat can be found, or where disease may have caused a drastic die-off of existing populations, transplanting is very much in order. However, the criterion of habitat suitability should never be ignored, and beavers should never be transplanted to questionable or unsuitable habitat. Also, a considerable background of experience in beaver transplanting by the Colorado Game and Fish Department has shown that additional criteria should be considered to insure successful transplants.

If at all possible, beavers to be transplanted should come from sites with habitat conditions similar to those of the transplant site. Beavers accustomed to an aspen diet will not immediately adapt to a diet of all willow, and vice versa; and "river" beavers will not readily adapt to the environmental conditions of small high-country streams. Finally, transplants should consist of mated pairs of adult beavers.

The important consideration is that transplants should be made primarily for the benefit of the habitat, and there must be a good and legitimate reason for making them. Animals to be transplanted should be carefully chosen, not simply "dumped" because they are unwanted elsewhere.



ECONOMICS

THE ECONOMIC relationships of beavers, that is, their impact upon human values directly and indirectly, positively and negatively, have been discussed in general terms in the sections dealing with ecology and management. The purpose of this section is to summarize just what these relationships are, and how they may be recognized and evaluated.

PELTS AND CASTORS:

THE MOST easily recognized phase of beaver economics is that of pelt value. This value can be assessed in definite monetary terms at any given time, and it is a positive value. It is a value placed upon the physical being of the beaver itself, and is in no way associated with the value of anything which may be affected by the activities of beavers.

Another positive and definite value associated with the beaver itself is that of castoreum, the product of the castor glands of beavers. The dried castors are sold by weight, and enter the market to be used eventually by the perfume industry as a base or fixative in the manufacture of high-quality perfume.

HYDROLOGIC INFLUENCE:

LITERATURE is replete with references to the positive value of water storage by beavers, but nowhere is this value defined. Water by the acre-foot can be given a definite monetary value, to be sure, but attempts to evaluate the role of beavers in the overall water cycle run afoul of many intangibles. That positive values exist is well recognized. The physical capacity of beaver ponds may be measured, but it is almost impossible to determine the increment to the water table and the additional volume of late-season stream flow resulting from the presence of beaver ponds in a stream drainage. The question of degree—how much can be attributed to beavers—must remain largely unanswered.

Personnel of the Beaver Investigations Project have observed streams which had ceased to flow any surface water by mid-August, the only available water in the drainage being that impounded by beaver dams. In at least one instance, on the south side of the Grand Mesa, the continued presence of beavers is the key to continued use of the range for livestock grazing, as no other stock water is present.

EROSION:

THE ROLE of beavers as either helpers or inhibitors in the processes of erosion has been discussed previously. Recognition of beaver influence upon the erosion history of any given valley is relatively easy; the evaluation of this influence is more difficult. It has been shown that over long periods of time, beaver ponds have little, if any, deterrent effect upon the erosion cycle. The assignment of positive values can thus be largely ignored. It has also been shown that accelerated erosion attributable to past or present beaver activity may be appreciable. In the absence of any standards for estimating the actual economic loss resulting from beaver-induced erosion, it must suffice to say that the potential for negative values to exist in any beaver-occupied valley is recognized.

OUTDOOR RECREATION:

A VERY considerable positive value accruing from beaver occupancy of streams and valleys is that of outdoor recreation in its many forms. In recognizing that this value exists, one is simply dealing with economic ecology, since the end result of such recognition is human use and enjoyment of the ecological conditions peculiar to beaver habitat. This value may be purely and simply esthetic; that is, appreciation of the presence of beavers in their native haunts, or it may be manifested more tangibly in, for example, a happy fisherman holding a string of beaver-pond trout.

If we could place an accurate and acceptable value on the contribution of beavers to outdoor recreation, this would be valuable in management of the beaver resource in several ways. It would provide a means for comparing the importance of recreation with that of other values, both positive and negative, associated with beavers; and the value of the recreation provided would give a measure of the management intensity or investment to be applied in maintaining the resource.

Clawson (1959) has discussed in detail the arguments both for and against the development of monetary measures of the value of outdoor recreation. These arguments, while intended to apply specifically to orderly planning, building, and development of recreational facilities, can, by implication, also apply to recreational facilities such as beaver ponds, which exist independently and are there for the taking. The chief argument cited in favor of the development of monetary measures is that any reasonable estimate of value is better than none at all. On the other hand, those who argue against such development claim that (1) it can't be done, and (2) it is undesirable to try.

Some of the aspects of beaver contribution to recreation can be measured. Differentials in trout production between beaver pond and stream habitats can be determined, and waterfowl, upland game, and big game production differentials can also be determined. The question then arises: If production differentials are in favor of beaver-occupied valleys, what are these differentials worth? Do we apply the economics of hatchery trout production, or is a beaver pond trout worth more than a hatchery trout? What is a brood of mallards worth? Who can place a value on the satisfaction of watching a family of beavers at work or play on a summer evening?

Clawson (1959) has shown that it is both theoretically possible and practically manageable to put monetary values on outdoor recreation, **in sum total**; that is, to evaluate recreation as opposed to the lack of recreation. The problem of getting accurate and dependable data is serious, but not insurmountable. Personnel of the Colorado Beaver Investigations Project have concluded that the additional problem of gathering data to evaluate the contribution of beavers toward the total value of outdoor recreation is not possible. There



Beaver pond trout fishing is the favorite of many Colorado anglers. This pond on Nutras Creek in Saguache County has produced many fine catches of brook trout.

is no standard of evaluation which is not completely arbitrary. As much as the wildlife manager might wish to place an accurate value on the recreation potential of beaver habitat, he must be content with simply recognizing that recreation values do exist and that management plans must be attuned thereto.

The phenomenal growth of an industry known loosely as "dude ranching," not only in Colorado but in all parts of the West, during the past 15 years is based upon the existence and occurrence of natural conditions which are considered to be attractive and desirable. A dude ranch must be able to offer to its clientele a maximum diversification of recreation opportunities, or suffer the stigma of being "second rate" or inferior. Many operators of dude ranches consider the setting of a stream valley having active beaver dams as being of prime importance in their business. The economic value of having naturally occurring beaver ponds present is considerable, especially since most dude ranch patrons demand easily accessible fishing sites. This is not the only value associated, however; the entire concept of esthetics makes a ranch having a beaver-occupied stream infinitely more attractive than a ranch lacking such a feature. Thus, beavers can exert an economic influence in this instance far in excess of their actual contribution to increased trout production.

Unfortunately, many dude ranch operators are short-sighted in their approach to beaver management. The writer has observed several instances where dude ranch beaver habitat contained beaver populations far in excess of carrying capacity. This condition is often allowed to remain unchanged on the theory that trapping of beavers will harm the quality of fishing. From the long-range standpoint, it is imperative that such operators recognize the fact that beaver overpopulations will ultimately deteriorate the habitat, and that for their own economic well-being a regular harvest of beavers is necessary.

DAMAGE TO HUMAN VALUES:

OFTEN, the economics of direct beaver damage to human values can be calculated closely. Thus, an assessment of crop loss occurring because of beaver interference with irrigation systems, or an assessment of time and money expended to repair beaver damage to structures, can be made which will put the economics of beaver damage into definite monetary terms. The problem of damage evaluation where the works of man are involved is far less complicated than the problem of evaluating damage to habitat by unmanaged beaver populations.

ECONOMICS AND THE WILDLIFE MANAGER:

IT IS APPARENT that beavers are capable of exerting a great deal of economic influence wherever they occur. The wildlife manager, in evaluating the overall importance of beaver dams in any given stream valley, must of necessity base his evaluation on economics, in spite of having to work with an almost total lack of definite monetary standards. There is no substitute for good common sense in making this evaluation.

It would be remiss to fail to emphasize once again that only by the most closely controlled management techniques can the maximum positive values of beaver occupancy be realized, while at the same time holding negative values at the lowest possible level.

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LITERATURE CITED

- Atwater, M.M. 1940. South Fork (Montana) beaver survey. *Jour. Wildl. Mgmt.*, 4(1):100-103.
- Bradt, Glenn W. 1947. Michigan beaver management. Michigan Department Cons., Game Div., 56 pp.
- Choquette, L.P.E., and D. H. Pimlott. 1956. Gastrointestinal parasites of beavers in Newfoundland. *Can. Jour. Zoo.*, 34(3):209.
- Clawson, Marion. 1959. Methods of measuring the demand for and value of outdoor recreation. Resources for the Future, Inc., Washington, D. C., 36 pp.

- Clements, F. E. 1910. Life history of the lodgepole pine burn forests. U. S. D. A. Forest Service Bull. 79, 56 pp.
- Cook, David B. 1940. Beaver-trout relations. Jour. Mamm., 21(4):397-401.
- Frery, Ladd G. 1954. Waterfowl production on the White River Plateau, Colorado. M. S. thesis, Colorado State University, Fort Collins, 93 pp.
- Grasse, James E., and Euvern F. Putnam. 1955. Beaver management and ecology in Wyoming. Wyoming Game and Fish Comm., Bull. 6 (2nd Ed.), 75 pp.
- Green, R. D. 1937. The susceptibility of beaver to tularemia. Minn. Wildl. Disease Invest., 3:110.
- Gregg, H. R. 1948. The magnificent accident. Sci. Mon., 67(2):73-82.
- Hall, Joseph G. 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. Ecology, 41(3):484-484.
- Hay, Keith G. 1955. Development of a beaver census method applicable to mountain terrain in Colorado. M. S. thesis, Colorado State University, Fort Collins, 143 pp.
- Henderson, F. Robert. 1960. Beaver in Kansas. State Biol. Surv. and Mus. Nat. Hist., University of Kansas, Lawrence. Misc. Pub. No. 26, 85 pp.
- Hodgdon, K. W., and J. H. Hunt. 1953. Beaver management in Maine. Maine Department Inland Fisheries and Game, Game Div. Bull. No. 3, 102 pp.
- Hoover, Robert L. 1955. Beaver ecology in the Longs Peak area of Colorado. M. S. thesis, Colorado State University, Fort Collins, 262 pp.
- Huey, William S. 1956. New Mexico beaver management. New Mexico Department of Game and Fish, Bull. No. 4, 49 pp.
- Ives, R. L. 1942. The beaver meadow complex. Jour. Geomorphology, 5(3):191-203.
- Jellison, W. L., G. M. Kohls, W. J. Butler, and J. A. Weaver. 1942. Epizootic tularemia in the beaver, *Castor canadensis*, and the contamination of stream water with *Pasteurella tularensis*. Am. Jour. Hyg., 36(2):168-182.
- Knudsen, George J. 1962. Relationship of beaver to forest, trout, and wildlife in Wisconsin. Wisconsin Conservation Department, Tech. Bull. No. 25, 52 pp.
- Landford, E. V. 1954. An outbreak of tularemia in beaver and muskrat in Waterton Lakes National Park, Alberta, Can. Jour. Comp. Med., 18(1):28-30.
- Lawrence, W. H. 1954. Michigan beaver populations as influenced by fire and logging. Ph.D. thesis, University of Michigan, Ann Arbor, 200 pp.
- MacDonald, Duncan. 1956. Beaver carrying capacity of certain mountain streams in North Park, Colorado. M. S. thesis, Colorado State University, Fort Collins, 136 pp.
- Neff, Don J. 1957. Ecological effects of beaver habitat abandonment in the Colorado Rockies. Jour. Wildl. Mgmt., 21(-):80-84.
- Olson, O. Wilford. 1949. Incidence of helminth parasites in beavers from the Platte River in Weld County, Colorado. Jour. Colo. Wyo. Acad. Sci., 4(1):64.
- Packard, F. M. 1940. Beaver killed by coyotes. Jour. Mamm., 21(3):359-360.
- Parker, R. R., E. A. Steinhaus, G. M. Kohls, and W. L. Jellison. 1950. Contamination of natural waters and mud with *P. tularensis* and tularemia in beavers and muskrats of the northwestern United States. Natl. Inst. of Health Bull. No. 193, USGPO, Washington, D. C.
- Presnall, C. C. 1943. Wildlife conservation as affected by American Indian and Caucasian concepts. Jour. Mamm., 24:458-464.
- Rasmussen, D. I. 1940. Beaver-trout relations on the Rocky Mountain Region. N. Am. Wildl. Conf. Trans., 5:256-263.
- Retzer, John L., Harold M. Swope, Jack D. Remington, and William H. Rutherford. 1955. Suitability of physical factors for beaver management in

- the Rocky Mountains of Colorado. Colorado Game and Fish Department, Tech. Bull. No. 2, 33 pp.
- Rutherford, William H. 1955. Wildlife and environmental relationships of beavers in Colorado forests. Jour. For., 53(11):803-806.
- Scott, J. W. Natural occurrence of tularemia in beaver and its transmission to man. Science, 91(2359):263-264.
- Seton, Ernest T. 1937. Lives of game animals. Doubleday, Doran and Co., Inc., New York. Vol. 4, pp. 441-501.
- Smith, A. E. 1950. Effects of water runoff and gradient on beaver in mountain streams. M. S. thesis, University of Michigan, Ann Arbor.
- Stegeman, L. C. 1954. The production of aspen and its utilization by beaver in the Huntington Forest. Jour. Wildl. Mgmt., 18(3):348-358.
- Swank, Wendell G. 1949. Beaver ecology and management in West Virginia. Cons. Comm. of W. Virginia, Div. Game Management, Bull. No. 1, 63 pp.
- Thomas, E. M. 1954. Wyoming fur-bearers—the beaver. Wyoming Game and Fish Comm., Bull. No. 7, 93-99 pp.
- Warren, Edward R. 1926. Notes on the beaver colonies in the Longs Peak Region of Estes Park, Colorado. Roosevelt Wildlife Annals, 1(1-2):192-234.
- Yeager, Lee E., and Ralph R. Hill. 1954. Beaver management problems on western public lands. N. Am. Wildl. Conf. Trans., 19:462-480.
- Yeager, Lee E., and William H. Rutherford. 1957. An ecological basis for beaver management in the Rocky Mountain Region. N. Am. Wildl. Conf. Trans., 22:269-300.

SCIENTIFIC NAMES OF PLANTS AND ANIMALS APPEARING IN TEXT

	Common Name	Scientific Name
Plants:	Aspen	<i>Populus tremuloides</i> (Michx.)
	Willows	<i>Salix</i> spp (L.)
	Cottonwoods	<i>Populus</i> spp. (L.)
	Alder	<i>Alnus tenuifolia</i> (Nutt.)
	Bog birch	<i>Betula glandulosa</i> (Michx.)
	Lodgepole pine	<i>Pinus contorta</i> (Engelm.)
	Big sage	<i>Artemesia tridentata</i> (Nutt.)
	Cinquefoil	<i>Potentilla</i> spp. (L.)
	Cattail	<i>Typha latifolia</i> (L.)
	Sedge	<i>Carex</i> spp. (L.)
	Waterlily	<i>Nuphar polysepalum</i> (Engelm.)
Animals:	Beaver	<i>Castor canadensis</i>
	Coyote	<i>Canis latrans</i>
	Bobcat	<i>Lynx rufus</i>
	Black bear	<i>Ursus americanus</i>
	Mink	<i>Mustela vison</i>
	Muskrat	<i>Ondatra zibethica</i>
	Mule deer	<i>Odocoileus hemionus</i>
	Elk	<i>Cervus canadensis</i>
	Squirrel	<i>Tamiasciurus fremonti</i>
	Marten	<i>Martes americana</i>
	Snowshoe hare	<i>Lepus americanus</i>
	Ducks	subfamily <i>Anatinae</i>
	Dusky grouse	<i>Dendragapus obscurus</i>
	Trout	Family <i>Salmonidae</i>
	Beaver beetle	<i>Leptinillus validus</i>