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WILLOW AND ASPEN IN THE ECOLOGY OF BEAVER ON SAGEHEN CREEK, CALIFORNIA

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INTRODUCTION

Like many other mammals, beavers thrive in sub-climax vegetation. Specifically, they often flourish where fire has been followed by appearance of Quaking Aspen, *Populus tremuloides.* This tree is the one most commonly felled for food and building material by beaver and its distribution is remarkably similar to that of the beaver.

Where beavers do occur in the absence of aspen, they usually depend on willow. Various species of *Salix* are found even more widely distributed than aspen, and very few beavers maintain themselves outside its range although they may temporarily subsist on such unlikely forage as sagebrush or cornstalks. As a matter of fact willow is often abundant in conjunction with aspen, and West and Rasmussen (1947) feel that willow, not aspen, is the key plant in beaver habitat.

The primary purpose of this study has been to analyze and interpret patterns of use of varying supplies of willow and aspen at 3 beaver colonies in the northern Sierra Nevada.

Several investigations similar to the present one have been most helpful and interesting for purposes of comparison. Notable are those of Aldous (1938) in Minnesota, Bradt (1938) in Michigan, Gese and Shadle (1943) and Tevis (1950) in New York, Haas (1943) in Utah, Haseltine (1948) and Hodgdon and Hunt (1953) in Maine, and MacDonald (1956) in Colorado.

THE STUDY AREA AND ITS VEGETATION

Sagehen Creek, about 8 miles north of Truckee in Nevada County, drains a basin approximately 12 miles long on the east flank of the Sierra Nevada. The stream empties into the Little Truckee River. Along its easterly course it drops from an elevation of 8000 to 5800 feet.

Quaking Aspen, *Populus tremuloides,* and 4 species of willow—*Salix cordata, S. glauca,* var. *villosa, S. Lemmonnii* and *S. argophylla*—constitute the principal forage species for beavers. The willows are found in wet sites or along the border of the stream for almost its entire length. Aspen occurs where the soil is relatively moist, but it is less restricted to the immediate vicinity of the stream than are willows. The distribution of aspen along the length of the creek is decidedly spotty.

Aspen stands typically spring up in the wake of forest fires. Most of the Sagehen basin has been lumbered and burned over. Mr. Charles B. White, a retired Truckee banker, recalls that much lumbering was going on in this area when he arrived in 1896, and it continued until about 1910. More than half of the 25 aspen trees aged by core-samples took root during the 1910-1928 period; the rest were established randomly from 1840 to 1890. This suggests that much of the present stand of aspen had its origin in fires immediately following the lumbering operations recalled by Mr. White.

Woody plants known to be cut by beaver on Sagehen Creek are:

Quaking Aspen	heavily
Willows	heavily
Mountain Alder	fairly heavily
Ceanothus velutinus	very lightly
Currant	lightly
Lodgepole Pine	very lightly
White Fir	lightly
Grasses	unknown extent

Although aspen and willow were the most important items cut by beaver, almost every woody plant was cut to some extent. White fir was often felled and was always barked in a characteristic way. Whereas the bark of the stump and lower trunk of felled aspen was almost always ignored in favor of the bark and twigs of the smaller terminal branches, the opposite procedure was followed with fir. There is apparently some ingredient present in bark or sap of the basal part of firs which is sought.

Mountain Alder, *Alnus tenuifolia,* especially in the upper reaches of the creek, is a conspicuous streamside plant and is used to some degree by beaver. Lodgepole Pine, *Pinus contorta,* is another conspicuous tree which is restricted to the vicinity of the stream and is often killed by flooding of the beaver ponds. Both the Jeffrey Pine, *Pinus jeffreyi,* and Ponderosa pine, *P. ponderosa,* are abundant on the upland slopes, the former occurring mostly above 6300 feet elevation.

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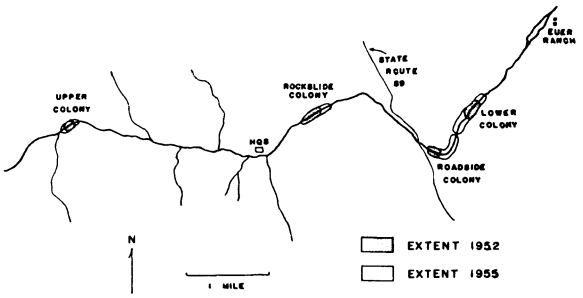

FIG. 1. Expansion of beaver colonies on Sagehen Creek, 1952-1955.

On the very highest slopes at the head of the basin and on one steep, cool north-facing slope farther downstream are stands of Western White Pine, *Pinus monticola*. White Fir, *Abies concolor*, Red Fir, *A. magnifica*, Mountain Hemlock, *Tsuga mertensiana*, and Sierra Juniper, *Juniperus sierrae*, complete the list of evergreens.

Ceanothus velutinus forms extensive stands of almost impenetrable chaparral on the burned over and logged over slopes at the head of the basin, and farther down the watershed on the south-facing exposures where it is mixed occasionally with Manzanita (*Arctostaphylos* sp.).

Bitterbrush, *Purshia tridentata*, and Sagebrush, *Artemisia tridentata*, particularly the latter, cover flatter, drier sites, forming unbroken stands in the lower reaches of the watershed.

DESCRIPTION OF COLONIES STUDIED

Figure 1 shows the locations and extent of 4 of the beaver colonies, 3 of which were studied in detail. For the purposes of this study, Bradt's (1938) definition of a colony was used: ". . . a group of beavers occupying a pond or stretch of stream in common, utilizing a common food supply, and maintaining a common dam or dams. They may or may not be living in the same lodge or burrows."

As shown in Figure 1, all the colonies expanded during the period of study. Only the Rockslide colony vacated any of the original colony site.

Figure 2 presents detailed maps of the 3 colonies and shows the extent of aspen, location of my sampling areas, and various beaver-made features such as dams, lodges and ponds. Owing to the nature of willow growth it was not practical to map its extent in the various colonies; it grew in clumps along the shores and on almost every little island, spit or exposed shoulder on the dams. Willow growth extends, roughly, from shore to shore the length of each colony.

The supplies of willow and aspen were highly variable from colony to colony. The Upper colony had abundant aspen but very little willow; the Rockslide colony had almost no aspen and an intermediate supply of willow; and the Lower colony had an intermediate supply of aspen and a great deal of willow.

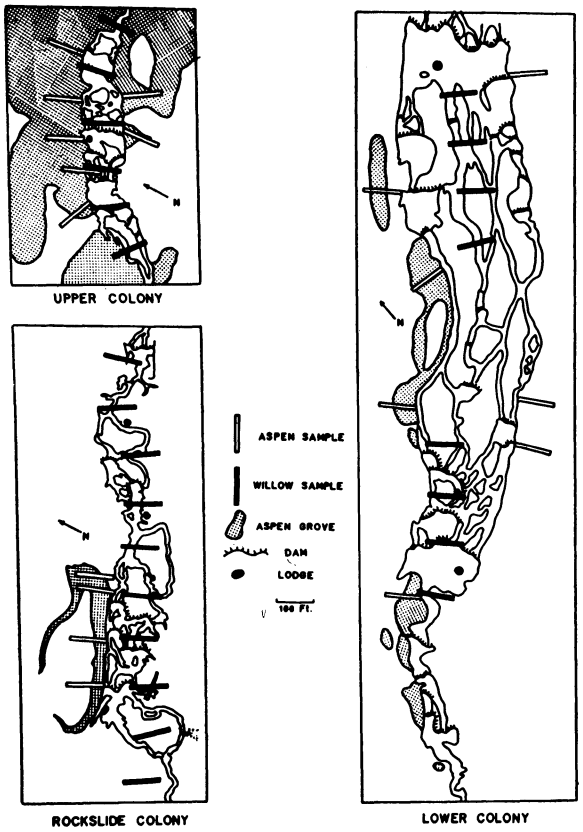

FIG. 2. Extent of aspen and location of sample plots on the three colonies studied.

POPULATION SIZE, ACTIVITY AND BEHAVIOR

For the results of the willow and aspen measurements to be most meaningful a census of each colony was necessary. Knowing the number of animals per colony during a given season permits one to calculate forage use on a beaver-day basis and thus make comparisons between the colonies. A census of each colony was made by applying the Lincoln Index method to the ratio of marked to unmarked animals seen during evenings of observation.

Trapping and Marking

Four Bailey live-traps, the type widely used by the state trappers in the West and recommended by Bradt (1938), Grasse and Putnam (1950), and Hodgdon and Hunt (1953), were used in the summers of 1953, 1954, and 1955.

In the past most field workers have had good success ear-tagging beaver with monel metal,

fingerling type fish tags, (Harris and Aldous 1946, Haseltine 1950, Rasmussen and West 1943). However, an obvious field mark was needed for the purposes of this study. Such a mark would permit an observer to obtain a Lincoln Index ratio on the basis of sight records rather than the less efficient method of re-trapping. In addition, activity and behavioral differences, if any, could be observed among individuals in a colony. The method finally adopted was notching the tail by means of a large-size pig ear-notcher. No more than 2 notches per animal were necessary. Beavers showed little or no reaction or bleeding and the marks have remained easily visible, in one case for 5 years. Recently David Taylor, studying these same colonies, has had good success marking beavers on the tail with waterproof spray enamel. These marks last at least a month and are much more easily recognized at a distance than are tail notches. In some cases scars and other natural marks on the dorsal surface of the tail were found to be reliable field marks.

Sexing the animals was accomplished by external palpation for the penis bone as described by Rasmussen and West (1943), and as demonstrated by Clyde J. Shehorn, state beaver trapper for the California Department of Fish and Game. The method of palpating the testes, described by Osborn, (1955) was tried several times during the 1955 season with indifferent success, probably because of inexperience on my part.

Population Estimates

In the 1954 season 5 individuals were trapped at the Upper colony. The breeding female and one kit were found in the traps dead of exposure, and another kit, although released alive, was in very poor condition at the time and was thought to have succumbed shortly after its release. An adult, probably the breeding male, and a yearling female were trapped, marked and released without injury. A 6th beaver, probably a yearling, was never taken in the traps but was occasionally observed. The colony is thought to have consisted of a pair of breeding adults, 2 yearlings and 2 kits at the start of the 1954 season. Following the trapping losses, 2 yearlings and the adult male remained.

Evidently the loss of the breeding female was a serious blow to the colony, for in 1955 only 3 animals were observed. They were the adult male and the animal taken as a yearling in 1954 plus an unmarked individual thought to be the same unmarked beaver seen in 1954. No kits were seen here in 1955, presumably because the 2-year old female was not in breeding condition. Osborn (1953) found that only about 20% of the 2-year olds examined by him had bred.

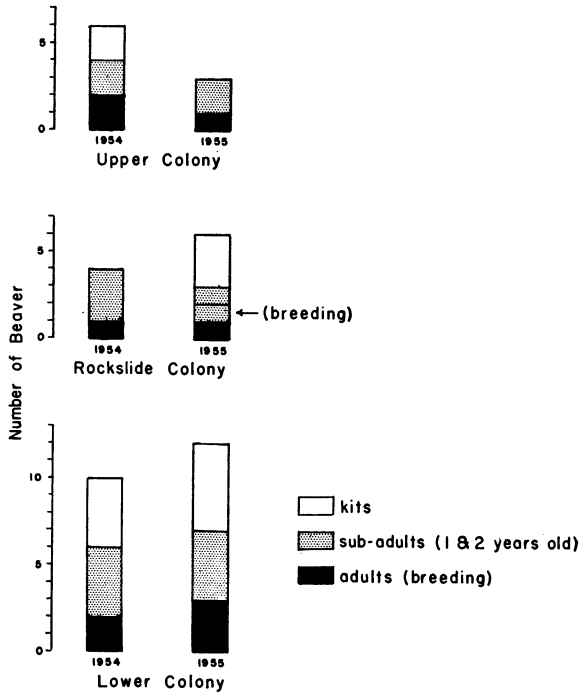

FIG. 3. Beaver population estimates for 1954 and 1955.

At the Rockslide colony the adult female also was killed in the trap in 1953. The subsequent population of this colony in 1954 was 4 animals, including an adult male and 3 smaller beaver, but no kits. It is significant that here, as at the Upper colony, no kits were seen in the season following one in which an adult female was killed, indicating that none of the 2-year old females had replaced its mother as a breeding female. In 1955 reproductive activity resumed and the population rose to 6, including the breeding male marked the previous season, a lactating female, another animal about the same size as the lactating female and three kits.

The only year in which beaver were trapped and marked at the Lower colony was 1955. In that year the population was thought to consist of 12 animals. An estimate of 10 beaver, based only on observations of unmarked individuals, was made for the previous year.

Figure 3 summarizes population estimates for the 3 colonies.

ASPEN

In this phase of the study the problem was 2-fold: 1) to measure the available amounts of aspen, of assorted sizes, and 2) to measure the rate at which the beaver were cutting the trees.

Methods

A sampling method was employed for calculation of availability of the different diameter classes of aspen trees, in terms of density per unit area. After the extent of aspen cover had been mapped, the density figures from the samples were projected to estimate the total amount of aspen available at the colony. Weight of bark available from each diameter class was obtained by referring to measurements made in Minnesota by Aldous (1938). Although growth characteristics of aspen may well be different in the Sierra, the use of Aldous' data was still the most practical method under the circumstances.

Sample plots, 10 by 100 feet in size, were laid out in a direction perpendicular to the shore line and were subdivided into ten, 10 x 10 foot squares. On the yearly runs of these samples, conducted at the end of August or early in September, note was made of the number and diameter of trees standing and felled on each 10 x 10 foot subsection. Placement of these "spoke" samples was not random. Instead, one or more plots were established in each large aspen stand, the number of plots depending upon the size of the stand. A deliberate effort was made to place the plot so that it would be as representative as possible of that stand. Locations of all these samples are shown on the maps of the colonies (Fig. 2).

On each visit to a colony the diameters of all newly-cut aspen trees were measured at stump height. As a stump was tallied it received a mark of red paint so that it would not be mistaken for a fresh cutting on subsequent visits. When cutting was at a maximum during the summer and early fall, visits were frequent, sometimes as often as once a week. In the winter, visits were at intervals of about 6 weeks. Every effort was made to find, mark and measure all trees cut since the previous visit. Because of the ease of finding newly-cut stumps and because re-runs made the same day rarely turned up stumps overlooked on the first run, it is believed that these counts are over 90% accurate and complete.

This method, which is essentially that used in a similar study by Aldous (1938), was used at the Upper and Lower colonies to determine absolute rates and amounts of aspen felled. At the Rockslide colony aspen use was so light that it was computed solely on the basis of the yearly runs of the samples already described.

Supply of aspen in the 3 colonies

The amount of aspen in the immediate environs of the colonies can be judged from a glance at the maps. Aspen cover at the Upper colony was extensive. There was very little of this species at the Rockslide colony and a moderate amount at the Lower colony.

TABLE I. Number of aspen trees within 100 feet of Pond

Year	Colony		
	Upper	Rockslide	Lower
1953	3180	400	3160
1954	2700	250	2190
1955	2300	200	1635

The question now arises: just how much aspen at a given colony is reasonably accessible to beaver? The tree growing 100 yards from shore can not be considered to be as available as one at the water's edge. Although distance from water certainly must decrease availability, somewhere it is necessary to draw an arbitrary line within which to confine the measurements. Hodgdon and Hunt (1953) state that beavers rarely traveled more than 100 yards from water. Hammond (1943) observed that they traveled 200 yards. Bradt (1938) considered that ordinarily 200 feet was the limit, but mentioned an instance of a beaver cutting aspen as far as 650 feet from shore. Only one of the 5 colonies studied by MacDonald (1956) cut 200 feet from shore, the average maximum distance being a little less than 150 feet. For the purposes of this study, however, I confined my measurements of aspen availability and aspen use to the zone within 100 feet of the stream since at least 90% of the cutting occurred this close to water.

Estimates of the aspen supply within 100 feet of shore in terms of numbers of trees are summarized in Table I.

Although the figures in this table portray the general trend of availability at each colony, a more accurate comparison is obtained by computing the weight of bark and twigs available from these trees. Such a comparison takes into consideration the differences in amount of food in trees of different diameters. Aldous (1938) and Stegeman (1954) determined the weight of bark and twigs available for aspen of various diameters. Figure 4, which compares availability of aspen among the 3 colonies on the basis of this criterion, was computed by applying Aldous' findings to these data.

Figure 4 shows that aspen supplies were shrinking at all colonies. By 1955 when this study terminated aspen was largely gone from the Rockslide and Lower colonies. The good supply at the Upper colony was dwindling.

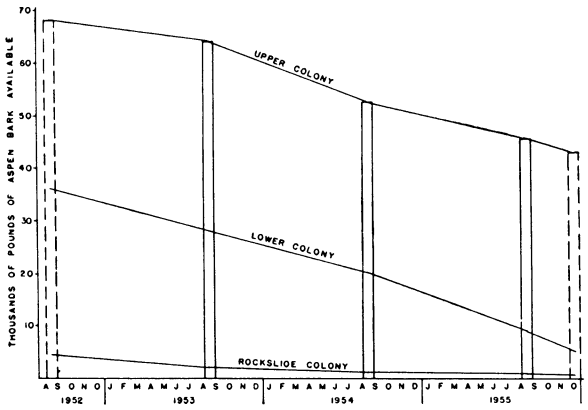

FIG. 4. Aspen availability in terms of green weight of bark and twigs. Dry weight is approximately 60% of green weight.

Distance from shore and relative use of aspen

Subdividing each spoke sample into 10, square sub-samples permitted an analysis of the relation of proximity of water to cutting at the 3 colonies. The results are shown in Figure 5. As would be expected, there is a trend for heaviest cutting to occur close to shore. A similar trend was noted by MacDonald (1956) in Colorado. It is also evident that the beaver will extend their operations farther from shore where the supply is much depleted, as at the Rockslide, than in a situation where aspen is abundant.

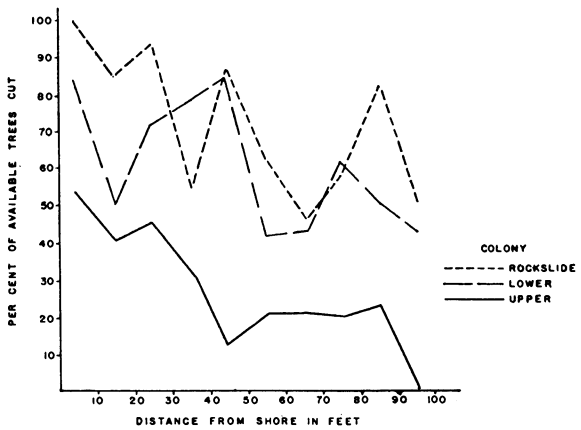

FIG. 5. Relationship between distance from shore and aspen use.

Seasonal cutting of aspen

Figures 6 and 7, based upon total counts, present distribution of aspen use at Upper and Lower colonies by year and by season.

The most striking feature of Fig. 6, in which rate of use is expressed as trees cut per day, is the high rate of cutting at the Lower colony compared to that at the Upper colony. This disparity is explained partly by the larger number of beaver at the Lower colony, but also it reflects the fact that beaver there felled a large number of relatively small trees whereas at the Upper colony fewer trees of larger average diameter were felled.

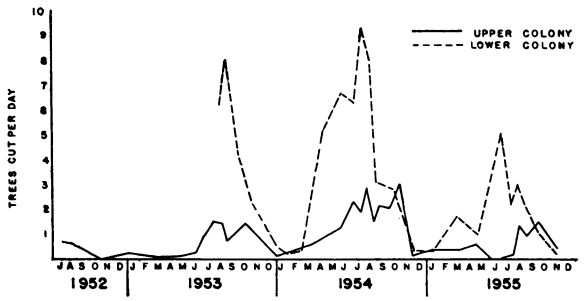

FIG. 6. Aspen use: trees cut per day.

To obtain a truer picture of the amounts of potential food handled at the 2 colonies it was necessary to compensate for the differences in average diameter of aspen felled. The conversion from trees cut per day to weight of bark and twigs cut per day is shown in Fig. 7.

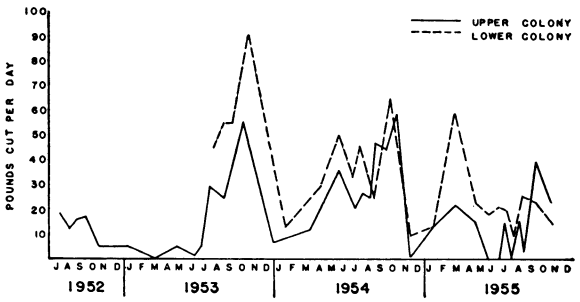

FIG. 7. Aspen use: bark and twig weight cut per day.

From this figure it is evident that the beaver at the Upper and Lower colonies are utilizing the aspen resource in nearly synchronous fashion. The major peak of activity in both areas occurs in late fall, and the time of minimum cutting is in mid-winter. These phenomena are timed by major seasonal changes in the weather. But within the periods of most active cutting the beaver appear to work in minor fits and starts which often are closely synchronized between colonies. I was unable to correlate these minor activity rhythms with changes in temperature or precipitation.

The period of most intensive cutting characteristically occurs in October when the food-pile is being built and dams and lodges are under repair. This trend is reflected in the major peaks referred to above and is in accord with the observations of most naturalists. An exception was found at the Lower colony in 1955 when most aspen was cut in March. There is no obvious explanation for this exception but it is noteworthy

that the beaver at the Upper colony also engaged in considerable cutting at this time.

The statement that mid-summer is the period of minimum cutting is frequently encountered. With one exception this situation did not hold true for the Sagehen colonies. Here the beaver usually fell a large portion of the season's quota during the summer. They cut least from December to March. The exception occurred at the Upper colony in the 1955 season when beaver felled no aspen whatsoever during the month of June. The fact that no kits were produced in this colony in 1955, due to the accidental death of the breeding female the previous season, may have been significant. These circumstances suggest that feeding of the kits may have a bearing on the mid-summer cutting of aspen.

Rates of use per beaver-day

As is evident in Fig. 7, the total quantity of bark and twigs from trees felled by beavers of the Lower colony exceeded that of the Upper colony both in 1954 and 1955. The actual ratio for both years was about 1.5 to 1. When account is taken of the number of beaver in each colony, on the other hand, it is apparent that the most aspen use on a beaver-day basis occurred at the Upper colony. A comparison of the three colonies for the years 1954 and 1955 is shown in Table II.

TABLE II. Pounds of aspen bark* cut per beaver day

Colony	1954	1955
Upper	6.2	5.4
Rockslide	0.65	0.03
Lower	3.7	2.1

* Computed by use of Aldous' (1938) conversion factors.

The most important point to be made regarding these figures is the relationship between availability and utilization; the quantity cut per beaver-day was greatest at the Upper colony where availability was greatest and least at the Rockslide colony where availability was least. This is shown graphically in Figure 8.

In using the word "utilization" it should be emphasized that beaver seldom eat all the bark from felled aspen. The unused amount varies with the size of the tree and depends also upon where it falls. Although the exact amount wasted was not determined for the Sagehen colonies, it was noted that beaver usually completely stripped bark only from branches or trunks up to 3 inches in diameter. If a large aspen happened to fall very near the water, however, almost all the bark was removed. Gese and Shadle (1943) stated that

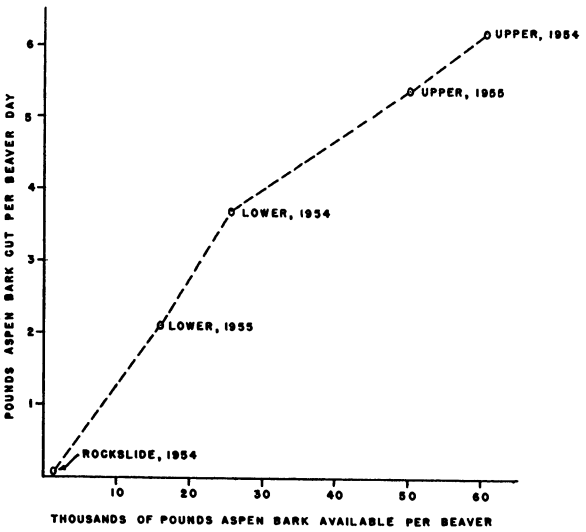

FIG. 8. Relationship between use and supply of aspen.

the bark of larger limbs is avoided by beaver because it tends to become corky.

MacDonald (1956) found that the average amount of bark used was 87% of that cut. Bailey (1927) estimated use as 50% and Aldous (1938) calculated the average use to be 36%. A figure of approximately 50% might be considered a compromise. Thus of 6.2 pounds of aspen bark cut per beaver-day at the Upper colony in 1954, 3.1 pounds is the estimated consumption. Stegeman (1954) listed 4.5 pounds per day as an average ration, derived from the work of several investigators who kept beaver in captivity. The estimate of about 3 pounds per day, which represents the closest approach to a pure aspen diet attained on this study area, compares favorably with Stegeman's estimate in view of the fact that other foods are always taken to some degree by beavers in the wild.

Size preference

The observation that beaver waste relatively more bark of large trees than small ones leads naturally to the question of preference. Do beaver tend to select aspen of one size class more frequently than others or is the pattern of cutting dictated primarily by relative availability of trees present? An analysis of preference in the field is not simple. Many factors such as local topography, distance from lodge or bank burrow, visibility or natural obstructions in addition to simple numerical abundance undoubtedly interact to influence a beaver's choice of which tree to cut. Since isolation of all the contributing factors is almost imposible in the field, I considered only the most obvious one, numerical availability.

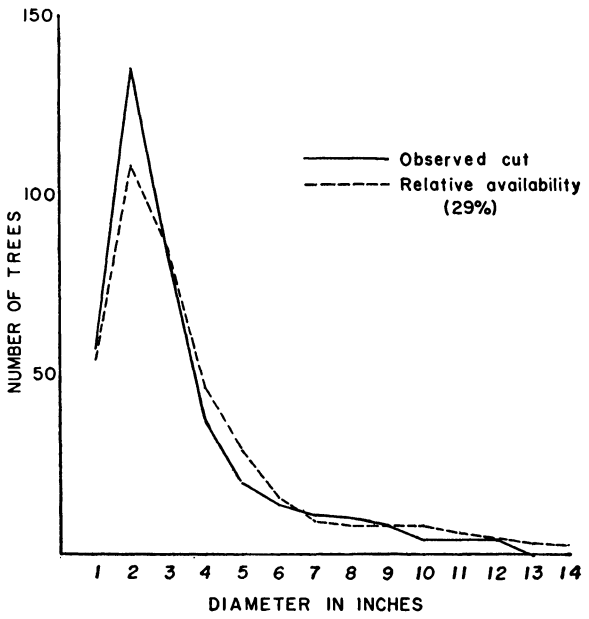

FIG. 9. Relationship of relative abundance of aspen of various diameters to number of trees cut.

Figure 9 summarizes the analysis made at the Upper colony. This graph is drawn from a complete count made in July of 1952. On this count every tree, cut or standing, within the area of use was tabulated. Area of use for this count was arbitrarily defined as the area extending from the water's edge to the most distant trees felled. The relative availability curve on this graph is a reflection of absolute abundance of the various diameter classes before the arrival of beavers.

It will be seen that use of 2-inch trees shows the greatest departure from the availability curve. More than 1300 trees were measured during the count and this departure, though small, proves to be significant at the 0.01 level when subjected to the Chi-Square test for homogeneity. The results of analyses of preference at the Upper and Lower colonies made by means of the spoke samples are similar but, being based on much smaller numbers of trees, are not significant at the 0.01 level.

Preference for trees of this size was indicated by Aldous (1938) and Hodgdon and Hunt (1953), although availability was not specifically documented by them. MacDonald (1956) concluded from his detailed study in Colorado that trees in the 1-3 inch category were preferred.

An attempt to explain this preference poses some interesting problems. The superiority of any size class could either be based primarily on its value as food or as building material. Since this preference for 2 inch trees appears to show a correlation with the amount of building going on at a colony, the latter alternative is favored. It was more marked at the Lower colony which was in a state of rapid expansion during the period of study than it was at the more stable Upper colony. Furthermore, as building declined during the period of study at the Upper colony, the differential preference for small trees also diminished. MacDonald (1956) noticed a similar situation in his most actively expanding colony, where cutting of 1-3 inch trees was very high.

Impact of beaver on aspen

Aspen cannot be regarded as a "renewable resource" within the probable life of any single beaver colony. The aspen steadily declines under pressure of beaver use, even in a situation where the supply is optimum.

The greater the supply of aspen at a colony, the more intense is the effort of the beavers to make use of it. Consequently, the amount of available aspen may be used as an index to the rate of consumption per beaver although it is not necessarily an index to the rate of depletion of the colony's supply.

Furthermore, the size composition of the stand is relatively unimportant since size-preference, though demonstrable, is very slight.

Hence, what might be described as the "aspen-consumption phase" in the life of a beaver colony is a youthful and transitory stage since aspen and beaver, in any combination, inevitably leads to relatively complete loss of aspen. Gradually the colony passes on to one of several more mature phases.

WILLOW

Willow is the 2nd woody staple of beaver diet, and it can sustain the animals in the absence of aspen. The Rockslide colony, for example, subsisted almost entirely on willow during the study period and a new colony became established early in 1954 near the mouth of Sagehen Creek far from any aspen. Since the Upper, Rockslide and Lower colonies differed so markedly in respect to willow supply, it became clear that a comparison of its use should be made to supplement the study of aspen use started first.

METHODS

Sampling of willow was begun in 1954 and continued more intensively in 1955. Transverse plots measuring 100 by 10 feet were marked out across each colony, usually at 125 foot intervals (Fig. 2). The plots were subdivided into 10 sections, each 10 x 10 feet. A willow clump having more than

half of its base within the boundary of the plot was considered "in" and its projected area was sketched on a diagram of the plot. These sketches were useful in measuring the proportion of each plot covered by willow. In the Lower colony the plots were in some cases much farther apart than 125 feet. Consequently, the coverage there was estimated to be about 3% in contrast to the 8% coverage at the other 2 colonies.

After fixing the boundaries of a plot, all cut stems ⅛ inch or more in diameter were painted red and on succeeding visits the newly cut stems were tallied and painted. In estimating use from these tallies it was necessary to compensate for variations in the amount of branching. Measurements on a lightly used area showed that, on the average, a vigorous willow stem cut at the usual beaver height of 12 to 18 inches above the ground had 3 branches. Where browsing had been heavy, on the other hand, most of the older, branched stems had already been cut and the beaver were relying on the unbranched shoots which appear annually after browsing.

Consequently a "branching factor" of 3 was applied to the tabulation of use at the Upper and Lower colonies as well as to the stands of vigorous willow on the lower end of the Rockslide colony. On the heavily-used sections of the Rockslide colony no corrective factor was necessary since the willow shoots were largely unbranched.

Availability and use of willow

Table III presents comparative measures of availability and use of willow in the 3 colonies for the period July-October, 1955. According to these figures the Upper colony had the least willow, the Rockslide colony an intermediate amount and the Lower colony the most. Percentage use was high at the Upper and Rockslide colonies and low at the Lower colony. If use is computed on a per beaver-day basis to compensate for the effects of different population size, the rate of consumption at the Rockslide colony is high, that at the Upper and Lower colony is low. There certainly is no obvious relationship between supply of willow and rate of use. Both the crude and more precise measures of use demonstrate that consumption was highest at the Rockslide colony where the supply was intermediate.

It should be pointed out that the high figure for the Rockslide colony is partly explained by extraordinary dam-building activity there. During the 1955 season these beaver were attempting to maintain a dam across the Hobart Mills water intake. Each time the dam was removed it was rebuilt by the beaver. However, when a reasonable allowance is made for the extra willow cut exclusively for construction, the trend for heaviest consumption per beaver-day at this colony is unchanged.

TABLE III. Supply and use of willow, by colony

	Colony		
	Upper	Rockslide	Lower
pounds bark available in July	570	2,040	11,580
pounds bark cut July-October	229	906	992
% cut	40	44	9
pounds bark cut per beaver-day	0.67	1.54	0.76

Role of aspen supply

Since Table III indicates that willow use is not obviously dependent upon the supply, there must be other controlling factors. One good possibility would be the amount of aspen cut in the various colonies. The amount of aspen cut per beaver-day during this same period was 6.7 pounds at the Upper colony, 0.1 pound at the Rockslide colony and 1.9 pounds at the Lower colony. A comparison of these figures with those for willow use is shown in Figure 10 and suggests an inverse relationship between consumption of aspen and willow. The data indicate that where most aspen is cut, as at the Upper colony, least willow is cut and where aspen consumption is least, as at the Rockslide colony, willow is most heavily used. Since the amount of aspen cut in turn depends upon the aspen supply (Fig. 8), we may go one step farther and say that use of willow is also inversely related to the supply of aspen. This is equivalent to saying that the supply of aspen controls in some measure the consumption of both aspen and willow.

The easiest way to interpret this relationship in terms of the beaver is to assume that they concentrate on the aspen, relying increasingly on willow as the supply of aspen diminishes.

Facets of the availability concept

The fact that aspen is the preferred food raises another question. If, as has been shown by Aldous (1938) and Bradt (1938), beaver may be kept for months on an exclusive diet of aspen, why do the beaver at the Upper colony where the aspen is very abundant bother to consume any willow? The explanation may lie in the intricate interac-

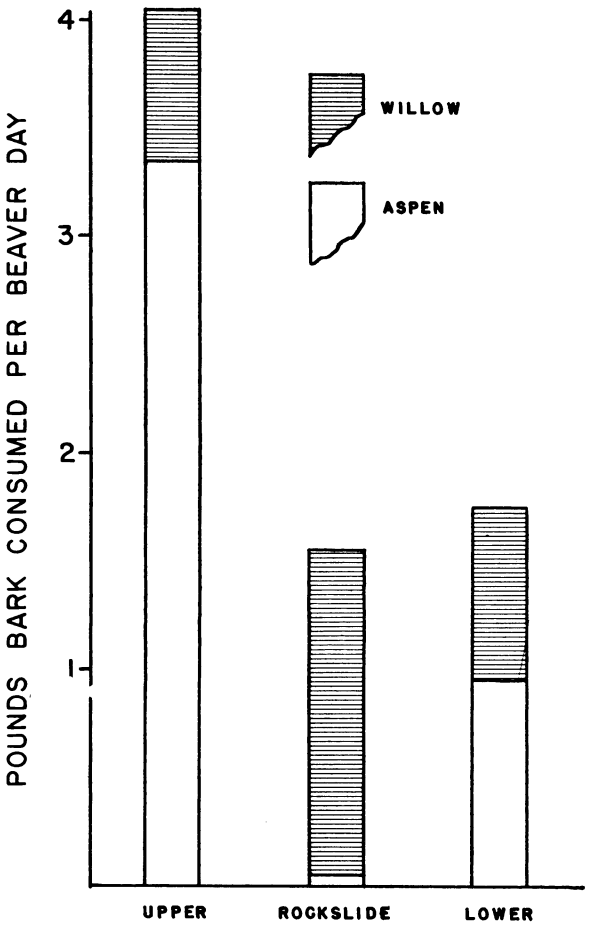

FIG. 10. Use of willow and aspen on the 3 colonies studied, July-October, 1955. Use of aspen estimated to be 50% of the cut.

tion of factors which, together, add up to availability. Factors such as absolute numbers of trees, distance from shore, topography, type of soil and presence and distribution of alternate forage have already been mentioned. Others probably contribute. The one which may explain the consumption of a substantial amount of willow even where aspen is abundant is a temporal factor. Not once during the 4 summers of observation was a beaver actually seen to fell an aspen. This activity was restricted to some time well after dark, when observation was not possible.

It was noted that the usual routine of a beaver upon emerging from the lodge in the early evening was to take a few turns around the pond in a tour of inspection and then to start feeding on willow. The beaver are undoubtedly hungry after a long day of confinement, but do not feel at ease about going ashore to fell or trim aspen until it is completely dark. During this period, therefore, aspen appears to be relatively much less available than willow. The latter may almost always be cut by an animal in the water or a foot or two from shore. That twilight behavior was the same in all colonies, regardless of aspen supply, probably is an important factor in explaining why a certain amount of willow is cut even where it might not appear to be necessary.

Year-to-year effects of beaver activity

It is evident from Table III that there is a downward trend in willow availability at all 3 colonies during the July-October period. But to evaluate the total effect of beaver one should consider a year-long record in which such factors as sprouting and die-back are also taken into account.

Die-back of willow occurred in all colonies observed and was also seen in willow untouched by beaver. Most of the die-back is thought to take place during the winter and it is encouraged by over-browsing. Actual removal of sprouts by the beaver and the additional loss by die-back constitute the "loss factors" affecting availability. Sprouting during late May and early June is the major "gain factor."

The amount of willow available fluctuates from year to year and within the seasons of every year, increasing when the gain factors outweigh the loss factors and decreasing when the loss factors predominate.

Figure 11 shows details of availability trends in willow on one of the intensive samples at the Rockslide and one at the Upper colony during a single year. Both graphs in this figure are similar in indicating that the willow supply in October, 1955, was below the October, 1954, level. Beaver use had been too heavy for a sustained yield on either area.

In other respects the 2 sample areas represent opposite situations and deserve some comment. The graph for the Upper colony sample indicates that the sprouting was almost sufficient to compensate for the extensive losses due to beaver work and die-back combined. Thus, only a small net loss resulted for the year. This situation is summarized by the columns on the right side of the graph.

At the Rockslide colony, however, it is clear that a heavy net loss occurred although beaver work was rather light. Die-back alone exceeded sprouting and this loss added to the loss due to beaver cutting produced the marked drop seen in the figure.

A vigorous stand can tolerate a rather large harvest by beaver, at least for one or 2 seasons, but willow which has been consistently over-

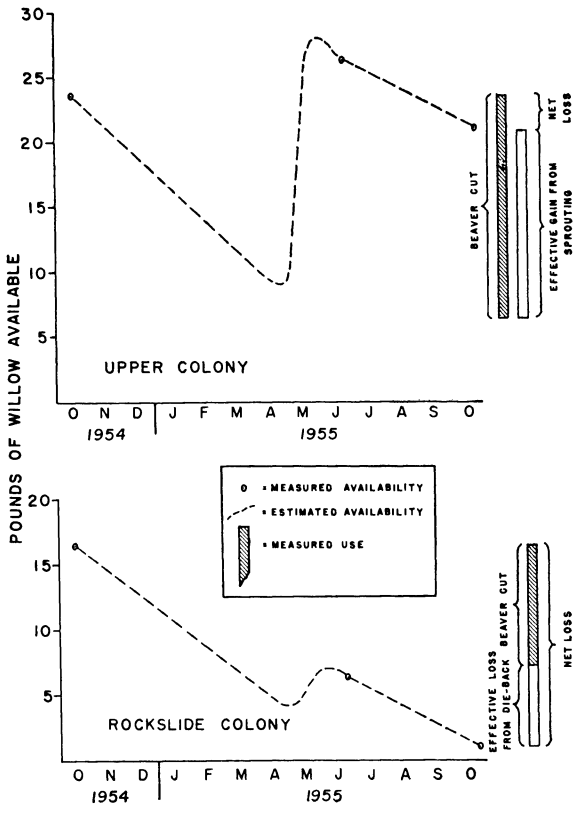

FIG. 11. Trends in willow supply and use on 2 intensive samples.

browsed, as at the Rockslide colony, will decline under a much smaller harvest. The decline in sprouting vigor following overbrowsing is the most significant relationship reflected in Fig. 11.

Although no intensive samples were run on the Lower colony, it seems almost certain that, in contrast to the other 2 colonies, willow was being cut on a sustained yield basis. One index of the condition of a willow stand is the average stem length. Not only was the average stem length greater than at either of the other colonies but, equally important, the July-October harvest, shown in Table III, was much lighter.

In attempting to estimate how much willow can be safely harvested by beaver, it seems clear that vigor of the stand is more important than total supply. MacDonald (1956) recognized this in estimating a safe harvest in terms of the current year's growth, another index of vigor. His suggestion of 20% of the current year's growth as a safe margin seems conservative to me but our data are not directly comparable.

Any estimate of a safe harvest of willow for a particular colony tends to imply that beaver colonies are fixed in location and that they are dependent upon a specific block of willow plants for their sustenance. On Sagehen Creek, where the distribution of willow extends for most of the length of the stream, this certainly is not true. In this type of habitat the beaver will gradually shift the site of their operations up or down stream as willow in the original colony area is overbrowsed. This was seen in a downstream shift of the Rockslide colony in 1954 and 1955. Overbrowsed sites, subsequently abandoned, will soon reproduce a healthy regrowth of willow, as Adams (1954) has noted. Of 29 deserted colonies examined by Haas (1943), only 4 were abandoned because of overuse of willow. The sprouting capacity of this durable plant makes it a mainstay of beaver economy, and even severe abuse will discourage it only temporarily. Seemingly, beaver can thrive indefinitely on willow by a form of "block cutting," or shifting their foraging periodically up and down the stream allowing overbrowsed sections time to recover.

SUMMARY

Two pairs of beaver were introduced on Sagehen Creek in 1945. Ten years later the number had increased to about 30 animals distributed in 5 colonies along the stream. Three of the colonies were studied for several seasons in order to explore the interaction between beaver and their 2 chief food-and-building resources, willow and aspen.

The rate at which beaver cut aspen was found to be correlated directly with the supply. On the other hand, rate of willow use showed no correlation with willow supply but was related inversely to aspen supply. These relationships are interpreted to mean that aspen is the first choice item; as it is used up the beaver take more and more willow.

According to an analysis at the colony where aspen was most abundant, the principal factor influencing a beaver's choice of size of tree to cut is the relative numerical availability of the sizes in the stand. A slight but significant preference for trees of the 2-inch diameter class was demonstrated. This preference is thought to be due primarily to superiority of 2-inch trees as a building material rather than as a food source.

The exceptional sprouting vigor of willow makes it much more tolerant of the inroads of beaver activities than is aspen. Even so, beaver have a tendency to overbrowse within the immediate colony area. The result is that sprouting vigor gradually declines and rate of growth falls behind rate of harvest.

Use of aspen never is on a sustained yield basis.

When beaver have consumed the aspen in one locality it is gone. Willow resprouts much more successfully than aspen, but the beaver still tend to eat it more rapidly than it grows. However, as one site becomes exhausted of willow, the beavers shift gradually up or downstream to better stands, thus permitting the original area to recuperate. Consequently, in terms of the entire stream, the willow is on a sustained use basis in a manner analogous to block-cutting as practiced by foresters. Whether it will remain so as the population continues to increase and expand into all habitable areas of Sagehen Creek cannot be foreseen.

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A MECHANICAL MODEL FOR THE STUDY OF POPULATION DYNAMICS

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INTRODUCTION

The machine described in this report was constructed at a time when analog computers were becoming fashionable. I had hoped to use it in a study of the complex changes in population structure that accompany changes in the reproductive rates and mortality rates of different age classes of populations of small mammals. It soon became apparent that the machine was capable of "solving" various kinds of problems put to it, but that preparation and calibration of the machine for each problem was too time-consuming to make