THE ECOLOGY OF THE BEAVER ON THE SNAKE RIVER FLOODPLAIN IN GRAND TETON NATIONAL PARK, WYOMING

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Project Number 200

This is a report on some of the initial investigations of beaver ecology carried out in Grand Teton National Park from May to October of 1974. It will describe methods and present data of immediate interest but will not attempt to detail information that will have significance only after the completion of the study and final data analysis. A sketch of the latter will be given in terms of methods and work completed. A minimum of two additional years is required to complete this study.

This study has been supported by the Yellowstone Environmental Study Center and the New York Zoological Society. I wish to acknowledge the valuable assistance and cooperation of personnel of Grand Teton National Park and the Wyoming Game and Fish Department, Dr. Oscar H. Paris, Director of the Jackson Hole Biological Research Station, and Dr. Jack C. Turner of the University of Wyoming, Department of Zoology and Physiology, my Ph.D. adviser. This study was based from the Jackson Hole Biological Research Station at Moran, Wyoming.

Introduction

Grand Teton National Park offers a unique situation for study of beavers because of the protection of both beaver and habitat in the park. An understanding of the ecology of the beaver in the park will insure this protection. Little has been known of the abundance and distribution of beavers in Jackson Hole. This study is investigating such ecological parameters as would be necessary for facilitation of naturalist programs and minimal management for the benefit of the beaver and the general public. In addition, this study is investigating the ecology of the species as it relates to the protected and undisturbed conditions.

Specific Objectives

A. The enumeration and evaluation of the abundance, distribution, home range, and dispersal patterns of the park's beaver population.

B. The determination of beaver habitat requirements, habitat utilization, and habitat modification with reference to cyclic activity and interrelationships with other wildlife.

C. The evaluation of beaver behavior patterns, particularly in relation to park use by humans.

Population Dynamics

Methods

Beaver were captured for marking with the Hancock live trap, a folding, suitcase-like aluminum trap weighing about 30 pounds. The traps are bulky and difficult to carry. The Avon raft used in this study could carry a maximum of three traps. As a result, it took from two to three days to move traps to the trapping site that was accessible only by raft. The traps were not received until the second week of June by which time much of the prime trapping time had passed. Beaver should be most trappable in a live trap when they are responding to the scent of another beaver, that time being May and June when kits are born and two year olds are forced from the colonies. The criteria for judging a site as active and a potential site for trapping were actual observations of beaver at the site, presence of scat, recent cuttings, or recent work on the lodge, den, or dam, if present.

The Hancock trap is set on a bank with one side submerged. Pieces of aspen eight to ten inches long were tied to the back side of the exposed portion of the trap. The bark on one side of the aspen was peeled off so that the odor of the aspen would be evident to the beaver. Aspen proved to be the best bait for live trapping as no success was obtained using cut alder, willows, or cottonwood. Two summer windstorms in the Park downed numerous aspen from which branches could be cut for bait. A drop or two of beaver castor was then placed on the aspen to further attract the beavers. Traps were placed wherever beaver activity was evident such as at a food canal, a scent mound, or a favorite foraging area. The trap was secured to the bank with a metal stake. Traps were occasionally camouflaged with grass but this did not improve success. All traps were kept clean and were occasionally washed to remove human scent.

Traps were checked for beaver at least three times through the night necessitating camping nearby. Traps were usually set by one hour before dark and were removed after sunrise. Traps were checked at 10 PM, 2 AM, and 5:30 AM except during July at high water when they were checked more often due to the rise in the river between 8 PM and 2 AM.

On capturing a beaver, data was immediately recorded on their behavior in the trap. The trap was removed from the bank and both the trap and beaver were weighed with a hanging scale. The trap was weighed after release of the beaver. Climatic conditions were recorded and the beaver was tagged on the ear with a monel number four self-piercing tag. Males were tagged on the opposite ear than the female for later identification. The beaver was then sexed by palpation for the testes. There is no external means of distinguishing sex. Occasionally, it was necessary to remove the beaver from the trap into a burlap sack for the sexing procedure. Reproductive condition was noted for the females. The beaver was checked for other distinguishing marks or injuries as well as parasites. Tail dimensions

were measured but total body length was impractical to measure. On several occasions beaver left fecal samples in the trap. These were collected and preserved for later food habits analysis. Finally, notes were taken on the beaver's behavior in the trap on handling and after release.

The classification of beavers as kits, yearlings, or adults was largely by body weight but exact aging of live beavers is not possible by any known methods. Part of the preliminary work for this study was carried out in the winter of 1973-74 when data from over 100 steel trapped beavers were obtained. The beavers were brought into the McConnell Brothers Fur Company of Laramie, Wyoming, by state trappers and the company agreed to allow me to work with the carcasses before and after pelting. Unpelted beavers were weighed and body measurements were taken. A pattern of marking the front incisors was developed so that the pelted carcasses could be identified with measurements taken from the same beavers before pelting. After pelting, the skulls and reproductive tracts were removed and returned to the laboratory. The premolar and molar teeth were removed from the mandible, decalcified, and the cementum layers counted. The first cementum layer is deposited at two and a half years (Van Nostrand and Stephenson, 1964). Body parameters other than weight did not correlate well with age. Weight correlated with age for about the first four years. Since kits are less than one year old, yearlings less than two years old, and adults greater than two years, the classification of beavers by weight into these broad categories is easily accomplished. Unless demographic techniques are used for population analysis, these categories should suffice for the evaluation of population dynamics. Attempts to discover a more exact method of aging will continue.

The size of the colony territory was determined for the linear distance on the river by the presence of scent mounds. Scent mounds may be located anywhere within the territory but are also located at territorial boundaries (Aleksiuk, 1968). The beaver territory away from the water's edge was subjectively determined either by locating natural boundaries such as steep slopes, changes in vegetation, etc. or the cuttings furthest from the water.

Trapping Data

A total of 16 different colonies were trapped over the first summer of this investigation resulting in a total catch of 30 beaver ranging from a catch of from five to zero per colony. Three colonies were trapped on two different occasions resulting in a total of 19 sets. Had trapping been carried out early in the summer before high water the success would likely have been much greater. In the second year of this study most trapping will be done between mid-May and mid-June.

The greatest number of beaver captured was in the 2 AM trap check (53%), followed by the 10 PM check (33%), and the 5:30 AM check (14%). The most beavers trapped was in June when 20 beavers were caught in 27 traps set. July was a difficult time to trap due to high water and the apparent lessened response to scent and trap success was six beavers in 43 traps set.

In August, no beaver were trapped in the eight traps set. In September, three were trapped from the 12 traps set and in October, three beavers were caught out of only four traps set. Between June and October a total of 94 traps were set; the trap success, therefore, was quite high (32%). The major limiting factor in numbers success is therefore the number of traps that can be set. The difficulty in moving the traps has been mentioned. There was no apparent relationship between trap success and climatic conditions at the time of trapping.

Of the three colonies trapped a second time, no catch was made at the colony from which beaver had been caught previously but success was obtained for two colonies that were retrapped from which no beaver had been previously caught. The type of trap used in this study is one that gives good success for beavers that are not trap shy. However, once a beaver is caught in the Hancock trap the chances of recapturing this same beaver at another time in the Hancock trap are negligible according to Grasse and Putnam (1950). Since recaptures are needed to determine the dynamics of the beaver population in the park, it will be necessary to supplement the Hancock trap with another type of trap in the second year of this study. This trap would be the Bailey live trap which is set entirely under water. Success with this trap, therefore, would be unrelated to the previous experience of the beaver.

Twenty-six of the 30 beavers trapped were tagged on the ear with tags numbered in sequence with the beavers as they were caught beginning with number one. Only partial data was obtained on three beavers that escaped during the handling process. No beaver was injured by the trap although a two year old caught in early June had a deep, healing wound that could have been a bite from another beaver. This beaver was caught at a time when the two year olds are being forced from the lodge and the wound may have been related to this. All of the six adult females caught in June and July were lactating. At this time, sexing of adults was simplified by the prominent nipples of the lactating female. Nipples should become prominent just before birth of the kits and remain so until the kits are weaned, probably about mid-July. All of the adult females examined appeared to be on a similar time schedule in terms of when kits were born and weaned although considerable variation is known to occur in some populations (Grasse and Putnam, 1950).

Table I is a summary of weight and tail dimensions for different sexes and age classes of beavers trapped in 1974. There is a preponderance of males to females (18/12) but this is likely due to the behavioral differences between sexes during the time when the young are being weaned, (see section on behavior). There is also a preponderance of adults in the sample which might be expected since they should be more responsive to the scent used because of their territorial habits. There are few kits but they did not appear until mid-July; two of the three kits were caught in October. The significance of the patterns of the data in Table I cannot effectively be evaluated until a larger sample is obtained.

Table I. Summary of weight and tail dimensions by sex and age group for beavers trapped in 1974. Numbers in parenthesis are metric equivalents.

Sex and Age Class	Number	Mean Weight, lbs (kg)	Weight Range	Mean Tail Length, inches (cm)	Tail Length, Range	Mean Tail Width, inches (cm)	Tail Width, Range
Adult Male	10	54 (119)	47-58	11.4 (29)	8.5-13.5	5.8 (14.7)	4.5-7
Adult Female	6	49 (108)	31.5-58	10.5 (26.7)	8-12.5	5.6 (14.2)	4.5-6.5
Two Year Olds, Males	7	41 (90)	34-46	10.1 (25.7)	9-10.8	4.8 (12.2)	4.3-5.5
Two Year Olds, Females	3	36 (79)	34-38	9.5 (24)	9-9.8	4.6 (11.7)	4.5-4.8
One Year Old, Male	0	-	-	-	-	-	-
One Year Old, Female	1	25 (55)	-	8.3 (21)	-	3.5 (8.9)	-
Kits, Male	1	18 (40)	-	9 (22.8)	-	3.8 (9.7)	-
Kits, Female	2	11.5 (25)	9-14	7.6 (19.3)	6-9.2	3 (7.6)	2.2-2.8

Visible ecto-parasites were not evident on beavers but in one instance, two large leeches (Hirudinea) were found attached to the abdomen of a beaver trapped in the oxbow at colony six. The leeches may have attached after the beaver was caught in the trap. Other ecto-parasites could have easily been mixed in the thick underfur since it was impossible to check the entire beaver. No attempt was made to distinguish internal parasites.

Beaver Population of the Study Area

In the summer of 1974, 22 of the first 27 miles of study area were carefully examined for beaver activity. The study area includes the major tributaries to the river between Jackson Lake Dam and Moose, Wyoming, or a total of at least 175 miles of stream and channels. This project will eventually encompass the entire Park, and, in addition, will include an area outside the Park for comparative purposes.

Between Jackson Lake Dam and Lower Schwabacher Landing a total of 33 beaver colonies were located on the river or its tributaries. This is a low figure since some channels have not as yet been examined. Also, it is very difficult to locate bank dwelling colonies since the bank dens are usually not evident from the river but rather require walking the banks of the study area in search of plunge holes which are good evidence of dens. Several active dens were located by walking the banks of the river channels and they would not have been discovered from a raft. The Grasse and Putnam (1950) study in Wyoming as well as most other studies of population densities of beaver have found that the number of beavers/colony are five on the average. Using this figure, the 33 colonies located should represent approximately 165 beavers. It should be stressed, however, that this figure is likely inaccurate and further work will verify the total number of colonies in the study area. Additionally, the average number of beavers per colony in the Park population will eventually be estimated from the data obtained in this study.

Figures 1-8 are maps of the study area showing the location of beaver colonies. In the maps, colonies are numbered and active lodges are filled-in triangles while active dens are filled-in circles. Abandoned lodges and dens are open triangles and circles. Note that many colonies have more than one lodge and/or den. The largest territory was that of colony three which extended for over a mile on the river. In the upper section of the study area, territories were packed one against the other as evidenced by scent mounds, leaving no space for establishment of new territories in this section. This "packing phenomenon" is more difficult to interpret in sections where there are multiple channels to the river.

The typical beaver colony in the Park appears to have one adult male and one adult female, one or more yearlings, and one or more kits and occupies a territory of possibly one half mile on the river. Assuming a reproductive rate of three kits per female per year and an average colony size of five, the 33 colonies discovered thus far would produce 99 beaver per year.

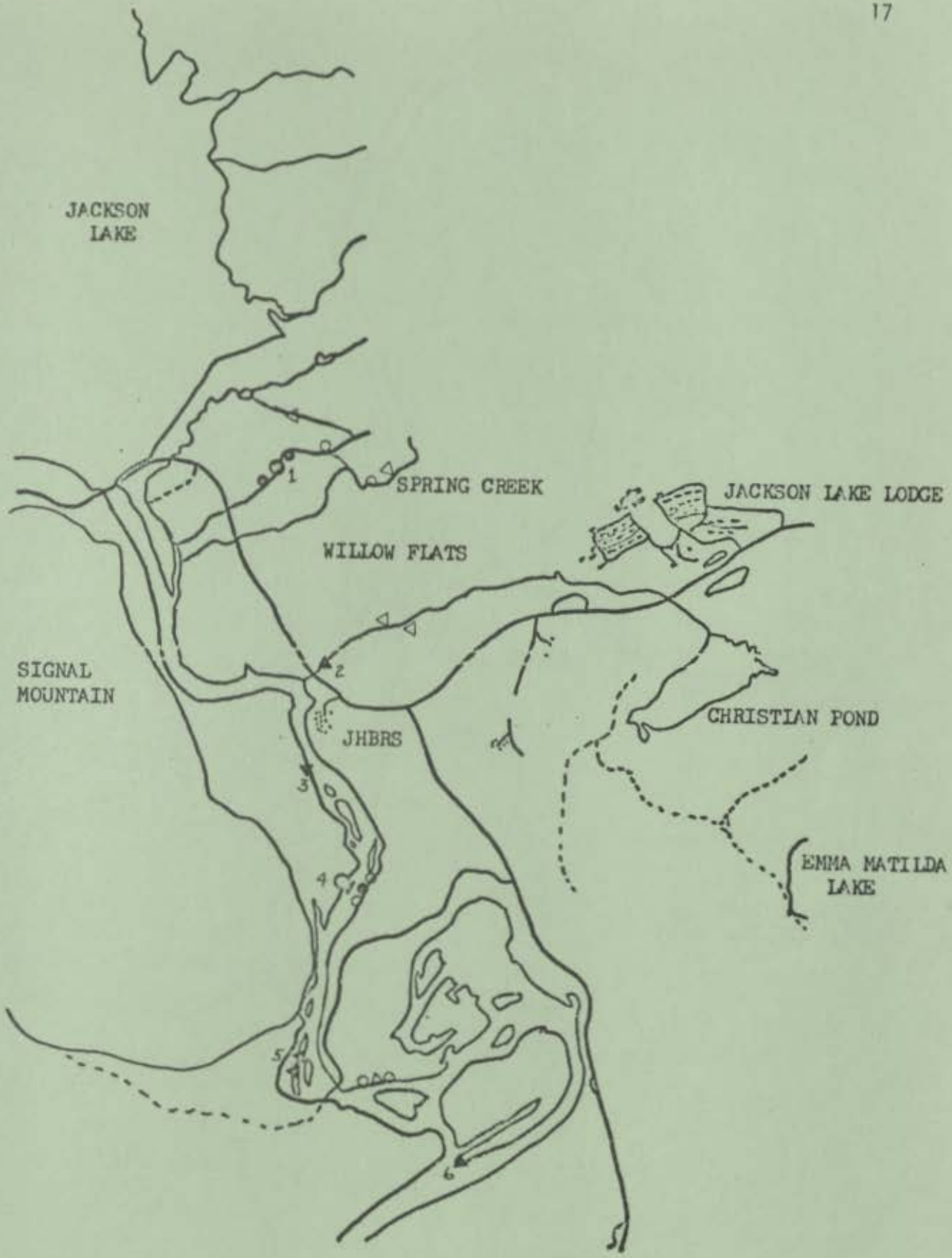


Figure 1. JACKSON LAKE DAM TO OXBOW BEND.
TOTAL RIVER MILES THREE.

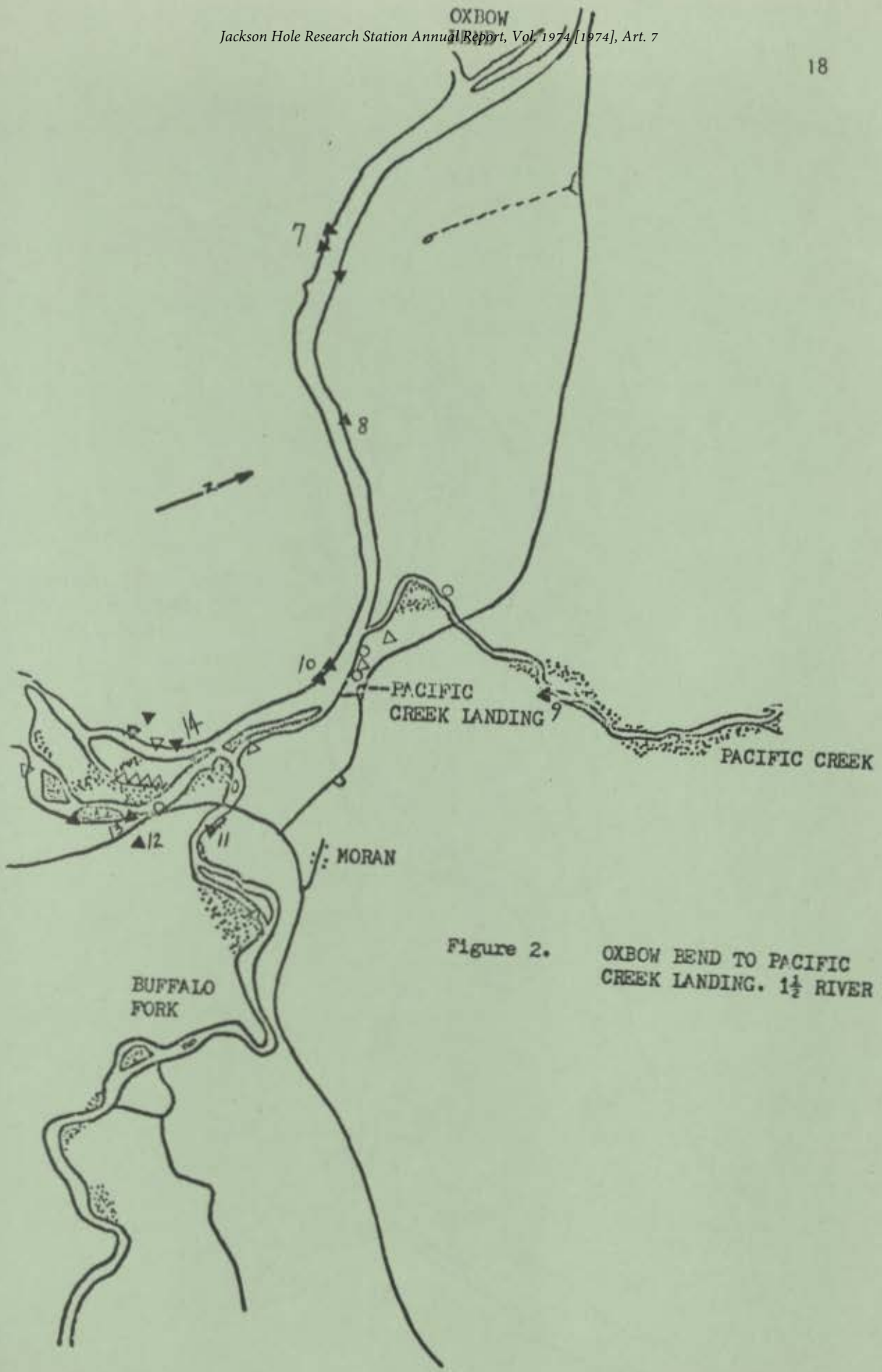
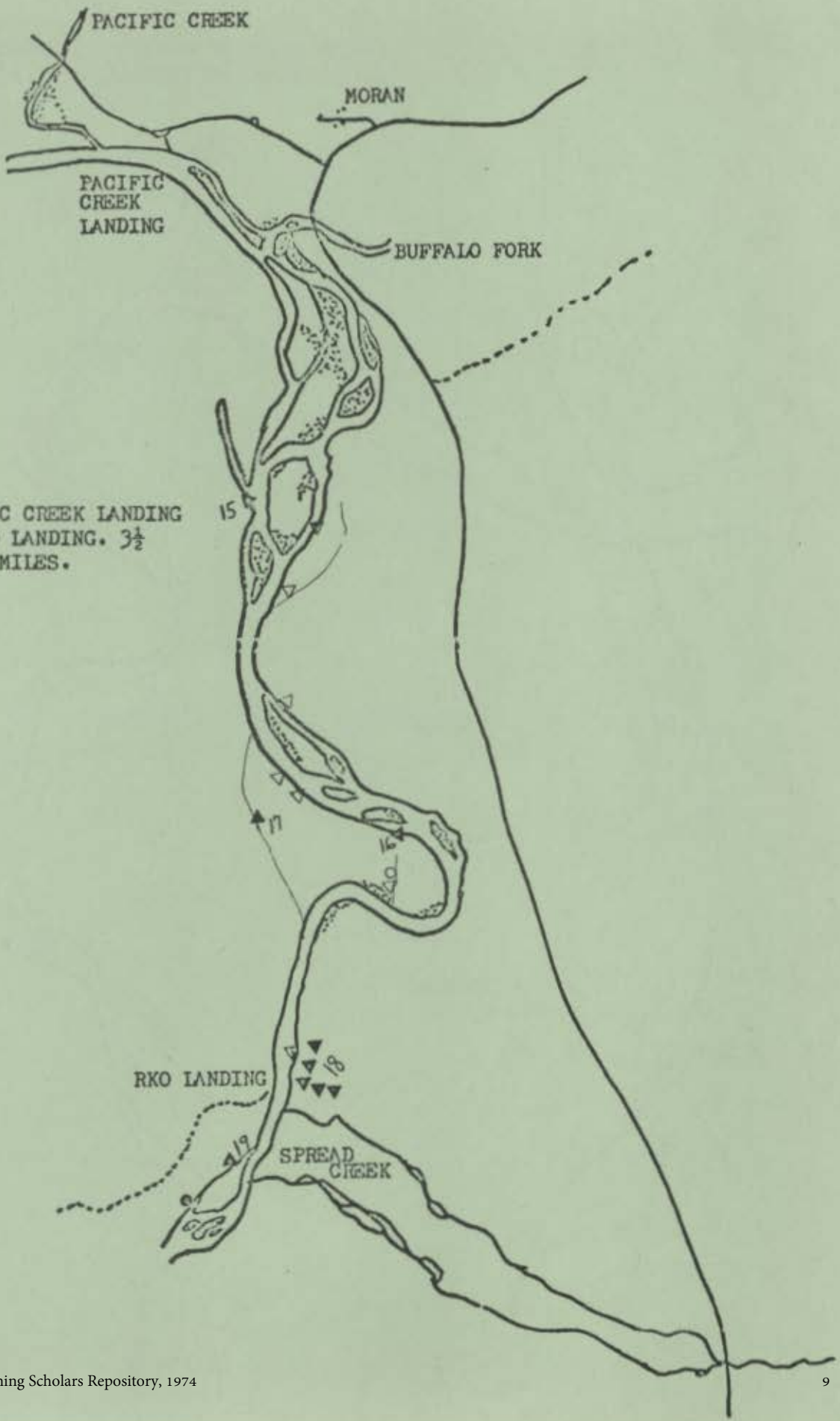
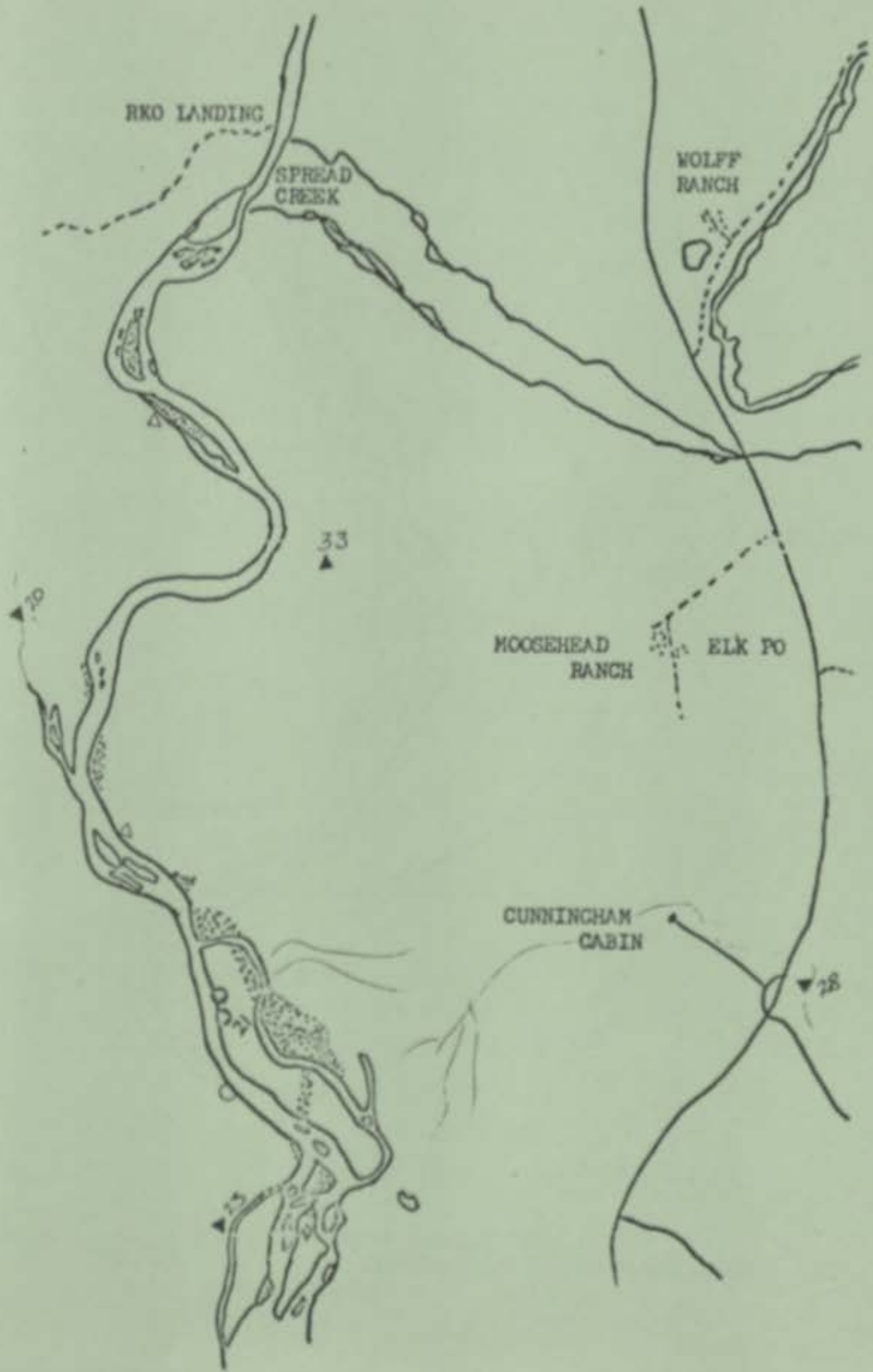


Figure 2. OXBOW BEND TO PACIFIC CREEK LANDING. 1½ RIVER MILES



3, PACIFIC CREEK LANDING TO RKO LANDING. 3½ RIVER MILES.

Fig. 4. RKO LANDING TO DEADMANS BAR LANDING.
PART A. RKO LANDING TO COLONY 23.



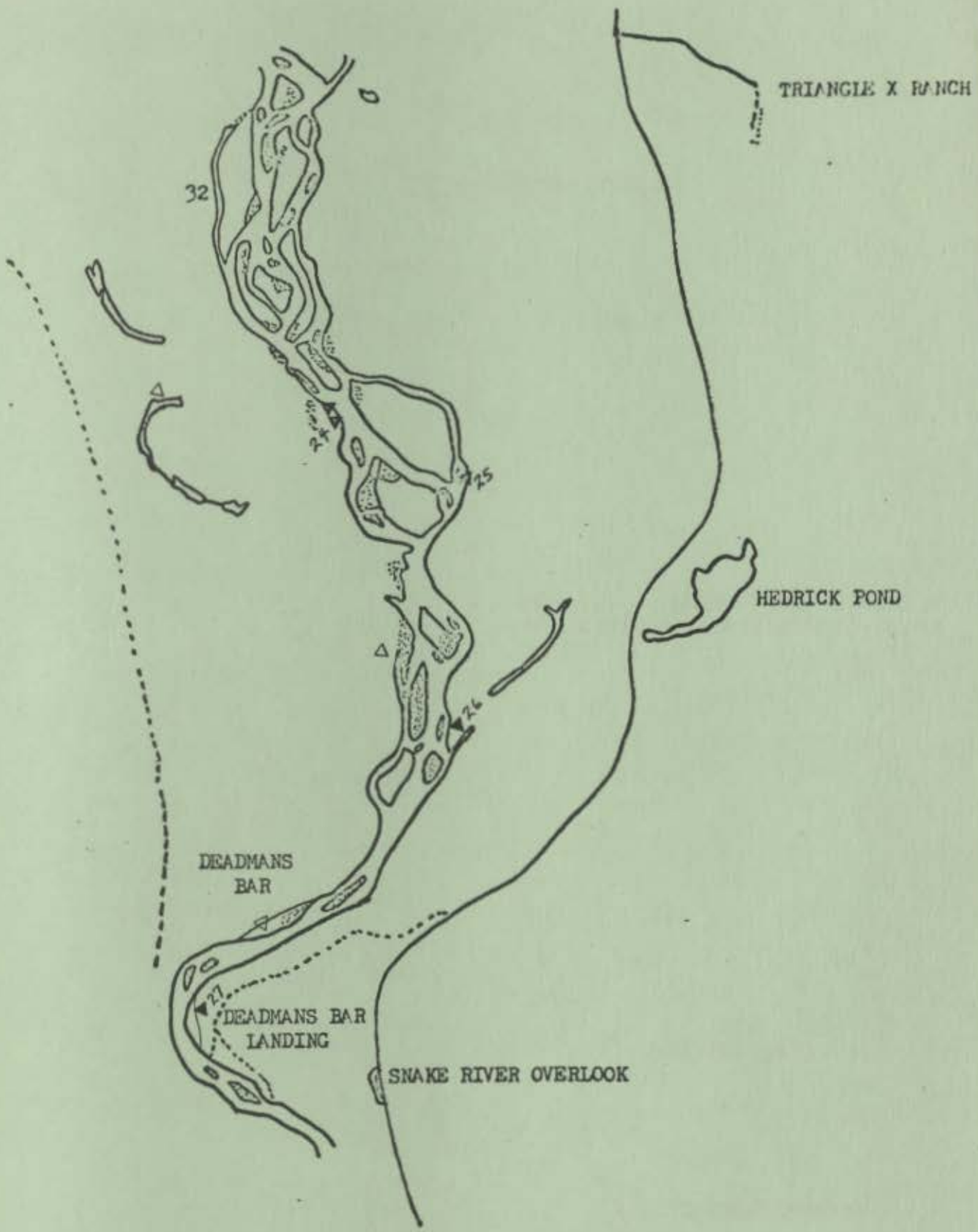


Figure 5. RKO LANDING TO DEADMANS BAR LANDING.
PART B. COLONY 23 TO DEADMANS BAR LANDING.
3 RIVER MILES.

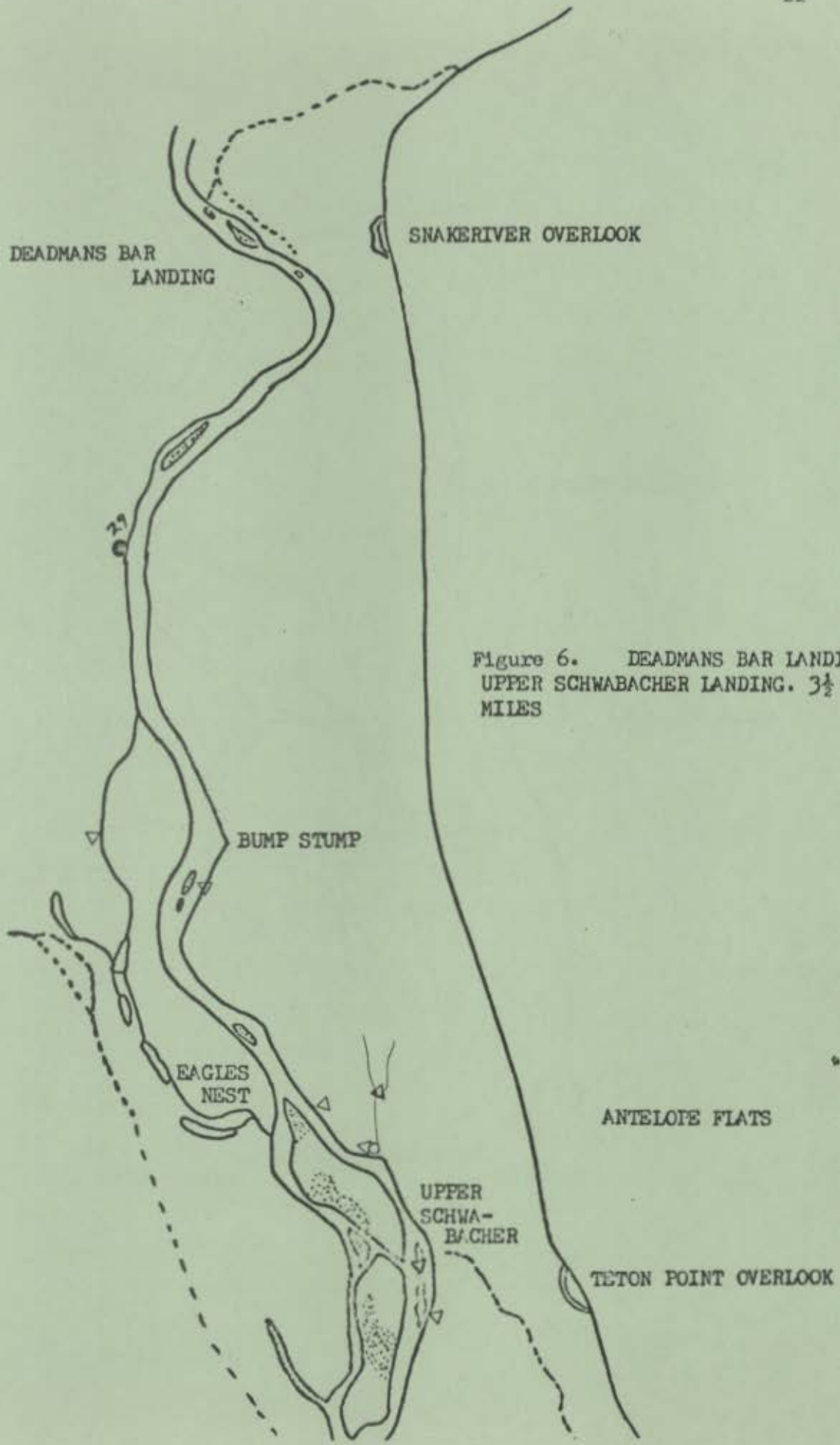


Figure 6. DEADMANS BAR LANDING TO UPPER SCHWABACHER LANDING. 3½ RIVER MILES

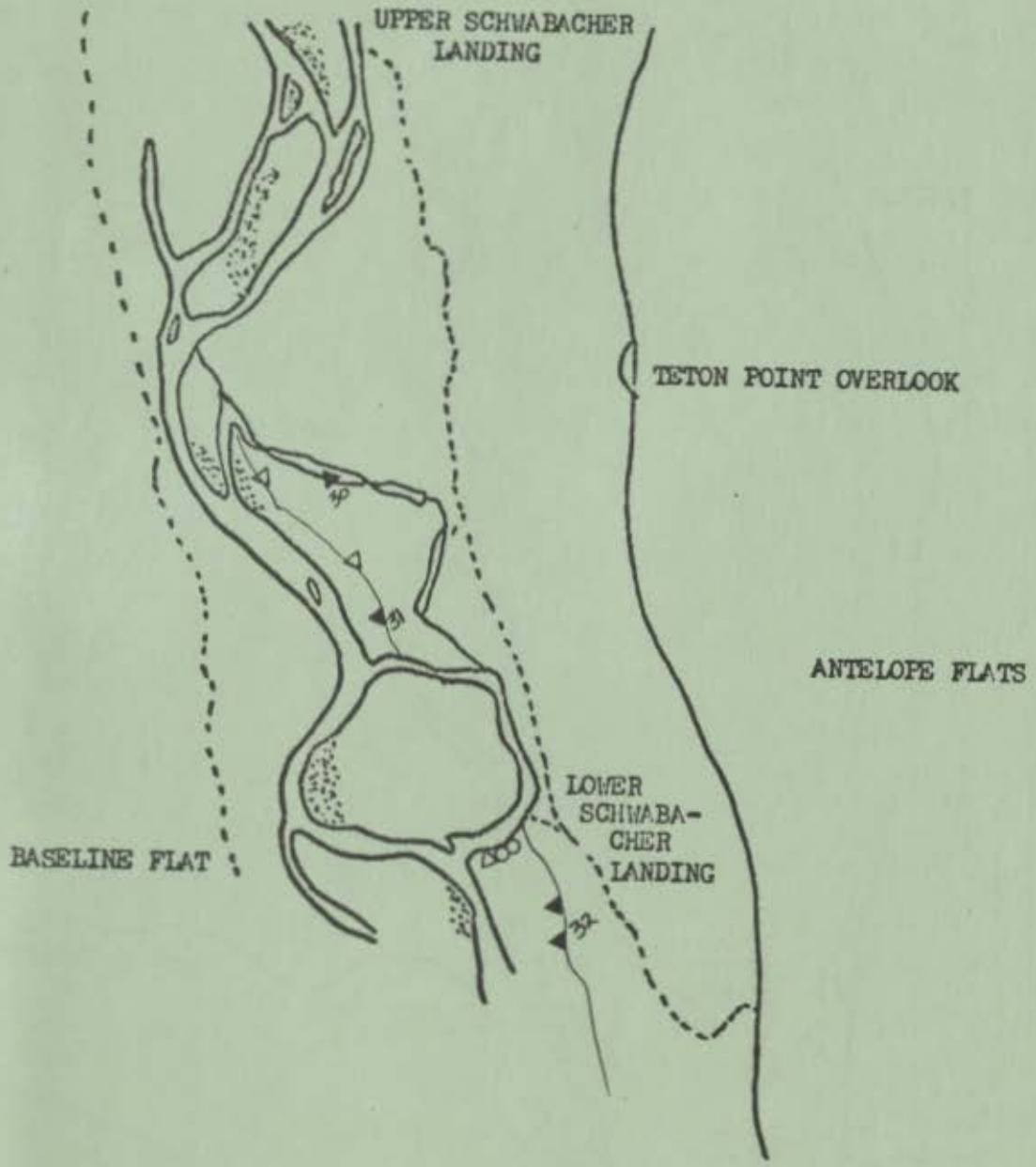


Figure 7. UPPER TO LOWER SCHWABACHER LANDING.
2 RIVER MILES.

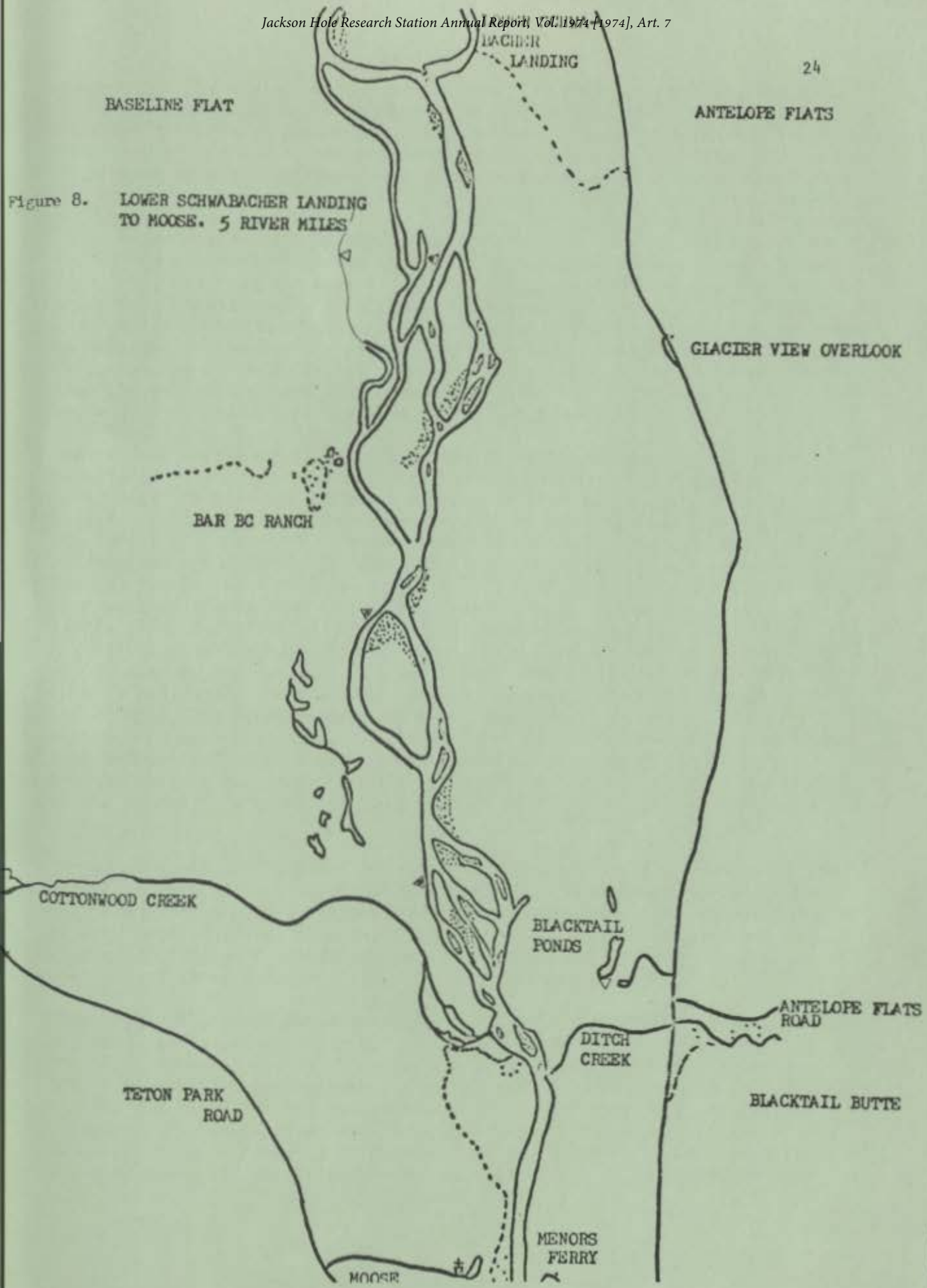


Figure 8. LOWER SCHWABACHER LANDING TO MOOSE. 5 RIVER MILES

Assume that the average colony consists of two adults, one yearling, and two kits. If the colony size remains stable over time in the population than the differences between reproductive rate and average colony size indicates at least a 30 percent mortality in the young each year and another 20 percent become transients each year until they establish new territories of their own. These transients, of course, are the two year olds that are being forced from the colony. In an exploited or steel trapped population, reproductive rate is likely not adaptive so long as removals do not exceed the population excess, that is, the number of two year olds forced from the lodge less the mortality in adults. The total population numbers, therefore, should remain relatively stable depending on the condition of the habitat. What happens then in an unexploited population like what might be expected in the Park? The possibilities are a lowered reproductive rate, increased mortality, or a very large outflux of two year old beavers from the Park or into marginal habitat or any habitat that might not normally be occupied had a stable population existed.

The rate of mortality of newborn beaver up until weaning has not been speculated in the literature. After weaning, the kits are trappable so that an estimate of mortality after weaning will be possible from data gathered in this study. Reproductive rate is also unknown for the Park population and may not be three per female per year under the apparent unexploited conditions. Trappers that will be removing any nuisance beavers from private lands within the Park have been asked to collect reproductive tracts from any mature females. Additionally, reproductive tracts from road kills will be held for examination. Only in this manner will it be possible to estimate reproductive rate as the number of fetuses per female and the mortality between fetal production and weaned kits can then be evaluated from trapping data and observation of the number of kits per colony. The Wyoming Game and Fish Department District Office in Jackson has been asked to watch for returns on the tagged Park beavers so that emmigration of Park beaver can be evaluated. This will require a considerably larger tagged population which should be available by the end of the second full summer of this study. To date, no returns have been made.

There were only a few cases of reported mortality in Park beavers in the summer of 1974. There were two road kills that were found and one dead kit, cause unknown, after the high water receded. Kit beavers may be preyed on by otters, coyotes, bobcats, large owls, and possibly eagles but very little information on predators has ever been reported. It is doubtful that any of these predators could overcome an adult beaver.

Finally, much of what has been described for the Park beaver population has assumed unexploited conditions. However, this may be a fallacy and the real circumstances may be that there is only a variation in the type and degree of exploitation between the Park's beaver population and a population outside the Park. First, due to the nature of beavers, they do require management in human use areas. If a beaver were to block a stream in the Park resulting in flooding to a main road it would certainly be removed since removing the dam is only a temporary solution. Secondly, the

extensive use of the Snake River by rafters may result in indirect exploitation by influencing the behavior of the beaver (see section on behavior) and where it will establish its territory. If all potential habitat is not utilized, the population cannot be maximal. Human influence could result in less than maximal habitat utilization. Thirdly, the effect of high and low water levels as controlled by the Jackson Lake Dam can be habitat abandonment. During high water in July of 1974, numerous beaver lodges and dens were nearly inundated. The effect on the kit portion of the population in terms of mortality is unknown but many nursing kits were obviously moved from the dwellings in which they were born and mortality rate may have been high. In late September, the water flow over the Jackson Lake Dam was reduced considerably as it always is at this time of year. Upon floating the Snake River in early October I found that nearly a third of the colonies in the first seven miles of the study area had abandoned their dwellings. Some channels that earlier supported colonies were completely dry. This necessitated that these beaver establish their colony elsewhere. The time between abandonment and the building of new dwellings may be critical to their survival in terms of cutting a food cache for overwintering. Additionally, the low water left large areas of exposed river bottom that the beaver must cross to get to forage. At some colonies, the beaver had to cross 30 meters or more of exposed area to get to the closest vegetation. At this time they would be very vulnerable to predators. These potentially exploiting conditions will be carefully evaluated in the next two years of this study.

Habitat Utilization

Methods, Results, and Discussion

A total of 102 beaver lodges or dens were located in the study area in 1974, 51 of these were active representing 33 beaver colonies and 51 were abandoned; 76 were lodges and 26 were bank dens or burrows; of the 76 lodges, 39 were active and 37 abandoned; of the 38 active lodges, 26 were primary and 12 secondary or accessory lodges; of the 26 bank dens, 10 were active and 16 abandoned; of the 10 active dens, six were primary and four accessory or secondary. A primary lodge is used here as the main dwelling or the one that the beavers were living in regularly. A secondary or accessory lodge or den was maintained but was irregularly used.

The typical beaver territory was defined as the furthest most scent mounds from the primary dwelling. The scent mounds were usually composed only of dirt that had been removed from the stream bottom but occasionally it included small wood cuttings or aquatic vegetation. The main ingredient of the scent mounds, castor oil, was easily distinguishable on mounds regularly visited by the beaver. Scent mounds were often located near the primary dwelling besides at territorial boundaries. They ranged in size from about 20 centimeters in diameter and several centimeters high to 60 cm in diameter and 50 cm in height. Characteristics of active and abandoned beaver sites have been prepared for 12 different colonies. Rather than present all of this data at this time, typical characteristics will be described.

The typical beaver lodge consists of cuttings from deciduous and coniferous trees and shrubs, grasses and sedges, moss, rocks, and mud. There were most often two underwater openions to the lodge and most lodges had at least one side on a bank rather than being completely surrounded by water. The lodge normally took the shape of an inverted cone, was between 3.5 and six meters wide and one or more meters high. All bank dens or burrows were found to have plungeholes located to the side or behind the den. These were usually covered with cuttings or were sometimes open. These are apparently used as accessory entrances into the den. Only about 40 percent of the colonies had any sort of dam within their territories and in all cases the dam building colonies were occupying the smaller side in channels of the river or tributaries. Dams varied in width from one to 25 meters and the constituents were largely the same as those found in the lodge. Beaver trails and food canals were common at all sites examined.

Stream flows, volumes, and substrates were quite variable throughout the study area as might be expected and this obviously influenced the presence or absence of beaver dwellings and dams. There are sections of the river that are not suitable for lodges or dens, particularly where there is fast water, eroding or gravel banks. Most of the study area on the river is not suitable for dam building due to flow rates.

The vegetation of the floodplain varies from the plants associated with the initial stages of sandbar succession to climax spruce-fir forest. The vegetation types of the entire study area are being mapped through the use of aerial photographs and on the ground observation. This will be correlated with the distribution and territory size of beavers in these vegetation types. Grass-sedge, willow-cottonwood, willow-alder, cottonwood-lodgepole pine, willow-sedge, and spruce-fir are the most common vegetation types and is representative of most of the seral stages of floodplain succession. Aspen is uncommon in close proximity to the river; that is, it is largely beyond the beaver's range.

Beaver food habits are being evaluated from actual feeding observations, cuttings, food piles and food caches, and by fecal analysis. All but the latter have been used as techniques for beaver food habits in studies reported in the literature. Beaver feeding habits at night when they are most active and when they can be the least observed are relatively unknown. The same is true for underwater feeding on aquatic vegetation. Fecal analysis will provide more accurate estimates of foods utilized and relative amounts. Additionally, night observation of feeding through the use of a starlight photomultiplier spotting scope will be more informative than observing only when sufficient light is available.

Fecal analysis by microtechniques requires that a reference slide collection of all potential forage and all parts of potential forage be prepared. The technique has been used for determining the food habits of a variety of animals, large and small. See Ward (1970) for a review of the technique. Individual plants can often be recognized in a slide preparation by cell characteristics, characteristics of margins of leaves and stems, etc. Subsamples of well mixed beaver fecal material are prepared in the same manner as the plant reference material using Hertwig's solution as a

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clearant, and Hoyer's solution as a mountant after the technique described in Ward (1970). The prepared slide of the fecal material is then compared with reference slides of known plant material to determine qualitatively what is being eaten. Several methods are possible for quantifying the relative amounts eaten. A special problem of analyzing beaver food habits by this technique is the great amount of woody material in the fecal material which is difficult to recognize as belonging to a plant species or even group of plants such as the Salix. Differential staining of the woody material using phloroglucinol which stains the lignin but not the cellulose of woody material is being attempted for differentiating plant characters. Success to date has been minimal with the stain. Seventeen fresh fecal samples were obtained in the summer of 1974 and reference slides of 40 different plant species common to the floodplain have been prepared. The analysis of the fecal material is presently in progress.

Beaver were observed feeding on Carex spp., Salix spp., and Populus angustifolia most often and they were at least once observed feeding on Pinus contorta, Pesudotsuga menziesii, Lonicera sp., and, in the traps, Populus tremuloides. The majority of the food piles contained Salix spp. although nearly every deciduous and confierous tree and shrub on the floodplain were seen in foodpiles at one time or another in addition to aquatic plants and several herbaceous forbs including Cirsium sp., Potentilla sp. and Lupinus sp. Food piles are prepared by the beaver each night and are usually utilized by the beaver the following night. It may serve as an immediate source of food for a hungry beaver when it first appears in the evening although some of the pile may be used for materials for dwellings. As many as 15 food piles have been seen within a beaver territory on a single check.

The majority of the tree cuttings in the study area were of cottonwood. The average height of the cut for 50 trees measured at colony five was 0.65 meters and the diameter of the cut trees varied up to 100 cm. On larger trees, only the tops and bark were utilized, the remainder being wasted. Beaver were seldom found to have moved greater than 40 meters overland to cut trees.

Winter cuttings at several colonies were evident by cut marks high up on trees. Part of the Park beaver population no doubt is icebound over the winter especially those colonies in small channels and tributaries that have been dammed creating ponds and in the upper sections of the river, especially in the oxbow. These beaver must rely on a food cache for overwintering, a large pile of cuttings usually in close proximity to the dwelling that can be easily gotten to from the dwelling. In October, evidence of food caches were seen at colonies one, two, five, six, seven, and twelve. These are areas with slow water flows which will likely freeze solid in the winter. Colony six had a very large food cache extending some 20 meters out from the lodge. It was two to three m. wide and was composed mostly of willows.

The phenomenon of cyclic beaver activity in a given area, that is, the pattern of establishment, habitat modification, abandonment, regrowth of the habitat, and re-establishment by beavers, is one of interest to wildlife managers and naturalists alike due to the potential predictability of the cycle and its implications in beaver transplanting operations and population trends. Investigations of this phenomenon are non-existent largely because the study of cyclic activity requires an unexploited population and historical data. Grand Teton National Park may be one of the few places in North America where this type of study is possible providing exploitation is minimal. Historical data is in the form of aerial photographs of the Snake River floodplain which date back many years and from which much information of the past conditions of the floodplain can be obtained. It will be assumed that for long established colonies, abandonment is the result of the beavers own modification of their habitat to less than marginal conditions; that is, the habitat has been denuded to the point that the beavers must establish elsewhere and the abandoned habitat will then undergo regrowth and succession and may eventually support beaver again. Blacktail Ponds is a good example in the Park of beaver modification of the environment to the point of abandonment and nothing will restore beaver to this area save the regrowth of suitable habitat. The number of years this will take is one of the points in question.

The occupied beaver habitat can be considered as part of a gradient, the most dissimilar habitats being optimal and marginal. The position of any beaver habitat at any given time along this gradient will be influenced by the length of time the beaver has occupied the site or the degree of habitat degradation, the condition of the habitat when the colony was established, etc. The abandoned beaver habitat can be considered as part of a gradient of habitats in various stages of regrowth and succession up to that habitat which is again suitable for beaver occupancy. The position of the abandoned site on this gradient will be influenced by the amount of time since abandonment, the successional stage of the habitat before abandonment, the degree of beaver modification of the site, etc. Complicating factors include channel changes and the disappearance of evidence of past activity (e.g., lodges) resulting from high water. Also, it is not known if or when beaver caused habitat degradation results in succession from a lower seral stage than that which existed, whether it progresses to a similar stage, or whether it bypasses the previous stage and succeeds to the next higher successional stage.

An example of the succession problem may clarify the statement above. Assume that beaver establish in a habitat that is in the cottonwood stage of floodplain succession. In time, the beaver will denude the habitat and most of the cottonwood trees will be removed. The question is whether the habitat after abandonment will regrow as cottonwood, whether it will be thrown back to a lower seral stage (willows), or whether regrowth will be as a higher successional stage (lodgepole pine). Obviously the age and substrate development of the original cottonwood stand will influence the type of replacement stage that is seen.

What needs to be measured then before the pattern of cyclic activity can be evaluated? Obviously, some idea of optimal and marginal habitat must be construed quantitatively. Some of this information can be obtained by comparing recently established sites and recently abandoned sites. Colony one and two, for instance, have been established very recently; colony two between June and July of the past summer. Several sites were found abandoned in 1974 that were active in 1973. Some idea of successional stages and rates of succession must be determined and this may be done in part from following aerial photographs of the floodplain over a number of years. Additionally, the age and condition of both active and abandoned sites need to be established.

Cyclic activity and floodplain succession are being measured by first typing the vegetation of each active territory being studied and the area adjacent to abandoned lodges being studied. This is done in conjunction with the use of aerial photographs and field verification so that the final result will be a map of the vegetation types and the area these vegetation types cover for each site being studied. Both active and abandoned sites are being aged, again through the use of historic photographs and by field verification. In the field, the site can be aged if the tree stand is of a similar age structure which most cottonwoods tend to be in a given area. Increment bore samples of cut tree stumps are compared with samples from standing trees to estimate how long ago the tree was cut. Also, cottonwood, like aspen, tends to sprout the year after being cut. These sprouts are usually from the base of the cut tree. The sprouts can be cross sectioned and the annual rings counted to estimate how long it has been since the tree was cut. The condition of the sites, in particular, the condition of the different vegetation types at each site under study, is determined by field vegetation analysis techniques for all potential beaver forage. A line intercept method is being used for estimating the trees and the shrubs and random sampling for forbs is by the use of a Daubenmire rectangle. At active sites, previously cut trees were marked so that the amount of cutting per year could be determined over the next two years of this study. Also, a random sampling of uncut shrubs were marked so that the degree of shrub cutting per year could be determined.

The cyclic activity pattern will be evaluated by comparing different aged sites, both active and abandoned, by the condition of the site. The comparison will be made through an ordination technique (Whittaker, 1967) involving setting up a matrix of the sites studied according to the similarity between sites in terms of the site condition, calculating dissimilarity coefficients, and hypothesizing the reasons for the dissimilarities. The final year of this study will test the hypotheses of cyclic beaver activity. Work was begun on evaluating cyclic activity in 1974 at colony two and colony five. However, aerial photographs are still needed to complete most of the study. It is hoped that at least twelve sites will have been analyzed by the end of this study.

The beneficial nature of the beaver in terms of creating new habitat for other wildlife is well known from the literature. At each active site in the study area, records were made of the wildlife using beaver habitat from observations, tracks, scat droppings, nests, burrows, etc. Numerous waterfowl have been observed in association with beaver habitat as might be expected. Moose, muskrat, water shrews, coyotes, osprey, otters, and

mink have also been observed. The relationship between moose, otter, muskrat, and beavers is especially interesting and will be given more attention in the next two years of this study. In particular, the potential competition that may exist between beaver and moose for food is of interest. See Rudersdorf (1952) for a review of this coaction.

Beaver Behavior

Methods, Results and Discussion

Behavior of beavers was recorded whenever they were sighted. Usually, binoculars or a spotting scope was used for planned observations. By October, a starlight photomultiplier spotting scope was readied for viewing night activity. Planned observations were most often at colony three behind the research station. The lodge, located on the opposite bank, was observed from good cover on a bank some 15 meters from the water's edge. In this manner it was possible to observe the activity of the beavers without being detected, at least by sight. It is possible that the beavers could detect my scent but they never showed alarm unless I was visually detected at which time their behavior demonstrated immediate awareness.

Beavers are primarily nocturnal and in a total of 21 planned observations at colony three, no beaver appeared earlier than one hour before sunset and in 17 of 21 observations the time of appearance was within 20 minutes of sunset to after sunset. The time of appearance, however, could vary with individuals of other colonies. Beavers are known to occasionally sunbathe and of a total of 112 observations of beaver, only one was a sighting of an undisturbed beaver at a time other than their usual activity period (11:30 AM) and this beaver did appear to be doing no more than sunbathing. The latest morning sighting of an undisturbed beaver was 6:30 AM.

The most common undisturbed beaver activities were swimming and feeding. Swimming was most often directional, to or from a feeding area, but cruising was not uncommon. In all evening observations of first appearance, the first beaver to appear would always cruise back and forth in front of the lodge for several minutes before leaving the immediate area of the lodge. Beavers were nearly always observed feeding out of the water. Upon cutting a stem of a shrub or a grass, the beaver would sit upright on its tail and hold the food in its hands as it ate. On several occasions a beaver was observed standing on its hind feet to cut a low branch off of a tree. On one occasion at colony 32, I observed a beaver cutting a cottonwood tree and using its tail as a prop to sit on. The sound of the cutting was heard from about 50 meters away.

Males and females of each colony trapped were tagged on opposite ears for distinguishing sex during observations. At colony three, the female

was tagged on the left ear, the male on the right ear. Kits, yearlings, and adults were easily distinguishable in the water or on land by their size differences. Therefore, it was not difficult to categorize observed beaver by sex and age groups providing they had been tagged.

The adult male appeared to be the dominant individual in the colony for all colonies observed and where the adult male was known. The adult male was the first beaver to appear at colony three in all planned observations. It would cruise in front of the lodge for several minutes before going upstream to feed. The female and yearlings did not appear until after the male had left the area. The male was seen before dark far more often than the female and they were seldom seen together. The female was seldom observed far from the lodge, especially early in the summer when she was nursing her kits. She was lactating when she was trapped and tagged on June 10. No kits of the year were observed at any of the colonies until July when one was trapped at colony eight. On one occasion at colony three, I was observing the adult male feeding next to the lodge. I was at the water's edge so he knew of my presence as he showed signs of awareness. The female suddenly appeared and started climbing the bank to the male. The male reared rapidly and knocked the female backwards, somersaulting her down the bank and into the water. The female did not reappear while I was present.

Beaver behavior in relation to disturbance by humans varied from curiosity to aggression. The majority of trapped beaver were very docile and easily handled. Aggressive beaver were adult males with one exception, that being a male yearling. Over 80 percent of the aggressive beaver were early morning captures at or after sunrise. About one third of the live trapped beaver gave an audible sound, a low huff caused by the beaver blowing through its nose. The sound was likely associated with the degree the beaver was upset in the trap and on handling as all of the aggressive beaver gave this sound almost continuously. Aggressive beavers would occasionally lunge and attempt to bite and the lunge was always accompanied by the tail slap. Some beaver showed great curiosity of the equipment that was carried with me during trapping operations. Beaver number five, a 57 pound lactating female captured at colony five did not enter the water for 20 minutes after her release. During this 20 minutes she visited the equipment several times. Other than the adult male, trap released beaver showed little interest if another member of their colony was in another trap close by.

Beavers are often disturbed from their dwellings during the day by rafters. The disturbed beaver showed various degrees of curiosity and alarm and usually gave the tail slap a number of times in the water. They would typically move downstream away from the lodge, slapping their tails continuously. If the raft continued downstream the beaver would dive and not reappear until it had gone upstream to the lodge. This appears as though it could be a diversion tactic to ward potential danger away from the rest of the colony. The disturbed beaver was most often an adult and, if tagged, would be recognized as the adult male. Some beaver could be disturbed from their dwelling by merely rafting the channel they occupied. Others could be disturbed from their dwelling by approaching close to the dwelling from water or land. A total of 33 observations of disturbed beaver were recorded.

Beaver contact with other wildlife was seldom observed. However, there were likely numerous contacts between beaver and otter since otter scat was observed around dwellings at colony three, four, five, seven, eight, ten, and thirteen. Otter were seen several different times, three times they were on or in a beaver dwelling. At colony four, three otter were observed from a distance of ten feet playing in the beavers' bank den. At colony three, seven otter were observed playing on the beaver lodge. At colony six, I witnessed a confrontation between an adult male beaver and two otter in which the beaver corralled the otter upstream out of the beaver territory. The colony at this time had newborn kits. There is a possibility that the otter, a carnivore, could prey on kit beaver. However, beaver do appear to be tolerable of otter in some instances. This relationship will hopefully be better understood as this study progresses.

Beaver are highly territorial, particularly in the early summer when kits are born and when the two year olds are being forced from the lodge. At this time there are many transient two year olds seeking out their own territory. The scent mounds at this time are visited regularly as the odor of castor scent on the mounds is quite evident. On one occasion, two adult males from adjacent colonies (six and seven) were observed in a confrontation at their respective scent mounds or territorial boundaries. The downstream scent mound for colony six was located within ten meters of the upstream scent mound of colony seven. Neither beaver crossed its own boundary but several times they approached each other, dove with a tail slap, and returned upstream and downstream respectively and again approached the territorial boundary. This went on for a full 20 minutes. Scent mound communication and territoriality may be an important means of beaver population size regulation in a given area according to a study by Aleksiuk (1968).

Many aspects of beaver behavior are not entirely understood in terms of the significance of the behavior. Behavior patterns obviously are quite variable for different individuals and different colonies. Continued observations over the next two years of both disturbed and undisturbed beaver during daylight or at night with the photomultiplier, should improve the understanding of some of these behavior patterns.

Summary

During the summer of 1974, 30 beaver were trapped from 16 different colonies. The majority of the beavers were caught in the middle of the night in the 2 AM trap check and June was the most successful month of trapping. High water in late June and July greatly hampered trapping operations. Male and female beaver were tagged on opposite ears for recognition of the sex during behavior observations. There was a preponderance of males and of adults in the trapped sample. Kits did not appear until mid-July after they were weaned. A total of 33 beaver colonies representing at least 165 beaver were located in the first 22 miles of the study area.

A total of 102 beaver dwellings, half of them active, were located in the study area. The majority of the dwellings were lodges and it was not uncommon for a colony to have one or more accessory dwellings. The largest beaver territory observed covered more than a mile along the river. Lodges and dams were quite variable in size and were built of whatever materials were available to the beaver. Stream flow rates, volume, and substrate limited the potential for lodge or dam building in some sections of the river but generally, the territories were packed one against the other, leaving little room for establishment of new territories. The vegetation of the floodplain included all the successional stages of floodplain development.

Beaver were observed feeding most commonly on willows but sedges, cottonwood, coniferous trees, and deciduous shrubs were also seen eaten. Food piles and winter food caches were mostly composed of willows but portions of coniferous and deciduous trees and shrubs, forbs, grasses, and aquatic vegetation were also found in food piles. The great majority of tree cuttings were of cottonwood.

Work was begun on the analysis of cyclic beaver activity with colony two and colony five being the first active sites to be examined. Vegetation analysis, tree and shrub marking, and aging of the sites was initiated. Results of markings will be determined over the next two years. A total of twelve active and abandoned sites will be compared by the end of this study.

Beavers are basically nocturnal appearing just before dark. They are readily disturbed from their dwellings during the day by rafters and they showed both curiosity and aggressiveness when disturbed or caught in a trap although most trapped beaver were docile and easily handled. The adult male appears to be the dominant individual in the colony. He is usually the first beaver to appear before dark and is most always the beaver that investigates when the dwelling is disturbed. The adult male shows definite patterns of protection of the adult female when she is nursing young and protection of the colony as a whole from both humans and other wildlife. Few beaver contacts with other wildlife were observed except for otter. Beaver were both tolerant and aggressive toward otters in the beaver territory.

Recommendations

Obviously, little in the way of recommendations related to findings of this study can be made at this early date. However, a couple of items can be recommended because of their obviousness. First, the sign at Blacktail Ponds Overlook is boviously no longer representative of the existing conditions there. It may be informative to the public to replace the sign or post a second sign describing just what has naturally occurred, that is, the beaver have abandoned the area due to their own degradation of habitat but that through the process of regrowth and succession, the area will likely support beaver again. Secondly, aerial photographs are

an excellent means of keeping up with the ever-changing floodplain not only in terms of its scientific value for wildlife and fisheries research but also for its practical value in search and rescue operations and predicting channel changes as well as accurate mapping. The 1974 series of aerial photographs of the floodplain showed drastic changes from the next previous series. It seems logical that such a series should be made at least every two years, if possible.

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