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A STUDY OF BEAVER COLONIES IN MICHIGAN

BY GLENN W. BRADT

Perhaps no other north American mammal has given rise to so many stories or to so voluminous a literature as has the beaver. Hearne (1795), Morgan (1868), Dugmore (1914), Bailey (1927), Seton (1929), Warren (1929), and others have written entertainingly about the manifold details of the beaver's life and its feats of engineering.

In view of this abundance of literature, it was with some trepidation that I began an investigation into certain phases of the life history and ecology of the beaver in Michigan. I was soon surprised to discover that most of the literature was of the casual observational, or "nature study" type, replete with references to statements made by Indians, fur trappers, and old woodsmen, corroborated or refuted by occasional personal observations and experiences. Very little planned research work seemed to have been done.

With the return of the beaver to a position of economic importance in Michigan, the state Department of Conservation was confronted with various problems concerning beaver populations and relationships, and it soon became evident that more accurate and intensive knowledge of the beaver was essential, if proper regulatory measures were to be adopted.

In cooperation with the Game Division of the Department of Conservation, I began an investigation of the beaver situation in the spring of 1929, which has continued to the present time. I have been able to spend a considerable portion of my summer vacation periods in the field each year, with occasional field trips during the school year, and have also maintained a small colony of beavers in captivity at the State College campus in East Lansing.

The first step necessary was to develop methods of catching the animals alive, determining the sex, marking them so that they could be individually identified if recaptured, and releasing them without serious losses from fright or injury.

Livetraps.—Fortunately, live traps were already available and could be purchased. The Biological Survey beaver trap, devised and described by Vernon Bailey (1927), was used successfully during the earlier part of the investigation. The trap was later replaced to a great extent by an aluminum alloy trap, much lighter and easier to handle than the former iron traps. These traps proved entirely satisfactory in every respect, rarely failing to catch a beaver when properly adjusted and suitably placed.

Beaver traps may be set in a variety of positions, according to conditions of water, food, runways, and other factors. The set most often used is prepared by tearing away a small section of a beaver dam to a depth of about one foot and a width of about two feet, permitting the water to pour through the opening in a miniature cascade. The trap is then placed just behind the opening, upstream, so that the beaver will swim against the trigger in approaching to repair the break in the dam. Since beavers are very active in repairing any breaks in their dams, this set can be depended upon to produce results in a high percentage of cases, and can be used night after night until all members of a colony using the dam have been taken. Beavers are so little disturbed by live trapping that they will often repair a dam a few feet from where one of their number is caught in a live trap, even pushing sticks against the trap in placing them in position on the dam. The set at the dam also offers the advantage of comparatively easy access in setting the traps and removing the captive animals.

Traps may be set at the foot of runways down which the beavers bring cuttings for use as food or in construction work. There is a distinct disadvantage in this method of setting a trap, however, since the poles or sticks carried by the beavers often spring the trap prematurely, or prevent the jaws from closing tightly, permitting the animal to escape. If the stream happens to be of the proper depth and width, traps may be set in the channel, catching the beaver as it swims up or down stream. A trap may be set on the base of a beaver lodge, catching the animal as it feeds or carries sticks to add to the lodge.

Traps must always be placed under water, as beavers are very suspicious of strange objects above the surface, but apparently they are quite oblivious to anything beneath the surface.

Occasionally it is desirable to attract the animals to a trap by the use of bait. This occurs most often when the beaver colony is located on a stream too large or too swift for the animals to dam, or on a lake or large pond where there is either no dam at all, or the dam is a considerable distance from the lodge or bank burrows in which beavers are dwelling. A simple method of baiting in such cases is to cut a number of fresh, leafy poplar shoots or twigs, and stick these into the bottom around the trap, with one or two close beside the trigger. The sight or smell of these freshly cut shoots is very attractive to beavers, who seldom fail to spring the trap while attempting

to sample the new food supply. Care must be taken to place the shoots in such positions that they will not interfere with the closing of the jaws of the trap, and where the beaver will be likely to swim against the trigger in investigating the fresh food material.

The use of bait is often necessary if one is to capture kit beavers still remaining in the lodge after the mother has been taken. Such kits are able to swim out and secure their own food after about the second week of life. These young animals may pay no attention to a broken dam, nor follow any regular channels or runways, but will search for any nearby food supply, and are easily taken in baited traps set near the lodge.

Losses of animals by injury in live traps is uncommon, such losses as do occur usually resulting from drowning. The traps sometimes tip over on one side, or slide down the slope behind the dam or lodge, covering the wire cage with water and of course drowning the unfortunate occupant. Such losses can nearly always be prevented, by tying the trap to a stake, and preparing the bed of the pond or stream properly for the reception of the trap before setting. Only 16 beavers from a total of 270 taken during the summer of 1931 were drowned, and many of these could have been saved by sufficient preventive forethought (Bradt, 1935, p. 512).

Handling and transporting beavers.—Various methods were tried for handling and transporting captured beavers from the pond or stream to a suitable place for sex determination and individual marking. The original iron frame traps were heavy and cumbersome to carry, and when these were in use the beaver was generally changed to a carrying case near the point of capture, and carried in this to the car, a matter of rods or miles as the case might be. To effect the change from trap to box, a rope or strap was slipped around the base of the tail while the beaver was still in the trap, then the jaws were opened and the animal swung into the open box. With the advent of the lighter, more compact aluminum frame traps, the trap was simply carried with the beaver inside. In case a trip of a mile or more was involved, a couple of poles were cut and tied on either side of the trap, permitting one man to walk at each end between the poles. Two men were not always available, however, and unaided I have carried many beavers in the aluminum traps for considerable distances.

There is little difficulty in catching beavers alive, but a great deal of hard work is involved, since the ponds and streams inhabited by them are often located at long distances from roads or trails, and often a thick cedar swamp or alder thicket must be penetrated before the water is reached.

Identification of sex.—Since there are no external indications of sex in beavers, a technique for field identification of sex had to be developed. Adult female beavers may be recognized during the nursing period and during the late stages of pregnancy by the four teats on the breast, but at other times of year the teats are inconspicuous and difficult to find.

The male beaver has a small os penis about one inch in length, which may be felt by inserting the finger into the genital opening just ventral to the anus. After some practice I was able to determine sex readily by this method except in the case of animals less than one year old. In the latter, the openings are so small that the insertion of the finger is not practicable.

This method requires that the animal be firmly held during the operation. This was accomplished by the use of a rectangular wooden box about 40 inches in length and 10 to 12 inches in diameter, closed at one end and open at the other. This box was set on end, with the open end upward. The beaver was then seized by the tail, held above the open end, and partly dropped, partly pushed head first into the box. With practice, this becomes a simple operation. A beaver held by the tail is unable to double upon itself sufficiently to bite the hand that holds it. It must, however, be held at arms length away from the body or it may bite some portion within reach, and the bite of a beaver is of serious consequence. Considerable muscular strength is required to poise a large beaver at arms length over the end of a box 40 inches above ground, the animal squirming violently meanwhile. A cylindrical tile of the proper diameter and length makes an excellent box for sex determination, as the smooth sides reduce friction and the beaver cannot resist so effectively when dropped into the opening.

Once inside the box or tile, the beaver is comparatively helpless, as it cannot turn around, and can be prevented from backing out. The tail is then held aside, the hind feet held also, and the operator proceeds with the sexing operation. An assistant is necessary to hold the box upright, and to hold either the feet or tail, the operator holding the member not so held. The beaver is a powerful animal, and if a box is used it must be strongly built and reinforced to withstand the struggles of the imprisoned animal. While the beaver is securely held in the box the marking operation is also accomplished.

Tagging.—The development of a satisfactory method of marking beavers so that individual animals could be readily recognized if recaptured proved to be a protracted and sometimes disheartening problem. The physical characteristics and habits of beavers prevent the use of the customary methods of tagging and marking live animals. The ears are very small, and too difficult of access to permit tags or punched holes to be practical. Bands placed on the legs would soon be torn off. Clipping of toe nails would be difficult to accomplish under field conditions, would require careful inspection of the animals under equally difficult conditions if recaptured, and might handicap them in swimming or feeding. No method involving damage to the pelt would be desirable. Only the flat scaly tail seemed suitable for marking.

Before I began this study Mr. H. D. Ruhl had already marked several beavers by riveting aluminum tags through the tail, and had released these

animals on the Gladwin State Game Refuge (Ruhl and Lovejoy, 1930). These tags were of the standard cattle ear tag type, bearing the words "Notify Conservation Department", and an individual number stamped on each one. A hole was punched through the tail of the animal, and the tag quickly riveted in position. A few taps with a hammer leveled the edges and made a neat looking and close fitting tag. The entire operation could be completed in less than 5 minutes, and the beavers seemed to mind it very little. A slight flinch as the punch penetrated the tissues of the tail, and occasionally a few drops of blood, were the only discernible effects.

Several of the tagged beavers were recaptured at intervals during the first year after release, and the tags were easily read and firmly in place. Apparently the problem of individual identification had been solved. Several hundred beavers were accordingly tagged and released during the nuisance beaver control work of 1931 (Bradt, 1933).

Unfortunately, about this time evidence began to accumulate indicating that after a year or so the flesh immediately surrounding the tag sloughs off, the tag loosens and falls out, leaving a rough hole to show that a tag had once been there, but leaving no clue as to the missing number on the lost tag.

Branding.—As soon as it became evident that the tail tagging method was a failure, branding methods were tried. Branding irons of suitable size were constructed, and a number of beavers on the Gladwin Refuge were caught, branded and released. Many of these had previously been tagged, and their identity had not been completely lost. The operation of branding proved unexpectedly simple. The white hot iron could be held against the surface of the tail until the white flesh beneath the scales was reached, yet the animal would never flinch. Apparently the surface and subsurface of the tail are not supplied with many nerve endings transmitting the sense of pain. The branding operation creates much smoke and odor, but in no case have I observed evidence of pain on the part of the beaver during the operation.

Brand numbers were easily read when fresh, and could even be seen when the beavers were swimming under water in the holding pen. Following the lapse of a year, however, only those numbers made up of straight lines, i.e. 1 and 7, could be accurately deciphered. Others were marred and obscure, due to a shedding or sloughing away of the scaly surface adjacent to the curves and angles.

Combinations of the figures 1 and 7 seemed adequate for the limited numbers of animals on the Gladwin Refuge, in which I was particularly interested at the time, and I continued to brand accordingly. These combinations were inadequate for any large number of beavers, however, and I soon adopted a code system, which avoids the use of the figure 7, as the angle of a 7 occasionally becomes so blurred as to occasion doubt as to the exact figure in question. With the code system a very large number of beavers

may be branded, using a single branding iron, and eliminating all curves and angles entirely. This system is illustrated in the accompanying diagram (Figure 1). Beavers marked with combinations of 1 and 7 in 1932 and 1933 still carried the brands in 1935 in an easily readable condition.

Places of study.—My first studies of beavers were conducted on the Gladwin State Game Refuge, located in the northwest corner of Gladwin County. The first beavers tagged in Michigan were liberated on this refuge by Mr. Ruhl in the fall of 1928, and here I carried on many of my subsequent investigations. Later the refuge was also used as a center for the investigation of beaver-trout relationships by J. C. Salyer (1935) and myself.

During the summer of 1931, I was engaged in the nuisance beaver control operations undertaken by the Department of Conservation and was able to accumulate much valuable information regarding beaver populations and distribution, as all reports were made on uniform blanks and these, including

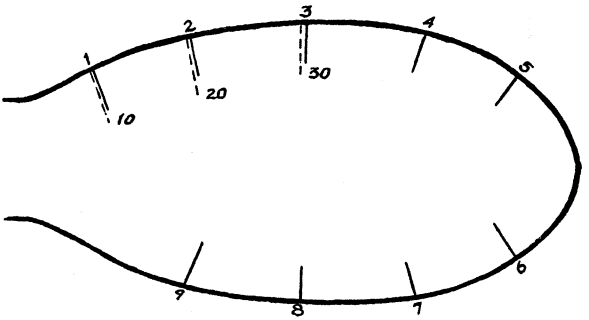

Diagram of the tail branding method used on beaver. Twin numbers, as 11, 22, 33, should be omitted.

those made by other workers as well as my own, were made available to me. A brief summary of this work was published in 1933 (Bradt, 1933, p. 509) (See also Table 1).

The summer of 1934 was spent in the field in northern Michigan carrying on a part of the beaver-trout investigation, and during the summer of 1935 I was in the field in charge of the newly inaugurated beaver-trout management program of the Department of Conservation.

Examination of carcasses.—In connection with this program, 207 beaver carcasses were purchased by the Department of Conservation from trappers during the open season in the spring of 1935. These carcasses were examined for sex, weight, external measurements, and condition of pregnancy. Of these, 138 were examined at the University of Michigan Museum of Zoology, 32 at the Department of Zoology, Michigan State College, and 37 at the Game Division of the Department of Conservation.

Captive beavers.—In the fall of 1929, the Zoology Department of Michigan

State College received 8 beavers from the Game Division of the Department of Conservation with which to conduct an experiment in beaver culture. Some degree of success has been attained in inducing the animals to breed in captivity, and data secured regarding breeding habits, size and sex ratios in beaver litters, and growth rates of young beavers.

Composition of beaver colonies.—The logical point at which to begin studies of beaver populations was obviously the unit of population, the colony. By "colony" I mean 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. While this definition may seem somewhat indefinite and difficult to determine, it is not so in the field. Beavers appear to maintain a system of territorial rights, and there is no evidence of overlapping of the colonies.

Estimates of beaver populations always assume some "typical" number of animals per colony as the basis for the estimate, and there has been much discrepancy as to the "typical" number that should be used. Apparently no systematic investigations had ever been carried on, the estimates being based on reports by Indians and trappers as to the number usually taken in a lodge when this was trapped out.

The data used in the following discussion of the number of beavers per colony were secured from several sources, each carefully examined as to accuracy. The largest single source of information was the reports of the nuisance beaver control operations in Michigan in 1931. Table 1 is a summary of the data obtained in this way, copied from my report published in 1933. By no means all of the colonies included in this table were used in the population studies, however, as no colonies were used unless it was certain that every member of the colony had been captured and recorded. To determine whether or not every animal had been taken, trapping was carried on until no more animals were caught for at least two days, and no evidence of beaver activity could be discerned. No repair work on the dams, no fresh cuttings for food, no tracks in the mud or sand along the bank for two days was accepted as evidence of absence of beaver. The traps were then removed, but approximately a week later, a return visit was made, and if no signs of beaver could be seen it was assumed that the colony had been entirely trapped out. If beaver sign was to be seen at that time, trapping was resumed and kept up until again no more beaver activity could be seen. In each case of this kind I have not included that colony in my tables, because there could be no certainty that a beaver had not come in from elsewhere in the interval between trapping operations. No colonies have been included in which there seemed a possibility of mistake in numbers of beaver actually living in the colony.

The colonies used were either trapped out by me, or by L. A. McIntire and A. M. Stebler, who employed exactly the same methods as I did in

carrying out and recording their operations. All reports were made on standard forms. The form and map accompanying the blanks were designed for use as data sheets for future compilations, and have proved most useful.

The figures available from the nuisance beaver work were supplemented by data gathered by me on the Gladwin Refuge and elsewhere, every colony used being subjected to the same criteria as to authenticity before being accepted.

Table 1 summarizes the work on nuisance beavers during the summer of 1931, but includes only those colonies from which we were able to obtain complete information regarding numerical composition.

Although the number of colonies and of individuals studied is insufficient to justify the drawing of definite conclusions, it appears that the number of

TABLE 1

NUMERICAL COMPOSITION OF BEAVER COLONIES

NUMBER PER COLONY	NUMBER OF COLONIES	TOTAL NUMBER ANIMALS
1	7	7
2	6	12
3	6	18
4	5	20
5	8	40
6	10	60
7	5	35
8	4	32
9	1	9
11	2	22
12	3	36
Totals.....	57	291

Total females, 50; total males, 60; total sex not determined, 181 (15 adults, 46 yearlings, 120 kits). Average number per colony, 5.1.

animals comprising a colony is decidedly irregular, and that the numerical average of 5.1 beavers per colony shown in Table 1 is of doubtful value as an index for estimating beaver populations over extensive areas. Nevertheless, since this figure is obtained by actual analysis of 57 colonies scattered over a large area of the state, it should be worth somewhat more than estimates made from one or two personal observations, or from reports of trappers and others based on haphazard trapping experiences.

Johnson (1927, p. 579) estimated beaver populations in the Adirondack Mountains on a basis of 10 animals per lodge. Morgan (1866, p. 135) stated that the trappers in the Lake Superior region estimated at the rate of 7 animals per lodge, and the trappers of the Rocky Mountain region estimated at the rate of 8 animals per lodge. Estimates of trappers and

woodsmen in Michigan are usually based on some number between 6 and 12 per lodge.

It is my opinion that the discrepancy between these estimates and the figure of 5.1 indicated in Table 1 may be explained on the basis of a common trait of human nature. Trappers tend to remember the lodges in which a goodly catch was made, and to forget those in which their catch was poor. They also very likely forget those in which only one or two animals were taken, with the thought that probably in this case they did not get all of the animals.

This idea may also explain the fact that most records of the number of animals in a beaver colony tend toward a certain uniformity. In case a colony was found to contain an apparent family group it was duly recorded, whereas if the group seemed to lack such an appearance it was not recorded but the assumption made that the entire group had not been taken.

My conclusion is, therefore, that while the figure of 5.1 beavers per colony could not be accepted as a true mathematical basis for the estimation of beaver populations over extensive areas, it is probably more nearly correct than are any of the higher average figures arrived at by casual or haphazard means. It could not, however, be used in estimating beaver population in any region in which trapping seasons are permitted.

The lodge as an index of population.—Estimates of beaver populations made by trappers and woodsmen are usually based on an average per lodge, the lodge apparently being considered as synonymous with the colony. Many beaver colonies, however, possess no lodge at all, the animals living in bank burrows entirely. This is frequently the case with beavers living in streams with high solid banks, permitting easy digging of burrows, and offering little inducement for the construction of lodges. Other colonies possess one lodge and several bank burrows, apparently each in use at the same time. Still other colonies possess two lodges in use, usually with several bank burrows in evidence as well.

Under such conditions it has never seemed to me that the lodge was a satisfactory unit upon which to base estimates of beaver populations. Consequently, I have undertaken an analysis of the available data regarding the population per lodge, dividing the colonies into those possessing no lodge; those having one lodge in use; and those having two lodges in use. I have never seen any beaver colony in which there were more than two lodges in use at one time. Occasionally one or more additional lodges may be discovered, but these have always been badly in need of repair, and were obviously no longer used by beavers. These old, run-down lodges are seldom, if ever, repaired again, the beavers seeming to prefer to build new lodges if needed.

Examination of 45 colonies indicates that the average number of beaver per colony with no lodge is 2.4, per colony with one lodge, 4.0, and per colony

with two lodges, 6.1. While, of course, these figures are not statistically significant, they do indicate the possibility that colonies using two lodges may be somewhat more populous than those using only one house. They also indicate the probable unreliability of estimates of beaver populations based on any average number of beavers per lodge observed.

Bank burrows.—I have been unable to determine whether or not certain individual animals in a beaver colony occupy the lodges and others the bank burrows, or whether the burrows and lodges are used indiscriminately by all members of the colony. Woodsmen and Indians have claimed that the male beavers are driven from the lodge before the birth of the young, and must remain outside until late summer, when the young are well grown. This sounds logical, and my own personal observations seem to be in accordance with such a view. I have never observed any evidence of antagonism between females with young and males, however, and I have observed the female and the male, in one case known to be the father of the kits, feeding and swimming together around the base of the lodge in which the young were lying at the time. Close observation did indicate, however, that the male was probably living in a bank burrow a few rods from the lodge, while the female and young occupied the lodge.

The underwater entrances to bank burrows are deep and narrow, and do not offer a suitable opportunity for the setting of live traps. Traps set *near* the entrances to burrows do not solve the problem of the actual occupants of the burrows, since beavers have a habit of swimming under water for some distance when they leave the lodge or burrow, and the beaver caught in the trap near the burrow entrance might actually have come from a lodge or burrow several rods distant.

It would probably be possible to use steel traps in determining which beavers use burrows, as these could be set in the entrance of the burrow, but this would necessitate the drowning of the animals, and I have not undertaken any measures that would result in the death of the beavers under observation.

The dam as an index to population.—There is a persistent popular notion that the number and size of beaver dams is an indication of the number of beavers in the colony making use of these dams. This idea has been contradicted by Johnson (1927, p. 578), but still persists among the general public. No evidence of correlation between the number of used dams maintained by a beaver colony and the number of animals in the colony is shown by my investigations. Such a correlation should not be expected, since the number and size of beaver dams depends on local conditions of topography, including stream flow, depth of water, availability of construction material, and distance between high banks, and little, if at all, on the number of beavers in the colony. Beavers construct dams to secure and maintain suitable water levels for their lodge entrances, and for safety and

convenience in food getting and storing, and the number and size of the dams varies accordingly.

Sex and age composition of beaver colonies.—Various estimates as to the sex and age composition of beaver colonies have been published. These are usually based on the population of the lodge as a colonial unit. My own figures are, however, based on the numbers taken per colony, and not merely per lodge.

Table 2 summarizes the data from 42 colonies studied. Only such colonies are included as were completely trapped out, and in which the sex and age were positively identified.

The numerical composition of these colonies has already been included in Table 1, so that the number of kits and yearlings is of no importance here. Sexes of kits and yearlings were not determined in all cases, but this is im-

TABLE 2

SEX AND AGE COMPOSITION OF BEAVER COLONIES

COMPOSITION	NUMBER OF COLONIES
1 female	1
1 female and kits	7
1 female and yearlings	2
2 females and kits (4)	1
1 male	6
1 male and 1 female	6
1 male, 1 female and kits	9
1 male, 1 female and yearlings	2
1 male, 1 female, yearlings and kits	8
Total	42

material in Table 2. All animals two years of age and over are included as adults in Table 2.

A typical beaver colony is shown by Table 2 to consist of an individual family, including the parents, the kits, and often the yearlings born the previous year. This corroborates the observations of the writer just mentioned. My observations of branded beavers on the Gladwin Refuge also bear out this conclusion, but indicate that the two-year-old progeny sometimes remain near the place of birth, and may live in the same pond with the rest of the family, although probably not in the same lodge or burrow. The fact that the two-year-old animals were not taken with the family group in any of the 42 colonies trapped out certainly seems to indicate that the two-year-olds are not usually members of the colonial family. Some of the single animals recorded in Table 2 may have been two years old, however. This would not affect the conclusions stated. The fact that males and females

were taken with kits in certain colonies does not prove that the males and females inhabit the same lodge with kits, as the males may have been living in burrows apart from the rest of the group, and still have been taken in the trap set on the dam. The dam, as previously stated, is the best place to take all members of a colony, whether they live in lodges or burrows.

Which beavers work on the dam?—There has been much speculation as to which beavers build and repair the dams, or at least which ones are most active in this work. Such conclusions as can be drawn from the animals studied by me indicate that males are the first to attempt repair work on broken dams, but that every member of the colony takes up the task if the male fails.

Number of young per litter.—There is no evidence that more than a single litter per year is ever produced. Small kits seen late in summer are readily explained as due to their having been born in July, at the latter end of the period during which young are produced.

My data regarding number per litter have been compiled from two sources. First, from the litters counted by me in the field, including those on the Gladwin Refuge and those taken during the nuisance beaver control work. Second, from the numbers of embryos per female taken during the spring trapping season of 1935. As stated previously, carcasses of beavers were purchased by the Department of Conservation from trappers at that time in an effort to gain information regarding sex ratios and other pertinent matters relative to a beaver-trout management program. These animals were weighed, measured, sexed, and conditions relative to pregnancy recorded at the University of Michigan Museum, at the Department of Zoology, Michigan State College, and by F. F. Tubbs of the Game Division of the State Department of Conservation.

Table 3 embodies the information secured from the animals examined during the trapping season of 1935, which covered the period March 15 to 31 in the Lower Peninsula, and April 1 to 15 in the Upper Peninsula. Since Table 3 includes data relative to sex ratios and localities as well as those relative to litter size, I have summarized the data regarding litter size in Table 4.

That the infant mortality is low in the beaver is suggested by the fact that the number of embryos per female and the number of kits per colony give practically the same figure for the average number of young per litter.

The results corroborated the reports of previous observers that 4 is the most common number of kits, and that all numbers from 1 to 8 occur. Whether or not 8 kits are born and actually survive has not been proven. I have personally observed two litters of 6 each on the Gladwin Refuge, and in each case every one of the young reached maturity.

I think it would be safe to conclude that an average of between 3 and 4

kits are produced per litter, and that in many cases these survive to become adults.

Sex ratios.—As previously pointed out, it was not found practicable to determine in the field the sex of living kits less than about 6 months of age. Hence, the majority of kits handled were not sexed. In several instances, however, I was able to follow the individuals of a particular litter through

TABLE 3

TABLE OF SEX RATIOS AND CONDITIONS OF PREGNANCY OF BEAVERS EXAMINED DURING SPRING TRAPPING SEASON, 1935

WHERE EXAMINED	PENINSULA	NO. EXAM.	MALES	FEMALES	SEX RATIO		NO. FEMALES PREGNANT	% PREGNANT	TOTAL EMBRY.	AVERAGE EMBRY.
					M	F				
Mich. State	U.P.	32	16	16	1	1	2	12%	3	1.5
Univ. Mich.	L.P.	113	55	58	.948	1	14	26%	61	4.3
	U.P.	25	13	12	1.08	1	7	58%	21	3.0
	Totals	138	68	70	.971	1	21	30%	82	3.9
Game Div.	L.P.	23	15	8	1.8	1	4	50%	18	4.5
	U.P.	14	9	5	1.8	1	1	20%	1	1.0
	Totals	37	24	13	1.8	1	5	38%	19	3.8
Grand totals	L.P.	136	70	66	1.06	1	18	27%	79	4.4
	U.P.	71	38	33	1.1	1	11	33%	25	2.3
Totals for Mich.		207	108	99	1.08	1	29	28%	104	3.7

TABLE 4

NO. OF KITS OR EMBRYOS PER LITTER	NO. OF OCCURRENCES	NO. OF KITS OR EMBRYOS PER LITTER	NO. OF OCCURRENCES
1	5	5	9
2	11	6	7
3	11	7	1
4	20	8	1

Number of litters studied, 65; number of young found, 242; average per litter, 3.72.

their first year of life, and to determine their sex as yearlings. This has yielded some positive information as to sex ratios in beaver litters. That sexes are born in approximately equal numbers is indicated by Table 5. Corroboration is also given for the conclusion that infant mortality rates among beaver are low, since in every case recorded in Table 5 I captured the animals as kits of less than two months of age, and recaptured them again as yearlings, no losses having occurred in the meantime.

A study of sex ratios among adult beavers is presented in Table 3, which includes the results obtained from sexing 207 carcasses purchased from trappers during the legal trapping season of March–April, 1935. Of these, 108 were males and 99 were females, a sex ratio of 1.08:1. This refutes the claim advanced by trappers that a heavy preponderance of males over females would be taken during a spring trapping season.

Salyer (1930) attempted to reconcile the trappers' claims of male preponderance with the approximate equality of sexes taken in 1935 by postulating a gross laxity in law enforcement during that season. According to Salyer, the state law requiring that traps be set at a distance of 50 feet or more from a lodge, burrow, or dam, was not enforced by conservation officers, which enabled trappers to catch all members of a colony indiscriminately. He inferred that had this law been enforced, a much greater proportion of males would have been taken by the trappers.

TABLE 5

SEX RATIOS IN LITTERS

NO. IN LITTER	SEX		NO. IN LITTER	SEX	
	♂	♀		♂	♀
4	2	2	2	1	1
4	3	1	4	2	2
4	2	2	4	2	2
6	2	4	4	2	2
5	3	2			
4	2	2	Totals 46	24	22

Number of litters studied, 11; number of kits found, 46; average number per litter, 4.18; sex ratio, ♂ 1.09 : ♀ 1.

I spent the entire season in the field, and my experience does not corroborate Salyer's theory. While some laxity of enforcement was apparent, it by no means reached the proportions inferred by Salyer.

The results of nuisance beaver control work in 1931 show that of the beavers examined for sex, 43 were males and 50 females, which likewise fails to bear out the theory of male preponderance at traps, as these animals were taken in spring and summer, many of them during the period of late gestation and birth of the young, exactly the time when, according to the trappers, the highest preponderance of males should occur. Even if it be true that males are often taken first in traps set on dams, trappers do not discontinue operations after the first animal is caught, and since females repair dams in every case after the male is removed, this would not result in any preponderance of males taken in traps.

The probable reason behind the trappers' theory that a large preponderance of males would be taken during a spring season seems to lie in the

prevalence among trappers of an erroneous method of sex identification. Mr. F. F. Tubbs, of the Game Division, and I carried on experiments during the 1935 season to discover whether or not trappers actually could determine sex in beavers. As the carcasses were brought to conservation headquarters for sale to the Department, we would ask the trappers to tell us which ones were males and which females. Despite the fact that these animals were skinned, exposing the external openings far better than is the case with unskinned animals, we found that females were generally identified as males. Unless the female was approaching parturition, in which case the teats are plainly evident, she would unhesitatingly be called a male by the trapping fraternity. The large castor glands, lying just above and behind the anus, were apparently taken for testes, and the lack of obvious nipples for further proof of maleness.

Had we depended upon trappers' identifications for our figures, the spring season of 1935 would have confirmed the thesis defended by Salyer, that males were taken in greater numbers than females at that time of year. Table 3, however, shows that the sexes were approximately equal. My conclusion, therefore, is that the theory of male preponderance in traps during a spring trapping season is due to erroneous methods of sex determination, and is contradicted by the evidence available.

Food.—Morgan (1868), Seton (1929), and others have attempted to list the kinds of plants used as food by beavers. A summary of these lists would be found to include nearly every plant growing within the range inhabited by the animals. Much difficulty is encountered in attempting to name the trees used as food because many trees are cut and dragged to the water to serve as material for the repair or construction of dams and lodges, as well as for food alone. It is seldom feasible to distinguish between these various usages of materials, so that trees may be included among the food plants that are really rarely, if ever, eaten. My observations indicate that beavers sample almost everything available as food, but their preferences are for a comparatively small number of trees.

The aspen group, the maples, and the willows seem to be preferred in the order given. Exceptions occur, however, which indicate some individual vagaries of taste.

I have observed a tendency toward the use of aquatic plants as food during the summer months, when tree cutting is at a minimum. Aquatic plants eaten under my observation include eelgrass (*Potamogeton*), duck potato (*Sagittaria*), duckweed (*Lemna*), water weed (*Elodea*), white water lily roots (*Nymphaea*), and yellow water lily roots (*Nymphozanthus*). I have watched beavers eagerly pulling and eating each of the above plants during summer evenings, and sometimes was unable to find that they were eating anything else at this time. Sometimes, however, the aquatic plants were supplemented by poplar bark obtained after nightfall.

The use of aquatic plants as food for beavers has been noted by the authors cited above, but I am inclined to think that the use of such plants is more extensive than has been heretofore recognized.

Very little has been published regarding the amount of food required by beavers. To secure accurate data regarding their food requirements in the wild it is necessary to know the exact number of trees cut during a definite period of time, and also exactly how many beavers were present during that time and occupied in cutting the trees and eating the food. It is rarely that these various factors can be known in the field. I have been able to secure data in which all of these factors were known on only two occasions.

In October, 1928, a pair of adult beavers was released by H. D. Ruhl on House Lake, Gladwin State Game Refuge. At that time there were no beavers on the refuge, nor in the vicinity, to the best of our knowledge. On June 12, 1929, when the beavers had been on the lake for 223 days, Mr. Ruhl counted the trees cut around House Lake, and measured the diameters of the stumps. Four kits were born on House Lake in May, 1929, but they were too small to cut trees at the time that Ruhl's count was made.

On May 29, 1930, 353 days later, I counted the stumps around the lake and measured the diameters. The 4 kits born on House Lake in May, 1929, probably began cutting trees soon after Ruhl's count, and continued to do so until after the count of 1930. Six kits were born in May, 1930, but these could not have been cutting until after the count had been completed.

The ground around House Lake was almost clear of undergrowth when the counts were made, and the work was carefully done, so I consider that the data obtained is as reliable as such data can well be under field conditions. The number of beavers present was positively known, as the result of live trapping and branding operations carried on before and after the tree counts were made.

Another tree count was made at Piper Lake, Ogemaw County. A pair of beavers migrated to Piper Lake from the Ogemaw Refuge during the first week of October, 1929. The date is known because the animals were seen crossing a road between the two points at that time.

I observed the two beavers swimming together in Piper Lake on July 5, 1930. No other beavers were living in the lake at that time, nor was there any evidence to indicate that others had been there meanwhile. The presence of other animals would not have been tolerated by the resident pair under normal conditions, and beavers were rare in Ogemaw County at that time. Hence, I feel that the assumption that this pair had occupied the lake alone during the period from October, 1929, to July, 1930 is justified.

Table 6 summarizes the data from House and Piper Lakes. The results indicate that a beaver in the wild cuts on the average .592, or approximately .6 trees per day.

Six captive adult beavers at Michigan State College consumed 180 trees

of diameters between 1 and 3 inches in one month, exactly one tree per beaver per day, or 365 trees per beaver per year. This agrees with Bailey's conclusion (1927) that "In feeding captive beavers in pens one small aspen one inch in diameter is generally found ample for one night's food supply for a full-grown adult". It should be kept in mind that captive beavers are unable to supplement their poplar diet by other foods as they can in the wild, which may account for the higher apparent consumption of poplar in captivity.

I have been unable to find any available formula for translating tree counts, with diameters of stumps, into terms of yield per acre of beaver food. Foresters use tables showing yield per acre of board feet or cord wood, but beavers eat bark and twigs, not trunks and large branches. Small trees are eaten much more completely than are large ones; trees with smooth bark are eaten more completely than those with rougher bark, even though the size may be equal.

TABLE 6

House Lake, 1929; 345 trees cut by 2 beavers in 223 days; .773 trees per beaver per day, 282 trees per beaver per year.

House Lake, 1930; 1040 trees cut by 6 beavers in 353 days; .491 trees per beaver per day, 179 trees per beaver per year.

Piper Lake, 1930; 283 trees cut by 2 beavers in 9 months; .524 trees per beaver per day, 188 trees per beaver per year.

Averaging the figures from the three counts; .592 trees per beaver per day, 216 trees per beaver per year.

In attempting to estimate the carrying capacity of an acre of poplar for beaver, many factors must be taken into consideration. Distance of the trees from water, slope of the ground, proportion of other trees in the stand, proportion of large trees to small ones, and other foods available, each influencing the number of trees needed per acre to supply a beaver colony.

For example, if the trees stand close together, many more will be lodged in falling, and so wasted from the food standpoint. Sometimes nearly one-half of the trees cut on a given acre are lodged against one another and wasted. Contrary to popular opinion, beavers are not sagacious woodcutters, and do waste much timber.

Beavers will not ordinarily cut trees more than 200 feet from the water's edge. Warren (1927) cited as unusual a tree 400 feet from the shores of Lily Lake in Rocky Mountain National Park, Colorado. Bailey (1927) said: "Beavers prefer to go only about 10 rods from shore for food, but in case of necessity they will sometimes gather food as far back as 20 or 30 rods." Orr (1935) said: "Aspen trees were cut for a distance of 2 or 3 or even 400 feet back from the edge of these small ponds, which is about the maximum distance that beavers will go to cut trees."

My own observations indicate that while the distances cited are valid, the animals may go much farther. Near House Lake, Gladwin Refuge, I found poplar trees cut and dragged to the lake from a measured distance of 650 feet. After the poplar had been cut to a distance from the shore of about 500 feet, the beavers practically ceased to cut poplar, turning their attention to scrub oaks instead. Oak trees are not ordinarily eaten by beavers, but they have furnished most of the bark eaten by the animals on House Lake for nearly 3 years. Macnamara (1929, p. 255) also mentioned the occasional use of oak as food by beavers.

The discrepancies between the number of trees cut per beaver in the two locations I explain as follows: The 2 beavers on House Lake during the period from October, 1928, to June, 1929, were adult animals, of large size, and the female bore and produced young during that period. These two adults would probably consume a maximum of food under such conditions. The 4 beavers added to the original pair for the second House Lake count were developed from kits to yearlings during the period under consideration, and were by no means as large as adults, even at the close of the period. Hence the total food consumption might well be diminished in comparison with that which would be consumed by 6 adults. The 2 beavers on Piper Lake were probably two-year-olds at the time of their arrival at the lake, and they did not produce young, a circumstance that presumably would lessen their food consumption somewhat as compared to adults producing young. Also the time of counting, July, was somewhat later, and beavers do not eat as much poplar during summer, then utilizing more aquatic plants and green herbaceous material. Hence, I conclude that the average obtained from all of the counts, 216 trees per beaver per year, represents approximately the requirements of a beaver under wild conditions better than any other available estimate.

Carrying capacity of poplar lands for beaver.—The average diameter of the trees cut by the beavers under my observation was 2.1 inches. According to Kittredge and Gevorkiantz (1929, p. 16), stands of poplar trees of about 2 inches average diameter include from 1500 to 3000 trees per acre, depending on the soil type and other factors. If we use 1500 trees per acre as a standard, and assume that one beaver will cut 216 trees per year on the average, one acre will support one beaver for about 7 years, or 7 beavers for one year.

If we use 3000 trees per acre as a standard, and assume that one beaver will cut 216 trees per year, one acre will support one beaver for about 14 years, or 14 beavers for one year. Of course these figures are only approximate at the best, as other trees and plants may also be available at the same time, and there will be some growth from sprouts to add to the supply. Thus 2 or 3 acres of poplar available to a beaver colony might easily last much more than 2 or 3 times as long as would 1 acre of equal stocking, due to the greater chance for new growth while the beavers searched less intensively for food material.

Using the figures as an approximation, however, we do have a rough means of estimating the carrying capacity of poplar lands for beaver. Since it has been shown that the average beaver colony in Michigan contains about 5 animals, it may with some degree of probability be estimated that one acre of poplar will support a colony for from 1 to 2.5 years, depending on the stand of poplar and other factors. Vague as this estimate may appear, it is certainly more dependable than other estimates have been in the past. A stand of large trees would probably be exhausted sooner, since there is usually more waste from lodging and also more waste from coarse bark uneaten. Stands of seedlings, very close together, might last longer, since they are eaten completely, and there is almost no waste due to lodging or uneaten material.

Emigration.—The experimental studies of beavers on the Gladwin State Game Refuge began with the introduction of 6 animals by H. D. Ruhl in the fall of 1928 (Ruhl and Lovejoy, 1930, p. 467). The experiment was expected to develop into an investigation of the dispersal and migration of beavers, through the marking and recapture of individual animals on the Refuge. The failure, however, of the tail tagging method of identification, which did not become evident until nearly 3 years had elapsed, and the subsequent difficulties encountered with the branding methods, delayed and partially nullified this line of investigation. The identity of many animals was lost when the tail tags dropped out, and with the uncertainty of the branding methods, and the rapid spread and increase of the colonies on the Refuge, I was unable to mark the young beavers as they appeared, so that presently I found the Refuge sprinkled with unmarked animals.

Only in the case of the colony on House Lake was I able to keep a complete and accurate record of the individual beavers from year to year. House Lake is about 10 acres in area, located close beside the Refuge keeper's lodge. It has no visible outlet, is spring fed, and is entirely unconnected with any other body of water.

An adult male and an adult female, each 3 or more years of age, were tail-tagged and released by Mr. Ruhl on House Lake, October 31, 1928. This pair produced 4 young in May, 1929, bringing the beaver population of the lake to 6 animals for that year. In May, 1930, 6 young were produced by this pair. In September, 1930, I caught every member of the colony, which included the adult pair, 4 yearlings born in 1929, and 6 kits born in 1930, or 12 animals in all.

At this time it was obvious that the tags were about to fall out of the tails of the adults, and they were branded, so that their identity would not be lost. The 4 yearlings were also branded, and their sexes recorded. The 6 kits were also branded experimentally, using much smaller irons than for the larger animals.

In September, 1931, I again caught the entire colony, which then consisted

of the 2 adults, 4 of the 6 kits born in 1930, and 6 kits born in 1931. The 4 animals born in 1929, now two years old, had disappeared from the lake, again leaving the population at 12 beavers. The brand numbers on the tails of the yearlings, branded as kits one year before, were now illegible, due to the large increase in size of the tails and of the individual scales of the tails during the year elapsed. A distortion of the tail, and a rough scar, were all that remained as proof of the previous branding. These animals were rebranded and released, the kits of the current year not being branded at this time.

Two of the 6 kits born in 1930 had also left the lake. The Refuge keeper reported having seen several sets of beaver tracks leaving the Refuge headed westward in April, 1931. How many, or which animals, left at that time we do not know. I think that these tracks were those of the two-year-olds, as I saw all 6 of the yearlings swimming on the lake at one time in July, 1931. The 2 yearlings must have left the lake between the middle of July and the second week of September.

In May, 1932, I captured the entire colony again, and found it to consist of the 2 adults, 4 female and 2 male yearlings, and a litter of very young kits, which I heard crying in their lodge. I released the female at once, and afterwards found that the litter consisted of 4 kits. Again the two-year-old animals had disappeared, and again the keeper reported tracks leading westward off the Refuge in April.

In April, 1933, I again caught the entire colony, consisting of the adult pair, and the 4 yearlings born in 1932. Once more there were no two-year-old beavers. The adult female was heavy with young at this time. Later observation showed that 6 kits were born in May, bringing the colonial population once more up to 12 animals.

In September, 1933, I caught the 2 adults from House Lake in Hoister Lake, about one-half mile east of House Lake, but separated by a brush-covered height of land. The kits born in 1933 had also accompanied the parents to Hoister Lake.

The food supply around House Lake was apparently running low at this time, all poplars having been cut to a distance of over 500 feet back from the shores, and the beavers reduced to getting most of their living from scrub oaks.

During the autumn of 1933, a pair of unbranded beavers took possession of the deserted House Lake, and produced 4 young in 1934. I did not get time to brand these beavers, but did catch them in 1935, when the colony consisted of 2 adults, 4 yearlings, and 4 kits, or 10 in all.

On December 20, 1935, the Refuge keeper caught, on the outlet to Hoister Lake, the original female beaver released on House Lake by Ruhl in 1928. Unfortunately, the beaver died in the trap. She seemed to be in excellent condition, weighed 48 pounds, and gave no evidence of decrepitude due to

age. She was at least 3 years of age in 1928 when released on House Lake, which would make her 11 or more years of age when killed. I know of no means by which the age of a beaver can be determined by inspection after the third year. Kits, yearlings, and two-year-olds are rather easily distinguished by size, and by breadth of tail, but after the third year there is apparently no criterion available for age determination. This female, with a known age of 11 years or more, offers possibly the only definite record of longevity in a wild beaver. Morgan (1868, p. 221) gave the ordinary duration of life for beavers as from 12 to 15 years. His judgment was based on reports from Indians and trappers.

Table 7 shows the sex, age, and numerical composition of the House Lake beaver colony from 1928 to 1933, and from 1933 to 1935.

The results of studies of the House Lake beaver colony indicate that the two-year-old animals leave, or are driven from, the colony shortly before

TABLE 7

SEX, AGE, AND NUMERICAL COMPOSITION OF HOUSE LAKE BEAVER COLONY, 1928–1933

DATE	ADULTS		YEARLINGS		KITS		TOTAL
	♂	♀	♂	♀	♂	♀	
October, 1928	1	1					2
September, 1929	1	1			3	1	6
September, 1930	1	1	3	1	2?	4	12
September, 1931	1	1		4	2	4	12
May, 1932	1	1	2	4	2	2	12
April, 1933	1	1	2	2	6		12
August, 1933							0

the birth of a new litter of kits. The yearlings are permitted to remain in the colony. This conclusion is corroborated by the data obtained during the nuisance beaver control work of 1931, where it was shown that no two-year-old beavers were taken by live traps from a colony containing kits. Morgan (1868, p. 135) reached the same conclusion.

I can offer some confirmatory evidence to support Morgan's statement that old beavers are hostile to their own young when these approach maturity at two years of age. It is a matter of general knowledge among beaver farmers that fighting occurs in the spring, before the birth of the young. It is also a matter of common knowledge at present that beavers fenced in an enclosure never increase beyond a certain rather definite number. My explanation of this is that the two-year-olds are attacked by the adults, and if they cannot escape by emigration they are killed. I have accordingly advised beaver farmers to live-trap all of their animals each spring as soon as the ice breaks, and to remove all two-year-olds, releasing the remainder again. In this way they could reap an annual harvest of pelts, and thereby

at least gain something, while otherwise they would reap no harvest at all (Bradt, 1934, p. 12). To the best of my knowledge no beaver farmer paid the least attention to my article or to my verbal advice, so I cannot cite evidence to prove or disprove my claims.

Some additional evidence supporting this theory may be cited from the enclosure on the Gladwin Refuge. In this enclosure a pair of adult beavers was liberated by Ruhl in 1928. Kits were produced by this pair in 1929, 1930, and 1931, as verified by observations, although the exact number of kits was unknown. In the summer of 1931 all animals were trapped out of the enclosure and only the 2 adults and 3 young kits were present. Since there is no reason to believe that any animals escaped, the missing beavers must have perished. The inference is that they were attacked by the adults, and due to the small area of the enclosure, were wounded and died.

While none of these lines of evidence is sufficient to justify a positive conclusion if considered alone, the cumulative effect is considerable, and certainly suggests that two-year-old beavers are driven from the colony by the parents in early spring before the new litter appears.

The fact that the migrating beavers struck out boldly to the west from House Lake, although there were no lakes and streams for miles in that direction, while there were lakes and streams within one-half mile to the south and east, indicates that beavers, like muskrats, do not hesitate to travel overland in spring. Whether or not the westward overland trek signifies an instinct to travel west, or merely an accidental occurrence, I cannot guess. Little Trout Lake lying just south of House Lake was occupied by other beavers during the history of House Lake occupancy, as recounted, but Hoister Lake to the east was not. Yet Hoister Lake remained untenanted by beavers until its invasion by the adults from House Lake in 1933. Consequently, I do not believe that any conclusion can be drawn from the evidence at hand regarding the reasons for the direction taken by migrating beavers, other than that they may not do the logical thing from a human viewpoint.

Importance to the beaver of emigration.—I have shown that the beaver colony is a family unit, composed of a pair of adult parents, the yearlings, and the kits.

The forced emigration of the two-year-old animals in the spring, just before the young are born, has a profound influence on the ecology and distribution of the beaver. As a consequence of this emigration, the beaver colony is limited to 14 or less animals, since litters of more than 6 young are rare, and the presence of two successive litters of 6 each, plus the adult pair, would be necessary to bring the total number per colony to 14. Actually the total number per colony rarely exceeds 12.

The limitation of the colonial inhabitants to 14 or less prolongs the period of occupancy for each site, as the addition of other mature beavers would materially increase the rate of tree cutting for food, and would exhaust the accessible food supply more rapidly.

The emigration of the vigorous young animals provides a method for the systematic dispersal of beavers, because the animals are obliged to seek new home sites, and since the members of a colony resent encroachments into their territory by strange animals, the new homes must be established in places not already stocked by beavers.

I have been unable to determine whether the two-year-old emigrants seek new mates, or whether brother and sister mating takes place. If new mates are secured, the emigration would result in outbreeding, with a possible increase in vigor, and a lessened tendency for hereditary defects. In regions with an extensive beaver population, it seems probable that emigration results in outbreeding, as wandering males and females would be likely to encounter others of the opposite sex. Beavers produce young in the spring of their third year of life, so that the wandering two-year-olds would have all summer and early fall during which to select new mates. In regions where beavers are scarce, the chances of meeting other animals would be lessened, and brother and sister mating might result.

It may be conjectured that the development of the beaver colony as a unit of population has been due to a continuation of simple family life. The young are accepted as members of the family because of the bond between mother and offspring. The yearlings, still sexually immature, and of relatively small size, are tolerated as a matter of course. The two-year-olds, almost as large as the parents, and possibly showing signs of sexual maturity, are objects of jealousy and are consequently attacked and driven from the family territory.

SUMMARY

The present study is an attempt to secure more adequate data regarding beaver populations and beaver ecology in Michigan. Methods of live trapping, branding, and determining sex of beavers have been developed.

The number of beavers per colony is irregular, varying from 1 to 12 animals. The numerical average of beavers per colony for the 57 colonies studied intensively was 5.1.

The number of beavers per lodge is not a satisfactory unit for use in estimating beaver populations over extended areas.

The number and size of beaver dams afford little indication of the number of beavers present.

The "typical" beaver colony consists of an individual family, including the two parents, the yearlings born the previous year, and the kits of the current year.

Every member of a beaver colony aids in maintaining the colonial dams.

The average number of beavers born per litter is between 3 and 4. There is only one litter per year.

The two sexes are approximately equal in number in the beaver, the number of males slightly exceeding the number of females.

The beavers studied cut between 200 and 300 trees each per year.

One acre of poplar (aspen) should support an average beaver colony from 1 to 2.5 years, depending on circumstances.

Yearlings are permitted to remain in the colony, but the two-year-old beavers leave or are driven from the home colony shortly before the birth of the second annual litter.

Beavers do not always follow water courses during emigration, but may undertake long overland journeys.

The emigration of the two-year-old beavers provides a method of dispersal, and tends to establish new colonies in areas not previously stocked with beaver.

The size and composition of beaver colonies is such as to permit the efficient and economical use of food supplies adjacent to small bodies of water.

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