SPATIAL AND ENERGY REQUIREMENTS OF BEAVERS[1]

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ABSTRACT

The relationship between energy intake and metabolic requirements of beavers (*Castor canadensis*) is discussed in regard to the spatial requirements of three colonies. A 26-pound yearling beaver requires 850 kcal of digestible energy, or 1.5 lb of fresh aspen per day, to maintain its daily metabolic processes with no additional growth. In order for such a beaver to attain maximum growth, 2040 kcal or 3.6 lb of fresh aspen/day are required. An acre of aspen produces 5,840 lb of food, so there would be sufficient energy to maintain a population of 10 beavers for 442 days if no growth of beavers occured. If one acre of aspen would maintain the population for one year, there would be 2.8 lb of fresh aspen/day which could be utilized for growth within the population.

This study investigated the spatial and energy requirements of beavers (*Castor canadensis*) in three colonies in Crawford County, Pennsylvania. The period of investigation was from 1 January 1959 through 1 January 1962. Data concerning energy intake of individual beavers per day were based mainly on the daily food consumption per beaver per day previously reported by Brenner (1962). Other authors have reported on the movements of beavers (Beer, 1955; Hodgdon and Hunt, 1955); the current study, however, attempted to determine the feeding ranges during the period when the individuals in the colonies were establishing their winter food cache. The relationship between the energy intake of beavers and the metabolic requirements of the species under natural conditions has also not been discussed previously. In the current study, the energy requirements were investigated in relationship to the feeding ranges of the colonies.

TABLE 1

Quantitative characteristics of three beaver colonies

Colony	Approximately annual population size	Pond		Feeding range	
		Circumference feet	Area square feet	Circumference feet	Area square feet
1	5	4,000	7,000	12,500	66,000
2	3	9,500	23,000	12,000	45,000
3	16	11,000	28,000	14,700	77,000

This study was undertaken at three ponds on State Game Lands 200, located 10 miles northeast of Meadville, Pennsylvania. The dominant vegetation consists of quaking aspen (*Populus tremuloides*), black cherry (*Prunus serotina*), and red maple (*Acer rubrum*), with black willow (*Salix nigra*) at the edges of the ponds. Herbaceous species were largely cattails (*Typha latifolia*), sedges, grasses, and spatterdock (*Nuphar advena*). Sizes of the ponds varied from 7,000 to 28,000 square feet (Table 1).

METHODS

Feeding ranges of the individual beavers within the colonies were determined through monthly observations of the food trails leading from the edge of the pond into the feeding areas. The circumferences of the utilized areas were determined with a Keuffel and Esser map measurer and the square feet determined by a polar planimeter.

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Daily food consumption per beaver was determined by measuring the diameter of every tree utilized on the study area. Utilization refers to the removal by beavers of any tree or its parts from the vicinity of cuttings, regardless of its ultimate disposition (Aldous, 1938; Brenner, 1962). Amount of food per tree was estimated based on the work of Stegeman (1954) in the Huntington Forest of New York State. In Stegemen's study, the average amount of food in pounds per tree was determined for the various diameter classes. This was done by cutting a total of 118 quaking aspen, representing size classes ranging from ½ inch to 10 inches in diameter. The height of each tree was measured, and all leaves and twigs up to ½ inch diameter (including outside bark) were cut and weighed. All bark was removed from 109 trees of 4 inches diameter that were representative of the stand. On State Game Lands 200, the population utilized only bark and small twigs for food; branches were not used for the construction of dams and lodges until after the bark had been removed. Stegeman's (1954) results on the amount of food per tree were therefore used to estimate the food consumption of the beaver populations. The methods of determining the daily food consumption and the size of the study area are described in greater detail by Brenner (1962).

SPATIAL REQUIREMENTS

The feeding ranges of three adjacent beaver colonies did not overlap (fig. 1). Two of the three ponds were occupied by a single family, the remaining pond by

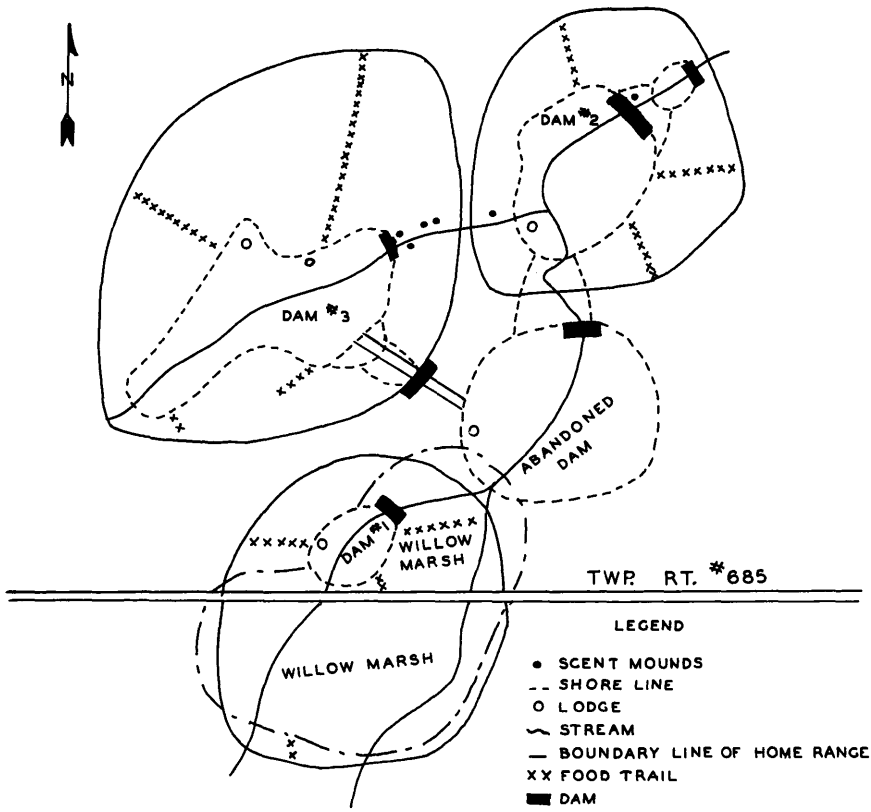

FIGURE 1. Feeding ranges of three beaver colonies (Scale: 1 inch=2,000 ft. In this figure a dam number indicates the colonies stated in Table 1.

two families. In this latter pond, both families established winter food caches and each spring both lodges contained an adult female with kits. This supports Hay (1958), who stated that a colony may have more than one lodge, but only one food cache per family. Joint utilization of the same pond was recorded in Russia by Semonoff (1953), who reported that the beavers showed a tendency to form colonies composed of related families. Therefore, a colony is defined in this paper as all the beavers that occupy a single pond, rather than just those animals in one family group.

The circumferences and areas of the three ponds, and the terrestial feeding ranges of the three colonies are summarized in Table 1. The areas of the feeding ranges do not include those parts covered by water. The sizes of the feeding ranges did not vary during the three years of the study. A black willow marsh surrounded the lake occupied by colony number one, the boundaries of the marsh indicated by the broken line shown in figure 1. Food trails originated at the edge of the pond or marsh, depending on the water level and availability of food. The feeding range of colony number 3 was larger than those of either of the other two colonies, and the available food supply averaged 700 feet further from the edge of the pond than that of the other two colonies.

Beavers usually feed close to the edge of the ponds; however, they tend to travel further for food during the period September through November, when establishing their winter food cache. The greatest distance traveled for food was 2,500 feet from the edge of the pond. The maximum distance these beavers would travel for food could not be determined during this study.

During the breeding season, in February and March, the beavers in all three colonies constructed scent mounds along the streams in their feeding ranges. These scent mounds were made of mud and vegetation. During construction, the beaver placed a mixture of urine and secretion from the castor (preputial) gland on the scent mound. These scent mounds were observed only during the breeding season.

ENERGY REQUIREMENTS

The daily food consumption of beavers has been the subject of many investigations. The results of some of these studies have shown variations of from 1.5–2.2 lb (Brenner, 1962), or 1.4–2.1 lb (Aldous, 1933), up to an average of 4.5 lbs of food/beaver/day (Bradt, 1947; Warren, 1940; O'Brien, 1938). It was determined by Brenner (1962) that, in the area studied, quaking aspen was the principal food of beavers. Cowan et al. (1950) reported that the energy content of fresh aspen is 1156 kcal/lb. Currier et al. (1960) demonstrated that beavers possess the ability to digest from 32 to 33 per cent of the cellulose ingested. Because crude fibre (cellulose) averages 28.1 per cent of the tree and the digestibility decreases as the percentage of crude fiber in the diet increases, a value of 50 per cent digestibility for the total tree may not be too much in error (Swift and French, 1954). Therefore, one pound of fresh aspen is believed to yield 580 kcal of available energy. Stephenson (1956) reported that a 26-lb beaver requires 850 kcal of digestible energy per day in order to maintain its daily metabolic requirements. However, Pearson (1960) suggested that this value should be 760 kcal of digestible energy per day. The daily food consumption of aspen for a 26-lb beaver, based on the above figure of 850 kcal, would be 1.5 lb or for a heavier adult beaver (35–40 lbs), 1.8–2.0 lb. Stephenson's (1956) laboratory determinations of 1.5 lb of aspen/beaver/day agree with the results of 1.5–2.2 lb of aspen/beaver/day obtained under field conditions (Brenner, 1962).

DISCUSSION

The daily food intake of beavers during the winter months (November through March), on Pennsylvania State Game Lands 200, was 2.2 lb of aspen, and the

daily food intake throughout the year was 1.5 lb (Brenner, 1962). This study also showed that herbaceous vegetation is an important factor in the diet of beavers during the summer months and that the utilization of herbaceous vegetation during these months enables a stand of aspen to support a population for a longer period of time.

The following discussion of a theoretical population of 10 individuals is based both on field observations of the three colonies on State Game Lands 200 and on the earlier study (Brenner, 1964) on the reproductive potential of beavers in Crawford County, Pennsylvania. Numbers of individuals within colonies did not appear to vary throughout the study. Earlier results (Brenner, 1964) indicated that the average potential litter size was 5.04 embryos per female and that resorption occurred in 16.7 per cent of the pregnant females examined. Because, in the majority of cases, there is only one reproducing female per colony, the size of the population would remain relatively constant; therefore, a theoretical population of 10 individuals is probably similar to the size of the average colony in Crawford County, Pennsylvania. If no growth of individuals occurred, the energy required to maintain a theoretical population of 10 individuals (2 adults, 2.0 lb of aspen/beaver/day; 4 yearlings, 1.5 lb of aspen/beaver/day; 4 kits, 0.8 lb of aspen/beaver/day) would be 15,259 kcal or 13.2 lb of fresh aspen per day. One acre of aspen on State Game Lands 200 produced 5,280 lb of food, so it would maintain a theoretical colony of 10 beavers for 442 days, 77 days longer than the previous estimate of one year reported by Brenner (1962). There would still be sufficient energy available to enable limited growth of young beavers during the winter months. If the theoretical population utilized 13.2 lb of fresh aspen/day (4,810 lb/year), there would be 1.030 lb of fresh aspen/year, or 2.8 lb/day, which could be utilized for growth of individuals within the population.

During the winter months, the main source of energy is the food cache. It is doubtful if the energy content of aspen would decrease appreciably during the winter months. However, the digestibility may decrease due to the possible leaching of nutrients from the stored food, reducing the energy content of the stored food and thus the useable energy per lb of food intake. At present, data are not available to support or reject this hypothesis. However, this should not affect the results of this study, because the energy requirements are based on the total food utilized by the populations throughout the year, including the food material stored throughout the winter months. These results are based on the assumption that the greatest amount of body growth occurs during the summer months when the population is utilizing primarily herbaceous vegetation for food.

The three colonies of beavers in the study area fed entirely within their feeding ranges; there was no overlap of ranges (fig. 1). Thus it is obvious that the food supply within the feeding ranges must have been sufficient to maintain the population. The range of movement of some mammals (*Rattus norvegicus*, discussed by Davis et al., 1948) is related to harborage and food supply, and radical changes in the environment may thus change the area occupied by the population. The same phenomenon probably holds true for beavers. The interaction of availability of food and water in relation to population size probably determines the size of the feeding range. The distance that a beaver will travel for food would be influenced by the distance of the food supply from the pond and the size of the impoundment. The population size would determine the amount of food required by the colony and could thereby influence the size of the feeding range.

The construction of scent mounds during the breeding season may serve as one mechanism for the establishment of a feeding range, as well as be a function of the breeding behavior of beavers. Carpenter (1958) stated that beavers mark their possessed territory, which is elaborately modified, by scent and also use various sound signals to defend the area. However, Carpenter (1958) did not

elaborate on what these possible mechanisms for marking the possessed territory might be or how they might operate within a colony or series of colonies.

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