THE EASTERN CANADA PORCUPINE - *ERETHIZON DORSATUM DORSATUM* L.

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FIELD AND LABORATORY STUDIES

ON

THE EASTERN CANADA PORCUPINE - *ERETHIZON DORSATUM DORSATUM* L.

By

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SCOPE AND CONTENTS:

The study, extending over two summers and one university year, was an endeavour 1) to determine the existence and nature of an innate activity pattern in porcupines under laboratory conditions, 2) to determine the behaviour of porcupines in their natural habitat, 3) to compare field and laboratory data on the behaviour of the porcupine and 4) to determine the home range of the porcupine.

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INTRODUCTION

In spite of the vast amount of work and voluminous literature written on the fauna of the world, there are still many aspects concerning certain animals about which little or nothing is known. Anderson (1919) points out that through the channels of the Audubon Society movements, local bird clubs, natural studies in public schools as well as through the technical guidance of scientific ornithologists, the objects and methods of bird study have become fairly well known. In the study of mammals, however, our knowledge has not been developed as broadly or systematically. To the study of the comparative anatomy and physiology of the major mammalian groups, particularly where such knowledge becomes of direct importance to humans, considerable attention has been focused. The ecology of species and their life histories, however, are less well known than corresponding relations in birds.

Domesticated mammals, because of long association with man, are best understood. Still much knowledge of the more intimate life history of many of the game mammals, such as deer, elk, moose, and bison, is either lacking completely or else the reports on them do not always agree. The decrease in numbers of certain furbearers has served to emphasize that

more knowledge about means of outwitting the animal during trapping seasons is not enough if at least the present population is to be maintained. Nor are the furbearers alone the only animals of economic importance to mankind. Many species of animals are of little value as food, fur, or skins, but are of great importance to man otherwise. Some are beneficial as predators on harmful species while others are detrimental to man as hosts to diseases. From an agricultural point of view, other forms are harmful by virtue of the damage they do to grain and fruit crops, and the predation on domesticated animals. Anderson (op.cit.) quotes Professor Hubert Osborn as saying, "Not a single farm product but is affected directly or indirectly by some animal activity." Taylor (1919) feels much is yet to be learned concerning the following: means of detecting presence of particular species; habitat relations; interrelationships of species; times of activity; migration, hibernation, and estivation; movements; habits associated with feeding and drinking; relation of characteristics and habits to existence and survival; breeding habits; nests, shelters and places of resort; present and former status; and other information on periodicity, effects of daylight and glands, weight, and dimensions. Even as late as 1946 Burt maintains that not enough is known about any kind of mammal to enable one to make a detailed statement of its economic status.

One of the commonest of our forest animals is the Canada porcupine, Erethizon dorsatum. This thesis is con-

cerned with an investigation of certain aspects of the biology of the animal. Although much has been written concerning this large rodent, yet despite its economic importance as a destructive animal in many forested areas, rarely has the animal been the focus of intensive field and laboratory study. Perhaps the lack of intensive investigation concerning the porcupine may be associated (1) with its partly nocturnal habits, (2) a lack of realization of the extent of the damage the animal is capable of causing in certain areas where forest and agriculture are the important industries, and (3) a possible reluctance on the part of would-be investigators to handle such an animal whose very nature and form demands caution and care in handling.

EXTENT OF INVESTIGATION

The studies embodied in this thesis followed two main approaches. These were (1) a study of certain aspects of the ecology of the animal in its natural environment, and (2) a laboratory study of the porcupine in an attempt to determine as near as possible under laboratory conditions, the innate behaviour of the animal in response to controlled factors such as light, temperature, and humidity.

Phase (1) of this investigation is based on field studies during the summer of 1952 at which time the writer was employed by the Canadian Government to carry on survey of porcupine damage to forest trees at the Acadia Forest Experiment Station in New Brunswick. Field work on the porcupine was also carried on at Snakeskin Lake in Hagerman and Burpee counties in Northern Ontario during the summer of 1953. The laboratory studies were carried out at McMaster University, Hamilton, Ontario, during the 1952-53 winter session.

Related Studies

Only during the last three decades has new understanding of the more intimate nature of certain animals been revealed through a study of their innate behaviour rhythms. Much remains yet to be tested in this methodical analysis of animal behaviour before a considerable measure of certainty

of correct interpretation can be claimed.

According to Welsh (1938), light production, colour changes, retinal changes, metabolic and general activity rhythms among animals may persist for long periods of time in the absence of changes in the external environment on which they are normally dependent. Numerous studies of persisting diurnal rhythms in animals have been made and various suggestions have been offered to explain the persistence, but in no instance has there been a satisfactory experimental demonstration of the complete chain of events which keeps the internal rhythm or cycle operating. Although much has been done in lower animal forms, the experimental study of diurnal activity rhythms in mammals has been confined almost exclusively to rodents, and among the rodents the albino rat has received the most attention.

Neither time nor space here would permit anything more than a few references to the work of others on the study of activity rhythms of animals. Nor can but a brief mention be made of the results obtained in the studies here cited.

Browman (1937) in studies of the albino rat, found peaks of daily activity, during normal day-night, or during controlled 12-hour periods of artificial light and darkness, occurred during the night or during darkness. Reversal of the light and darkness caused a subsequent reversal of daily activity. Constant artificial light for a period of weeks

was found to cause fluctuations in the daily activity rhythms of the female rat. Peaks of activity occurred for five or six days during the solar night, then, after one to three days of irregular activity, the peaks occurred during the solar day. Rats in constant darkness, and blinded rats, were found to maintain the rhythm of daily activity with which they entered the dark.

Richter (1927), studying the albino rat, found active periods at intervals varying from one to two hours. Also the activity within each period is slight at the beginning, but increases as the period advances and reaches the maximum usually near the end. Richter associated these one to two hour activity peaks with the gastric movements of the animal and also a four day activity rhythm with the ovulation cycle of the female.

Johnson (1926) showed a well defined and persistent daily rhythm existed in the activity of the forest deermouse, Peromyscus. Peromyscus kept in constant darkness as long as seven months still continued to exhibit daily periodicity. Reversed illumination resulted in a reversal of activity period. Attempts to establish artificial days of sixteen hours length failed. Young mice born in darkness, and kept for six weeks with their parents, were found to have an activity period which corresponded with their parents', which at the time was not in phase with the period of darkness outside. Johnson believed that the persisting activity rhythm of

Peromyscus is not produced by, nor dependent upon, environmental conditions, but rather is of an internal physiological rhythm.

Davis (1933) observed both the 1 - 2 hour feeding rhythm and the 24-hour activity rhythm in Microtus. The longer cycle was found to have its peak immediately after sunset--even when the animal was fed different foods and at different times. The average amount of activity was found to fall away slightly during the night while after sunrise it became much reduced. Placed in darkness, the twenty-four hour rhythm of Microtus was maintained and though the pattern was somewhat different in character, the peaks occurred at the same time, i.e., just after sunset.

Wolf (1930) found the Japanese dancing mouse to be more active at night between 6 p.m. and midnight, and a second period of activity to occur in the early morning hours. These activity periods were maintained in constant darkness except for slight shifts in the onset of activity. Records were obtained on mice born and raised in darkness and a marked periodicity in activity was found, although it was not correlated with outside day and night. Wolf recorded feeding and general activity separately and found the feeding period so regularly distributed over periods of high and low activity that he concluded there was no apparent connection.

Griffin and Welsh (1937) found daily periods of activity for bats to occur in the early evening and a second

period of lesser activity usually occurring in the early morning.

An internal twenty-four hour cycle of metabolism was shown by Werthessen (1936, 1937) to occur in rats and man during thirty-six hour fasts. In both, the rate of oxygen consumption and carbon dioxide production were high at the beginning of the run, dropped to a minimum at about the 16th hour, and then rose to a second maximum near the 24th hour. After this, unpredictable variations set in.

A review of the literature has failed to reveal a single instance in which continuous activity recordings had been made using the porcupine. The most extensive experimental study of the porcupine appears to have been that carried out by Sackett (1913) on the learning processes of the animal.

THE PORCUPINE

Distribution

Anderson (1946) indicates that one species of Canada porcupine is currently recognized in the genus Erethizon. Although six sub-species are known to exist, by far the greater number belong to either the black-haired eastern porcupine, E. d. dorsatum Linnaeus, or the yellow-haired western porcupine, E. d. epixanthum Brandt. The yellow-haired porcupine ranges over the plains and mountains from Turtle Mountain, N.D. and Wood Buffalo Park westward, while the black-haired porcupine is found mainly to the east of that but occasionally occurring as far west as northern British Columbia. In the overlapping zone intergredation occurs. It is because of this intergredation that Anderson considers the two types as belonging to one species instead of two.

According to Taylor (1935), "the porcupine is found, with certain outstanding exceptions, throughout the forested area of the continent of North America, mainly in Hudsonian, Canadian, and Transitional Zones". The animal is well adapted for its occurrence in an extended series of habitats which confine many other plants and animals.

Kingsley (1888) notes that the North American genus Erethizon is a transitional type in habits and form between

the Old World ground-loving, non-climbing porcupine and the highly arboreal species of South America. Some of the latter possess prehensile tails.

Habitat

Porcupines are found commonly in forests, containing rocky ridges, and coves, and have turned up in such exceptional habitats as the tundra, grasslands, cities and farm crops. Because of the great diversity of its feeding habits, the porcupine possesses a great capacity for readily adapting itself to a wide range of habitats. Dicks (1938) suggests the possibility that the relatively high humidity of the coastal areas may be a limiting factor in the distribution of the species rather than availability of food.

Maps showing the extent of distribution of the Erethizon porcupine occur in the works of Baird (1859), Anderson and Rand (1943), and Hamilton (1943).

Dens

The porcupine is an expert climber not only of trees but also of the rocks among which it finds dens. The dens serve mainly for shelter against winter rains and snows. Here also the young are born. The exact length of time that the newborn stay within the dens with the parent has as yet not been determined.

The dens used by porcupines vary considerably in size, depth, and form. Dens examined by the author at the Noonan Ledges near the Acadia Station varied from small

shelters formed by overlapping rocks to narrow crevices of sufficient height to admit a human adult with ease. The depth of such dens as shown in Figure 1 was found to extend fifteen feet or more back from the entrance, the whole length showing signs of having been occupied. Judging from the amount of recent pellets found in such dens it would appear that the number of occupants varies directly with the size of the dens. Hamilton (1939) writes, "The larger dens may house a number of animals of mixed sexes, while the small cracks or shallow retreats in the rocks are used by single females as farrowing dens. It is comparatively easy to locate dens by the large number of damaged trees in the vicinity. Usually the porcupine shows a marked preference for den sites which have a southeasterly or southwesterly exposure."

The porcupine is a very untidy housekeeper, the floor of its den being littered with pellets and bits of sticks. In all the porcupine dens I had examined I failed to find any specially prepared nests, although frequently winds carry small amounts of dead leaves within the dens. The smell of urine is prominent throughout the den even long after the porcupine have left it. The lack of recently dropped pellets in the dens during the summer investigation was considered as an indication that the dens in question had not been used by porcupines for a month or more previously.

Nor are rocky crevices the only type of abode suitable as dens. Windfall trees frequently serve for shelters, particularly during the summer months. An odd porcupine residence was found in the form of an abandonned oil-drum stove shown in Figures 2 and 3.

Figure 1 - The deep narrow crevices among the rocks of the slopes at the Noonan Ledges frequently accord ample protection for porcupine against cold winter rains.

Figures 2 and 3 - An abandonned oil-drum stove which had been used as a den by porcupine. Pellets fill the drum to the level of the door opening.

Description

The name, derived from the Latin words meaning "pig" and "spine", is an excellent descriptive word, for the porcupine is covered dorsally by a characteristically dense coat of sharp spiny quills. The ventral surfaces of the body, face and legs are free of quills. The eyes are small, black, and bead-like. The ears are almost completely hidden by the long hair and quills behind the eyes. The squat, strongly arched body is supported by short stout legs which are covered with stiff hairs. The padded paws are naked, tough, and leathery; the forepaws bearing four, sharp, grooved claws, the hind possessing five claws. The gait is plantigrade. The blunt, triangular tail serves a triple function, that of defence, sensory, and as a supporting appendage.

Taylor (1935) claims the weight of mature porcupines ranges from 15 to 43 pounds. One animal I captured at the Acadia Station weighed approximately 30 pounds. Others taken by me ranged from 12 to 25 pounds. Generally I found the captured male to be somewhat larger than the female. Shapiro (1949) lists weights of animals captured by him as follows:

Males	Females
23.5	17.7 (gravid)
20.0	
13.5	13.5
10.0	13.0 (gravid)
9.5	
8.6	10
6.0	9.9 (gravid)
	9.9
	6.3
	6.0
	5.0

Weights in pounds of captured porcupines
(Shapiro 1949)

Two specimens kept in captivity by me for experimental purposes from September 1952 until May 1953 exhibited winter and spring pelage changes. The room in which the animals were caged was unheated until after Christmas. In mid November both animals, but particularly the male, developed a dense coating of long, fine, black hairs which practically hid the quills except when the animals were aroused. This undoubtedly aids considerably in enabling the porcupine to withstand, as it does, the rigors of the most severe winter. During March, with the onset of warmer weather, the female

was noted to shed large numbers of quills and hair in a relatively short time. The change in coat of the male was observed to occur later and more gradually. Struthers (1928) claims that porcupine kept in captivity where the temperature never drops below 50° Fahrenheit do not grow a thick winter coat. Colour variation is not unusual in this species of porcupine--ranging from light brown to black. For example, Brown (1948) describes the find of a yellow-haired eastern Canada porcupine. Generally these animals are dark brown or black. Albino porcupines, although extremely rare have been noted by Shiras (1906, 1911), Struthers (1928), Benard (1941), Anderson and Rand (1943).

The quills of the porcupine are actually modified hairs. Messer (1947) claims that they are formed from numerous hairs joined together. Commonly the quills lie flat against the animal's body and point caudad. The quills are loosely attached by a slender root embedded in a specialized layer of muscles just below the skin. Contraction of this layer causes the immediate erection of the quills when the porcupine is stimulated. The tip of the quills are covered with microscopic, overlapping retrose scales. The barbed action of these scales combined with the muscular activity of the victim move the whole quill inward once a penetration is affected. A white crystalline substance with myriad of microscopic air spaces forms the core of the quill. These numerous air spaces render the quill buoyant in water, and

aid the animal in its swimming. Gabrielson (1928) suggests the possibility that the softening of the quills, and the consequent reduction in their efficiency as a means of protection, causes the porcupine to seek shelter of rocky ledges at the time of wet weather. Concerning the effect of moisture on porcupine quills found in the digestive tract of porcupine predators, Quick (1953) writes, "The porcupine quills found in the specimens reported here were examined under a compound microscope. All except one short quill were found to be frayed at the base. It appeared that either digestive or abrasive action, or both, had begun a reduction of the quills. Several quills found 'free-floating' in the abdomen appeared to have lost effective penetrability. Microscopic examination revealed that the barb scales were either worn away or very soft. Body fluids might have a tendency to soften the quills. The fact that quills were found piercing the stomach lining and other organs indicates that some time is required to reduce the quill to relative harmlessness. Variations in the length of the quills found show that such a process is possible. Some quills, it was noted, were reduced to lengths of about four millimeters. Those found in the organs of the abdominal cavity probably were ingested with hide and flesh."

Senses

Before discussing the behaviour of the porcupine, a few remarks concerning the means of directing those activities

of the animal may be appropriate here. A consideration of the external senses based on field observations of the porcupine may explain many of the modes of response of the animal to its environment.

On numerous occasions, particularly at the Snakeskin Lake location, I had been able to approach closely to porcupine feeding on aquatic vegetation before they showed any apparent signs of recognizing my presence. This delay of response suggests that either the sight of the porcupine is not very well developed or else, as in many other animals, there is a natural reluctance to respond to slight and gradual environmental changes. The majority of the enemies of the porcupine approach swiftly. A slowly approaching object, therefore, may not be considered as a potential source of danger. Once I had been discovered standing near by, the animals stopped feeding and turned from side to side sniffing the air. A note of annoyance generally followed during which the porcupine would chatter its teeth for varying lengths of time. Further response varied from one animal to the next. A few, after a pause of two minutes or more, resumed feeding along the shoreline. Others, however, generally moved slowly toward the shelter of the forest a few feet away. Spencer (1950) notes that porcupine, like many other animals, seem to discern and take alarm at a moving object but pay little or no attention to a motionless one.

The sense of touch, on the other hand, is widely employed by the porcupine. While climbing, each step forward

is explored and tested with the forepaws before the full weight of the body is applied. Descent from a tree is accomplished backwards, the tail shifting from side to side "feeling" the trunk slowly and deliberately. Descent along sloping large branches of trees, however, is accomplished while travelling forward. The long stiff hairs which project beyond the quills of the body also appear strongly sensitive to touch. On numerous occasions I have gently touched the long hairs of the back of quiescent porcupines. The response was invariably an instantaneous bristling of the quills and a turning of the tail in my direction.

The sense of smell among porcupines appears to be fairly well developed and is frequently used in feeding. The animals were often seen to sniff along a twig until they reached leaves but a few inches away. One might suggest, therefore, that limitations in the development of the porcupine's eyesight are compensated for by the greater development of the sense of smell.

Like the sense of sight, field observations indicate that the sense of hearing may be poorly developed in the porcupine. Particularly while feeding or resting, porcupine appeared to fail to detect many warning sounds of danger which would have frightened away a more keenly aware animal. Animals feeding along the shore of Snakeskin Lake could frequently be approached with ease by walking in shallow water along the shore. A possible explanation for this may occur

in the fact that none of the natural enemies of the porcupine are aquatic, and therefore, the animal may have no reason to fear danger from that direction. In the woods, however, a snap of a twig was found to be sufficient warning to alert any porcupine. The response was invariably a retreat to safety, moving cautiously at first and then, if danger persisted, retreating in haste. As with other animals, one might assume the association of certain sounds with the concept of impending danger, while other sounds, by the process of conditioning, are merely attributed to the natural environment and are, therefore, disregarded. While observable responses to such crude auditory stimuli do not appear to be the best criteria for measuring hearing, yet only one study could be found in the literature concerning the extent of the range over which the porcupine may actually hear. Sackett's psychological studies (1913) showed that the porcupine respond more sensitively to sounds of lower than higher vibration rate such as the rustling of leaves or the rumbling of distant voices. He suggested that the vocalization of the species indicates a fairly wide range of tonal discrimination. The female possesses a high-pitched scolding yelp, while the more quiescent male courts in a muffled humming tone. Authors who have attempted to describe the vocalization of the porcupine include Batchelder (1930), Wade (1931), Seton (1932), and Saunders (1932).

Several features of particular interest concerning the voice of porcupine were noted along the shore near the

camp site on Snakeskin Lake. Almost invariably it was the high-pitched cries of the females that repeatedly awoke me during the nights and necessitated investigation. From the ten to twelve foot elevation of the promentory upon which the tent had been pitched, a porcupine could be detected for several hundred feet along the shore by using a powerful flashlight. If the area was searched during the hours between 9 p.m. and 2:30 a.m. in response to the sound of snapping of twigs along the shore, generally either a baby porcupine or a large non-vocal male animal was found. On the other hand, if search was made in response to the high pitched voice of the female, not only could she soon be found, but almost invariably there was another porcupine near by as well. The second animal was either a large male, another female, or a young animal. The female generally appeared to be either more intolerant of the presence of other porcupine, or perhaps, maintained contact with her young by calling. Also, more often than not, only during the evening hours did the noisy encountering between female porcupine and others of the same species occur. Female and young driven in different directions from the camp site during the night hours could frequently be heard vocally approaching one another near the upper reaches of the wooded ridge behind the camp. Nightly activity and vocalization generally began shortly after sunset and ceased as late as 4:45 a.m.

Movements

The movements of porcupine are of two main types,

seasonal and intraseasonal or daily feeding movements. According to Gabrielson and Horn (1930) seasonal movements are definite and pronounced. They are governed by climatic factors and depend upon the rainfall and the nature of the winter precipitation. In the more humid Northwest, the spring movements consist of a slow and deliberate migration from the cliffs and lava runs to mountain meadows and valley farms in search of succulent food. With the approach of the first cold rains, there occurs a more rapid movement back to the shelter of the dens, in which the porcupine remain for varying periods during stormy weather. The fall and winter feeding in these regions is usually within a quarter of a mile of the rim rocks. With the melting of the snow in the spring, and the growth of ground vegetation, the animals resume their ground feeding habits, moving again from the cliff regions as the season advances. Even in localities where there are no marked elevations, the movement is toward locations which offer greener food during the summer. In the drier regions, where both water and the resultant abundance of vegetation is lacking, Gabrielson claims the migration extends over a greater area than in the more humid coastal regions. In general, these movements depend upon the availability of food and shelter. Seasonal migration has also been noted by Struthers (1928), Couch (1932), Taylor (1935), and Spencer (1946, 1950).

The intraseasonal, or strictly feeding movements of

the porcupine are less definite, and, although they are in the general geographical direction of the seasonal migrations, they are simply foraging activities. A more detailed discussion of this aspect of the study is given under the section on home range.

Natural History

In spite of the abundance of popular literature on the porcupine, there exists, however, gaps in accounts of the life history of the animal. Frequently literature discussing the same phases has been found to be contradictory and thus leaves the impression that much more study of this animal is indicated.

Curtis and Kozicky (1944) suggest that porcupines are not usually considered as gregarious when absent from large permanent dens. Although Seton (1929) sometimes found a dozen gathered at a lumber camp, he maintained that these were accidental meetings. They are drawn together, not for each other's company, but for attractive foods not found elsewhere in the area. It is only during the mating season that they aggregate in groups. Breeding generally occurs during September and October. Even in mid-July, however, a male porcupine at Snakeskin Lake was seen to assume mating behaviour by the presence of a female, humming to her and showering her with urine as he stood up on his haunches and approached her. Following breeding, they return quickly to their solitary ways. With a gestation period of about seven

months, as indicated by Shadle (1948), young are usually born during April and May. Generally only one offspring is born at any one time, although in personal conversation with forestry personnel at the Acadia Station, reports of two young a year were made. These reports, however, were unconfirmed and the possibility exists that one female was caring for her own and one of separate parentage may have been noted instead. The possibility of two young is also mentioned by Keyes (1934). Kay (1932) claims he had killed a female porcupine as it was crossing his field in June with five immature ones following her. Seton (1929), on the other hand, maintains that twins in each family appears to be the general rule. It would be interesting to determine whether any correlation exists between the litter size and the latitude at which the animals are studied.

During the study I did not have the opportunity of observing a live porcupine younger than approximately one month old. Seton (1929) claims the young of the porcupine are well developed at birth, having teeth, open eyes, half inch quills, and being fully clothed with black hair. The placenta dries and drops off within twenty-four hours. Spencer (1930) notes that a newborn porcupine taken prematurely by him in a caesarean operation, was capable of walking within fifteen minutes of emergence. One of the first noticeable habits of the young animal was the characteristic flips of the tail when disturbed. Hamilton (1939) states that the young are very precocious and eat leaves and tender

shoots within a day or two of birth; however they apparently nurse for about a week.

Play among young porcupine is described by Hamilton (1939), Shadle (1944), Tryon (1947), and Spencer (1950). The young soon become independent of the parents. Nevertheless they frequently follow the parent female as she moves about foraging for food. At 2:00 a.m., June 29, 1953 at Snakeskin Lake, I stood for more than a quarter of an hour holding a flashlight on a mother porcupine two feet away as she suckled her young near the edge of the lake. A male animal fed on aquatic plants which had drifted ashore ten to twelve feet away. This specimen may, or may not, have been the male parent of the young. Several baby porcupine marked during the study at Snakeskin Lake were seen repeatedly with the same marked adult parent animals. Tyron (1947) suggests that the instinctive tendency of the young to follow closely anything moving away from it serves in the wild to keep the young close to their parent.

Although generally a docile animal, porcupine do on occasions strike at one another with the tail and make noisy, snapping movements with the prominent incisors. Kay (1932) describes fierce fighting between two male porcupines. Unlike most other victims, however, the porcupine possesses the ability to extract some of the quills received in such encounters. Cameron (1949) relates an occasion during which he observed a porcupine removing quills which had become em-

bedded in the body. With the hope of observing the method of copulation among porcupine, I had allowed on several occasions the two animals I had in captivity to move freely about in a large room for several hours. Frequently the male became sexually aroused and, standing on its haunches approached the female. She, however, being quite unreceptive, promptly struck the male under the jaw with her tail. Six or seven quills became firmly fixed in the skin. He withdrew sufficiently to be out of range of further blows and deliberately curling his claws as best he could, managed to extract four of the larger quills. I removed the remaining quills when he returned to the cage.

The growth of porcupines is rapid during the first seven months, followed later by a much slower rate. "If this change in growth rate coincides with the onset of puberty," suggests Tryon (1947), "it would appear that the male porcupine of this species (Erethizon epixanthum) can perhaps mate in December of its first year." Shadle (1951), on the other hand, suggests a porcupine can sire in sixteen months after birth. Struthers (1928) maintains a more conservative view that male and female porcupines reach maturity at the end of the third summer and autumn respectively.

Porcupines are generally monogamous, although cases of repeated mating have been noted by Shadle (1948) and Struthers (1928). Struthers believes that the species may breed twice each year, as he has seen young ones weighing two or

three pounds in September and in January. Considerable discrepancy appears to exist among various narrations on the position assumed during copulation among porcupines. Taylor (1935) cites three accounts of observed copulation related to him. The description of the posture assumed by the animals differed in each case. Shadle (1946, 1948, 1951, 1952) describes copulation among porcupine kept in captivity.

No certain methods for determining the age and longivity of porcupines in their natural habitat could be found in the literature. Taylor (1935) estimates the life span of Erethizon epixanthum as being about twelve years. Brown (1925) claims that a Malaccan porcupine (Hystrix lingcauda) received at the Philadelphia Zoological Garden on March 10, 1903, died on April 11, 1921--with a life span of more than eighteen years. Perhaps the latter species have a natural life span which is considerably greater than that occurring among Erethizon.

The fisher (Martes pennanti) and man are among the most successful enemies of the porcupine. Attacks on porcupine by fisher are described by Schoonmaker (1938) and Abbot (1945). Other authors describing attacks by coyote on porcupine include Sperry (1933), Keller (1935) and Murie (1951); Hamilton and Russel (1939), Rollings (1945), Vos (1953) on attacks by bobcats; Musgrave (1927) on attacks by mountain lion; Weaver (1939) by gray fox; and Kendall (1944) described attacks by hawks and owls.

DESCRIPTION OF STUDY AREAS

The Acadia Forest Experiment Station

Located approximately fifteen miles northeast of Fredericton, New Brunswick, the Acadia Forest Experiment Station encompasses 34.5 square miles of forest within the limits of the Burpee Game Refuge.

The area, underlain by the Carboniferous Formation, is of the rolling plateau type, the general topography sloping from a 600-foot elevation in the northeast to a 100-foot level in the extreme south. The land is unsuitable for farming, the over-burden being sandy, gravelly soil with occasional outcrops of sandstone. The tributaries of five small streams constitute the only water-ways of the Station area. The area is typical of much of New Brunswick with forest composed of even-aged stands, for the most part of fire origin, with many age classes being represented. Prevalent forest types are balsam-fir, black spruce, pine and intolerant hardwoods such as maple and ash.

Under the present working survey plan, north-south blazed lines ten chains apart have been cut through the forests of the Acadia Station. This pattern extends across the entire forest from the east boundary to the west. Each of these blazed lines then had permanent working plan plots of

1/10 acre established along its length 10 chains apart. Each of these sections of an acre was marked by aluminum stakes bearing the number of the plot. In addition a square sheet of aluminum also bearing the number of the plot was nailed to the tree nearest the center. Almost 2,800 such permanent working plan survey plots were established on the Acadia Station.

Noonan Ledges

Situated two miles west of the northwest corner of the Acadia Station, yet still within the limits of the Burpee Game Refuge, exists the Noonan Ledges--a typical porcupine denning area. The ledges extend approximately for one mile in a north-south direction. A densely wooded valley 200 to 300 feet across separates the steep rocky slopes. Along the borders of the ledges, among the boulders and crevices, numerous porcupine dens were noted. Noonan Brook, which empties into Indian Lake south of the Station, flows along the base of the western slope of the ravine. Despite the shallow depth of the soil, white and wire birch, aspens, maples, spruce, fir, and white pine are plentiful, particularly in the valley and just beyond the top of the ledges. These provide ample feeding material for the concentrated porcupine population which appears to have inhabited the region in the past. Dens along the upper third of the slopes of the Noonan Ledges were usually found to show signs of having been inhabited by porcupines more frequently than those along the lower levels. This preference for dens along the upper lev-

els may be governed by the fact that less snow would tend to accumulate there during the winter, or a greater availability of food in regions beyond the rim of the ledges. In an investigation of a randomly selected area of two acre size along the eastern slope of the Noonan Ledges, I found evidence of 102 dens of various sizes having been occupied periodically in the past seasons. No recent pellets could be found in the dens during the mid-summer investigation.

Snakeskin Lake

For a period of five weeks commencing on June 8, 1953, the investigation here described was carried on in Northern Ontario. Situated approximately 25 miles north of Parry Sound, Ontario, Snakeskin Lake as seen in Figure 4 extends in an east-west direction, partly in the county of Hagerman and partly in the county of Burpee. Of glacial origin the lake lies between high, bare rocky surroundings which at some points along the north shore rise seventy to eighty feet above the level of the lake waters. The south shore has more gradual elevations and fewer rocky outcrops. The lake, almost four miles long, ranges in width from little over 150 feet across at the narrowest portion to approximately 3/8 mile across the widest region. While the average depth of the lake, based on six readings taken along the center of the lake, measured 26 feet, numerous shore inlets and protected coves were shallow enough for the growth of patches

of water lillies, rushes, and horsetail.

The prominent species of trees surrounding the lake were maple, elm, birch, pitch pine, spruce, cedar, and alders. Several dense alder swamps drain into the lake from both the northern and southern shores.

A mill clearing and an abandoned farm were found along the sand road which passed by the western end of the lake. Another clearing approximately twelve acres in area was located along the southern shore 1¾ miles from the road. An unoccupied log cabin and a stable were located in this clearing. Two other shacks are located at widely separated points along the north shore approximately ¾ and 1½ miles respectively east of the clearing. Several logging trails led to the water's edge from the southern woods. Along the greater extent of the shoreline, numerous drift logs and trees have been washed up onto the rocky shores by wind, wave, and ice. These play a leading role in the activity of the porcupines observed along the shoreline--particularly as shoreline extensions used by the animals in acquiring aquatic vegetation growing in water.

A brief note concerning the names I had designated for various points along the lake should be interjected at this time. The camp was located along the north shore at the end of a slight promentory approximately 1 3/8 miles from the western end of the lake. The shoreline indentation immediately west of the campsite is referred to as Camp Cove. The

narrowing of the lake ¼ mile west of the camp is referred to as the West Narrows, while a similar narrowing ¼ mile east of the camp is designated as East Narrows. On the southern shore 3/8 mile southeast of the camp is the Clearing--an abandoned farm of approximately twelve acres area and now grown over by shrubs, alders and weeds. Buildings still standing on the clearing include a log cabin referred to here as the Shack and used only seasonally by hunters, a small horse stable also of logs, and an outhouse. Behind the buildings was an old stump which had at one time been saturated with salt solution to attract porcupines and thus protect the buildings. Only a small fraction of the large stump remains and is still frequented by porcupines. Immediately west of the clearing is an area named West Cove--the location of the most frequent observation of porcupines at Snakeskin Lake.

Figure 4 - Snakeskin Lake and surrounding territory. Georgian Bay lies to the left of the map, Parry Sound, Ontario at lower center.

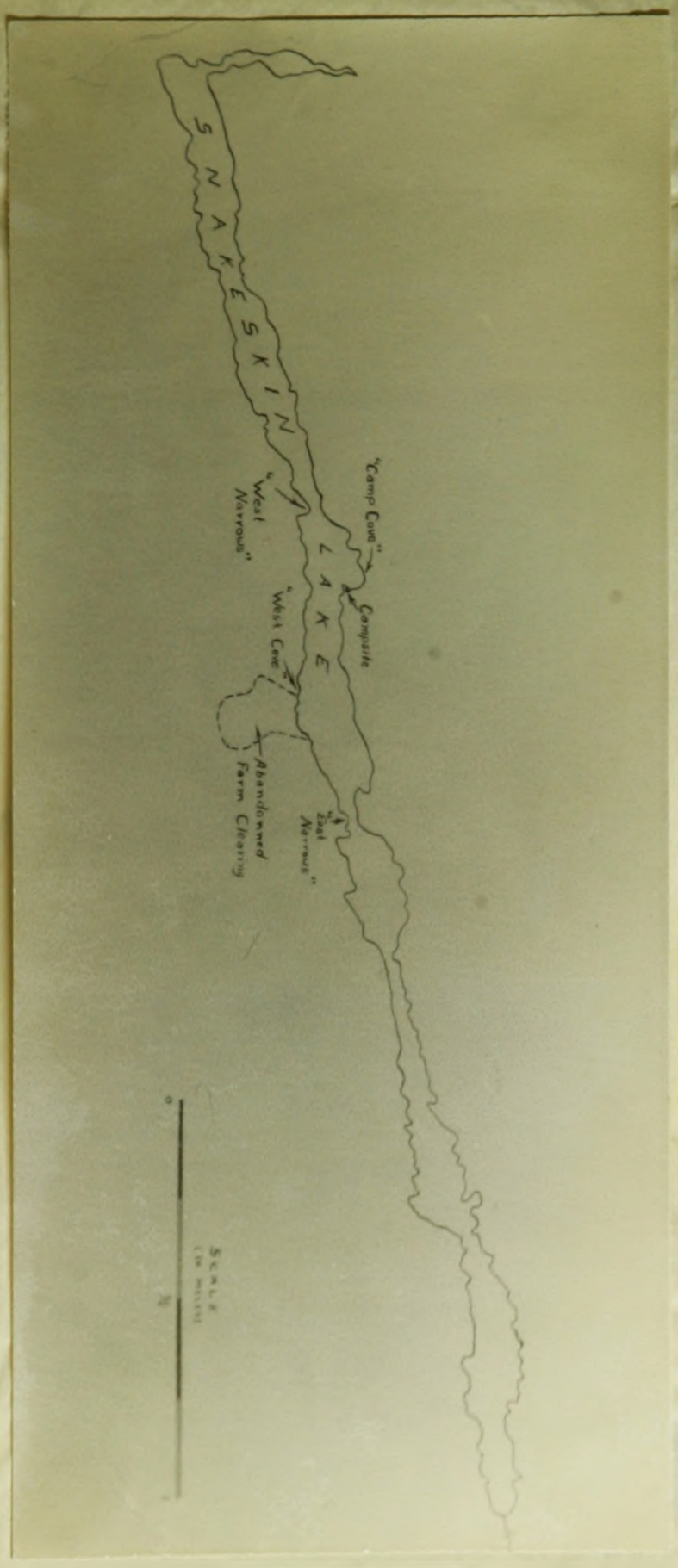

Figure 5 - Snakeskin Lake showing campsite and surrounding area.

METHODS

The ecological studies of the porcupine carried on at the Acadia Station were done in connection with the survey of damage by porcupines to the forest trees, and in studies at the Noonan Ledges. Many of the observations recorded at the time were included under sections describing the porcupine and its habitats.

In order to become more familiar with the topography of the Station and the biology of the porcupine prior to the actual damage survey, I spent several weeks of extensive random searching for porcupines over a greater part of the 22,000 acres of the Acadia Station. Because of the limited transportation facilities, much of the road travel accomplished in this phase of the study was done after supper hours when a large army jeep was available for this purpose. This time of day proved rather favourable for such observations.

During the course of recording the damage data, observations on the porcupine were noted whenever possible. In travelling from one working survey plot to the next, either my student assistant or I concentrated on following the often obscure N.-S. blazed line, leaving the other free to follow a zig-zag course to note the presence or evidence of porcupine. Denning areas encountered during the survey were briefly examined at the time, the exact location with reference to plot

numbers marked on the field map, such as shown in Figure 6, and the area listed to be re-examined once the damage survey itself was completed.

In an endeavour to learn more concerning the feeding habits of the porcupine during the summer months and on the nature of the parasites which appear to infest the digestive tract of most or all porcupines, it was hoped that one porcupine a week could be killed, brought to the Station laboratory where the viscera were to be removed and preserved in gallon jars using 15 per cent formaldehyde solution. During the course of the summer, the viscera--including stomach, intestines, heart, lungs, and kidneys-- of twelve porcupines were preserved and forwarded first to the National Herbarium, National Museum, Ottawa, and then to the Institute of Parasitology, Macdonald College, Quebec, for analyses of stomach contents and parasites respectively.

In order that the results of the extent of damage inflicted by porcupines on the Acadia Station might be better understood, it was felt desirable that some estimate of porcupine population be made. Such a study as described by Curtis (1944) could best be carried on after a light snowfall when the animals could be followed by their footprints, and no longer would the concealing element of foliage be present. Such a population survey as described by Curtis, necessitates the employment of many more individuals than could be afforded for a similar study at the Acadia Station. An alternative

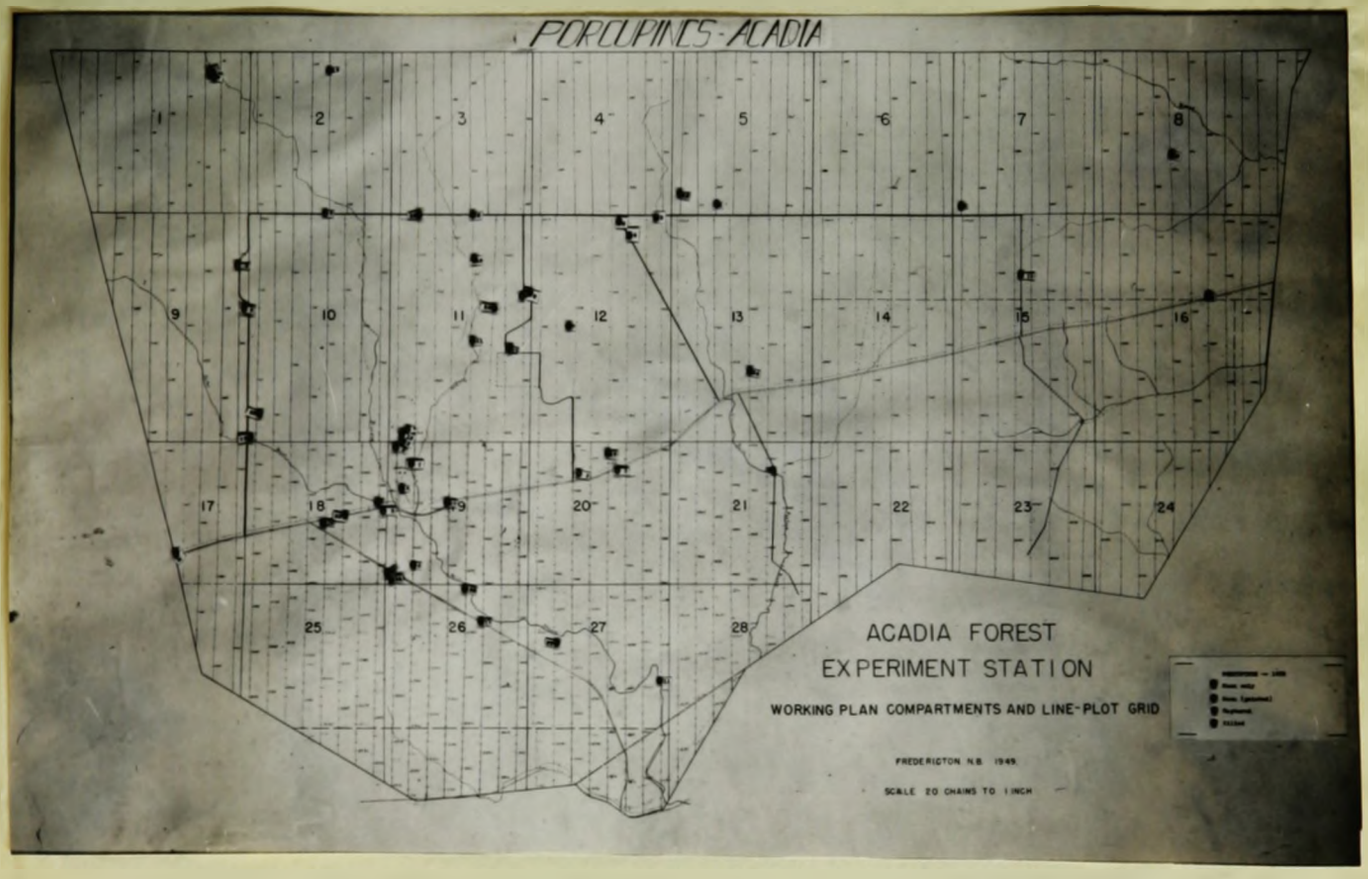

Figure 6 - Map of the Acadia Forest Experiment Station, Sunbury County, New Brunswick, where the survey of porcupine damage was made during the summer of 1952.

plan was instituted whereby each individual working in the forest at Acadia was to submit a weekly census sheet recording information on any porcupine encountered on the Station during the week. Further questioning of the census takers added more information. The location of each observation was plotted on a large map of the area.

A brief note may be made at this point on methods employed in the capture of porcupine both at Acadia and at Snakeskin Lake. Several methods are described by Taylor (1935) and Spencer (1950). At the Acadia Station I employed a simplified method in capturing porcupine. Whenever animals were encountered in the woods at times when no available transportation back to the Station quarters could be had, it was found that the animal could be frightened up into selected trees where they would remain for several hours before venturing down again. During this interval arrangements for the capture could be made. Trees for such use were chosen with the point of view of facilitating the capture--choosing either a small tree for the animal to climb, or else choosing a tree beside which stood another which could be climbed at the time of the capture. Then tapping the nose of the porcupine with a leafy branch, the animal can be made to descend to waiting cages.

An alternative method of capturing porcupine while alone was to endeavour to capture the animal with a noose. Using a short stick, the animal can easily be cornered. Then,

moving very slowly so as not to frighten the animal, a noose of strong cord 2½ to 3 feet in length can be carefully placed over the porcupine's head, or preferably behind the front legs. Once tied, the animal could easily be led back to the road and lifted into a tool box in the jeep. Using this method it was found possible to capture animals without causing any bodily harm or loss of a large number of quills.

Occasionally it was found possible to turn the specimen over on its back with a stick. With the stick then placed across the animal's chest, a noose could be placed over either hind foot just above the ankle. Animals so tied could either be carried short distances while lifted completely off the ground, or be allowed to walk along a directed route.

Snakeskin Lake

Whereas the studies on the ecological aspect of the porcupine at the Acadia Station had been carried on incidental to the survey of the damage, studies at Snakeskin Lake were designed more specifically to study the animal itself. The main emphasis of the studies here were as follows:

(1) to determine the nature and periods of activity of the porcupine in its natural environment;

(2) to determine the possible home range of the animal during summer months in such an environment, and

(3) to determine, if possible, whether any correlation exists between activity records derived in the laboratory with activity as observed in the field.

In order that a porcupine encountered at various locations on the lake from time to time could be recognized as the same animal, it was necessary that a marking scheme be worked out which would not only be lasting but also simple enough in method that it may be accomplished easily.

For marking animals various methods are advocated in the literature. Among these are tagging the ear or other parts of the body, toe clipping, ear notching, marking with paints or dyes. Tagging as a means of identification, it was felt, would present two serious disadvantages in marking such an animal as the porcupine; first--the constant danger that the tag may be pulled out either accidentally or intentionally by the animal; and secondly, the use of a tag of any practical size would still necessitate repeated capture of the animal each time it was to be identified. The same objection was anticipated toward the use of ear notching or toe clipping as a means of identification. To attempt recapture of a marked animal when found resting far out on a limb of a tall elm tree at a height of 40 to 60 feet above the ground would not only prove impractical but also somewhat dangerous. A method whereby an animal encountered even at such height might easily be identified from the ground would be much more ideal. For this purpose the best solution appeared to be to mark the animals with paint. Six cans of paint of white, red, yellow, orange, blue, and pale green colours were included in the equipment.

Once the means of marking had been decided, there re-

mained the problems of (1) capturing as many porcupines as possible in a five weeks period, (2) the means of applying the paint so as to distinguish one painted animal from another, and (3) the search for animals already painted in order to determine the home range.

Curtis and Kozicky (1944) describe a type of funnel-shaped net of sheet metal used by them in tagging the ears of small animals. I employed a similarly shaped net. The net is shown in Figure 7. The net consists essentially of three pieces: (1) a 12-inch hoop from a wooden nail keg, (2) a strip of fine mesh chicken wire, 30 inches by 48 inches, and (3) a binding piece of ordinary bale wire. The narrow end of the net, tapered to 4 inches in diameter, was closed off by two perpendicular lengths of bale wire. The whole net weighed but a few ounces, yet was strong enough to hold the largest porcupine captured.

The capture of animals encountered along the shoreline or in the clearings was relatively simple while using the described net. Each time an endeavour was made to approach as near as possible to the animal before it became aware of danger. To achieve this, various tactics proved helpful--such as approaching slowly, quietly, toward the wind, and whenever possible, walking in water rather than chancing the accidental snapping of a twig underfoot. Porcupine feeding on water lillies and other aquatic vegetation along the shore seldom appeared disturbed by the slight additional

Figure 7 - The wire net used in the capture and marking of porcupine at the Snakeskin Lake location of field study. (Rule over the end of the cone is in place only to show relative size.)

splashing sounds which might be caused by a person walking along the shore or the paddle of a canoe. Once, however, the porcupine sensed danger, the animal would cease feeding and begin to chatter its teeth as it slowly looked about. If no pursuit was made, the animal either resumed feeding after several minutes, or else moved away slowly into the woods. If followed, it immediately began to run, thus making capture difficult by darting this way and that under brush, thickets, and fallen trees. Generally it was found that the followed porcupine resorted to escape by climbing a tree only after other evasive methods proved unsuccessful.

More frequently, however, it was found possible either to approach the porcupines without causing alarm or else get close enough to facilitate easy capture either by overtaking the animal and putting the net down over the animal from behind, or, as occurred on a few occasions, by holding the net directly in the line of retreat. In the latter instance, the animals ran directly into the net. Once inside, the net need but be turned upright and one foot placed on the larger edge of the hoop. The animal is harmlessly trapped and then painted with ease.

In the course of the studies at the Acadia Station and at Snakeskin Lake, four separate methods of marking porcupines with paint were used. These were as follows: first, using an oil can container with a long spout and a thumb-controlled plunger mechanism for forcing the paint from the

can. Such an apparatus had advantage that the animal might easily be marked even from several feet distant. The necessity of a paint solvent to wash the apparatus clear of paint before it hardened inside discouraged its use at Snakeskin Lake. Secondly, using the net, it was but a simple matter to merely pour a small quantity of paint through the wire netting onto the animal. The use of a wire netting rather than the more enclosed sheet metal type of net not only facilitated painting, but also by pouring only a small quantity of paint onto the animals and allowing them to turn somewhat in the net, the paint was found to smear over large enough a body surface so as to be identified from fifty to a hundred feet away.

A third method of applying paint was found useful when only a small amount of thick paste remained in the bottom of the can and would not pour. There again the net was used. The paint was applied at the end of a stick which could then be touched to the animal. Such a method was particularly applicable when it was desirable to paint only the top of the head, about the snout and paws, or on other limited regions.

The fourth method required neither net nor snare of any sort. On several occasions, such as at the old, much-chewed stump in the clearing at the Snakeskin location, it was found possible to come up behind a porcupine so preoccupied chewing at the saltlick that it could be marked before it be-

came aware of danger. On other occasions, porcupines feeding from the end of rocks or logs projecting out into the lake could be cut off from retreat and if approached slowly, preferred rather to be painted than to dive off to swim ashore. At other times, porcupines found sleeping in small trees could be painted by climbing to a slightly higher level than the animal and pouring paint down over it.

The use of various coloured paints in marking porcupine has several distinct advantages over other methods which might have been used. First, by the use of assorted colour combinations and various patterns over the body of the animals, a large number of animals can be painted without conflicting repetitions. Secondly, the paint appears not to harm the animals. Third, the method is rapid. An animal can be caught and painted in a few minutes. Then too, even if the animal swims away, very little, if any, of the paint washes off. Animals found weeks after having been painted can be recognized just as easily as immediately after the marking had been applied.

During the five weeks at Snakeskin Lake, forty-five porcupines were painted. As more and more porcupines were painted, it became necessary to use two colours on the same animal. Table I lists the colours and patterns used on the forty-five porcupines painted at Snakeskin Lake.

TABLE I

Porcupines and Colour Patterns Used in Painting them at Snakeskin Lake

Porcupine	Date	Point of Capture	Pattern Used
P_1	June 10/53	West of Camp	Yellow on right side
P_2	June 11	Behind tent	Yellow on left side
P_3	June 11	Atop ravine behind Camp	Red on right side
P_4	June 11	West Cove	Red on left side
P_5	June 11	Shack landing	Red mid rump (large)
P_6	June 11	Shack landing	Red mid rump (small)
P_7	June 11	Shack outhouse	Red tail (large)
P_8	June 11	Stump	Red band on neck
P_9	June 12	At canoe at Camp	Orange on right side
P_{10}	June 15	¾ mile NW of Camp	Orange on left side
P_{11}	June 15	Stump	Yellow mid rump and tail
P_{12}	June 15	West Cove	Yellow head and tail
P_{13}	June 16	W. edge of Clearing	Yellow right body, white left body
P_{14}	June 16	Clearing landing	White head, yellow rump
P_{15}	June 17	Stump	White on right side

TABLE I - continued

Porcupine	Date	Point of Capture	Pattern Used
P_{16}	June 17/53	Shack outhouse	White on left side
P_{17}	June 18	Stump	Red on right, yellow on left side
P_{18}	June 18	West Cove	Red on left, yellow on right side
P_{19}	June 19	Camp Cove	Red on left, white on right side
P_{20}	June 19	Same, W. shore	Red on right, white on left side
P_{21}	June 24	Camp Cove	Yellow snout, neck, tip of tail
P_{22}	June 30	In front of tent	Blue right front
P_{23}	July 1	West Cove	Blue on right side (Baby of P_7)
P_{24}	July 1	Camp landing	Blue tail (Baby)
P_{25}	July 1	Across lake from Camp	Blue rump and tail
P_{26}	July 1	South shore, West Narrows	Blue top of head
P_{27}	July 1	W. of West Cove	Blue on left side
P_{28}	July 1	Camp Cove	Blue band on neck
P_{29}	July 2	Extreme S. of Clearing	Green left rump (small)
P_{30}	July 2	West Cove	Green on left side

TABLE I - continued

Porcupine	Date	Point of Capture	Pattern Used
P_{31}	July 3/53	West Cove	Green head and tail (large)
P_{32}	July 3	West Narrows	Green head, Blue tail (large)
P_{33}	July 4	West Cove	Green right, blue left
P_{34}	July 4	¾ mi. W. of Camp S. shore	Green left, blue right.
P_{35}	July 5	Camp Cove	Green left head, blue right rump
P_{36}	July 5	Camp Cove	Blue head and tail, green rump
P_{37}	July 5	West Narrows, S. shore	Green head, blue tail (small)
P_{38}	July 5	E. of West Narrows, N. shore	Green snouth, right paw, both sides and tail
P_{39}	July 5	Clearing landing	Green head and tail, blue rump
P_{40}	July 5	West Cove	Blue snout, , tail, mid rump
P_{41}	July 5	Behind Shack	Blue right head, green left head
P_{42}	July 6	W. of West Cove	Green right head, blue left head
P_{43}	July 6	West Cove	Green band on neck, blue tail (Baby)
P_{44}	July 7	West Cove	Blue mid neck to rump (Baby)
P_{45}	July 7	Camp Cove	Green mid snout to neck

To determine whether animals found at considerable heights were marked or not, and if so, in what manner, usually presented no great difficulty. A loud shout or a well hurled stone was sufficient to cause the animal to move, during which time the pattern of marking could usually be determined if present. To catch and paint such animals, however, presented a more difficult problem. To throw sticks and stones--even when often striking above the animal--more often than not would cause it to climb higher and even more out of reach. To climb such trees of 20- to 30-inch d.b.h. whose lowest branches too were at a considerable height, proved impractical.

One successful solution was found to entice such animals to climb down from their lofty perch. When it was found that neither sticks, stones, nor shouts could arouse one such animal from its sleep, I went back to camp and returned with a .22 caliber rifle. A shot which chipped a piece of bark an inch or two in front of the sleeping porcupine's snout was sufficient to waken the animal. It began to climb further out onto the limb but another similarly placed shot caused the animal to retrace its steps. Within two minutes it had climbed backwards to the ground and made off into the dense thickets.

The same procedure was attempted with another much larger and less cooperative porcupine. Three shots caused this animal to descend approximately one-half way to the ground but then it darted up another large branch. Since I had no

marking paint with me at the time, I permitted the animal to climb to safety. With careful aiming, however, it is felt that the method might be used successfully in capturing porcupines which would otherwise have to be allowed to go unmarked until such time as they might be caught on the ground. Perhaps a sling shot would prove just as effective and practical.

The hopes of finding a porcupine early in the day and then observing its movements throughout the whole day in an endeavour to determine the nature and periodicity of its activities were difficult to realize. On numerous occasions animals found in the clearing were observed for varying lengths of time from some distance. Eventually the animal became cautious and gradually moved toward the woods, stopping frequently at first, turning around to listen, and then moving away with increasing speed. Their actions were no longer typical of feeding porcupines. In the woods definite pathways of retreat are followed until at last, if the pursuit is continued, the animal climbs a tree.

Rather than concentrate on the activities of one typical porcupine throughout the day, therefore, it was felt that a large number of observations on as many porcupines as possible would give an activity picture more characteristic of the animal as a whole. The date, hour, location, and activity of each animal encountered were recorded in the field with the hope that a summary of all the observations would give a gen-

eral pattern of activity of a typical porcupine day.

Several difficulties and limitations were encountered in searching for the porcupines I had painted and released. The fact that I was alone limited the area of forest through which I could search in any unit of time. Whenever the canoe was combined with woods travel, it was always necessary to circle about to return to the point at which the canoe had been pulled ashore which involved time.

To search and study the entire length of the lake and its surrounding area would have been impractical for one individual. Since I was camped approximately one-third of the way up the lake on the northern shore, the main location of study was centered in an area a mile in each direction from the camp. Several visits were made each week by canoe to the western end of the lake, while the eastern extremity of the area was visited but three times in the five week period.

Although no strict schedule was followed as to which part of the woods were to be searched each day, an attempt was made to alternate observations along the north shore with those along the south shore. For several daylight hours after rains the search was limited to travel by canoe or to searching in the vicinity of the clearing across the lake.

Nor could any definite procedure be followed during the search in the woods. Tins of one or more colours and the net were carried on all occasions of travel through the woods or on the lake. Tall elm trees which projected above the

dense canopy of maples were particularly searched, mainly from atop rocky outcrops, clearings, or ridges. Numerous swamps of various sizes were crossed throughout the search and pathways followed as far as possible.

The nature of much of the Snakeskin Lake forest added another difficulty in the search for painted procupine. In many regions the dense regeneration of young maples ranging from three to ten feet high hid the ground, while another canopy at twelve to twenty-five feet almost shut off the view of the sky and taller trees. It was often only by chance alone that some animals were found. By staggering the hours of meals, and by checking each sound of porcupine heard about the camp during the night--even to the point of arising four or more times in one night and at as late as 4:45 a.m.--an almost twenty-four hour cycle of observations was made. Also on two occasions a search was made on the shoreline and clearing across the lake as early as 5:45 a.m. A heavy mist blanketed the area. No animals were found stirring at that early hour. On several occasions porcupines were observed and followed as they moved along the shore from approximately 8:00 p.m. until well after midnight. Animals observed by bright moonlight or by the white paint used in marking them, could be easily followed in the canoe. Wherever in the course of the porcupine's travel a steep rocky ledge at the water's edge necessitated a detour, the animal was heard going off into the woods for a short period of time and then returning just beyond the obstruc-

tion. A daylight examination of the line of travel followed by the porcupine showed a clearly worn pathway had been followed. The path deviated from the shoreline wherever a precipitous obstruction occurred. On several other occasions as well, porcupines were observed travelling definite pathways for several hundred feet after which the paths became so divided and faint as to be no longer clearly discernable. Sackett (1913, page 72) in his use of the maze in studies on the learning process of the Canada porcupine commented on the pathways as follows, "No one, however, can follow the natural trails of the porcupine without feeling that these animals tread a maze every time they creep out after food. Their paths, particularly in the fall and winter months, are sometimes worn deep into the ground, winding for miles through the underbrush, ferns, laurels, and shrubbery; they go around large rocks, over smaller ones, under logs and over stone walls, creeping in and out with almost endless branching, crossing and shunting. When the more formal problem of a laboratory is interpreted in the light of this instinctive behaviour of the animal, the superior ability of the porcupine in maze running may be explained upon a lower basis and in a more natural fashion than is otherwise possible."

Experimental Methods at McMaster University

In an endeavour to determine whether porcupine possess an innate pattern of activity, and the nature thereof, two ani-

mals were used in experiments at the McMaster Biological Research Station. Of the two animals, the larger male porcupine--"Uncle Baldwin"--was studied during most of the experimental work until his death in late April. After this time studies were repeated employing the female porcupine--"Minnie". The female had also been used during an eight day recording period just prior to Christmas.

The activity studies were designed to be carried out in two phases: (1) under as near to normal conditions as possible; and (2) under controlled experimental conditions. The term "normal conditions", as used here, meant the allowance of natural variations in temperature, light, and relative humidity. Under "controlled conditions" an attempt was made to limit or control each of these factors by enclosing the animal and instruments in a large box in which there was a continuous source of light at first and continuous darkness later. Temperature and relative humidity could be kept more or less constant within the box. With captivity, it was realized that the habitual freedom of movement, the natural selection of food, and many other influencing factors had been radically altered. Yet it was felt that once accustomed to the new surroundings, if an innate pattern of activity existed within the animal, such a pattern would eventually be revealed. To determine the nature of such a pattern, a means of continuously recording the activity was devised.

Figure 8 shows a drawing of the apparatus used in recording activity of the experimental porcupine. A captivity

cage containing the animal was fastened by two bolts to one end of a piece of half-inch plyboard strip five inches wide and six feet long. The other end of the plyboard was clamped almost perpendicularly against one wall of the room. The back of a chair placed under the plyboard between the wall and the suspended cage provided a moveable fulcrum.

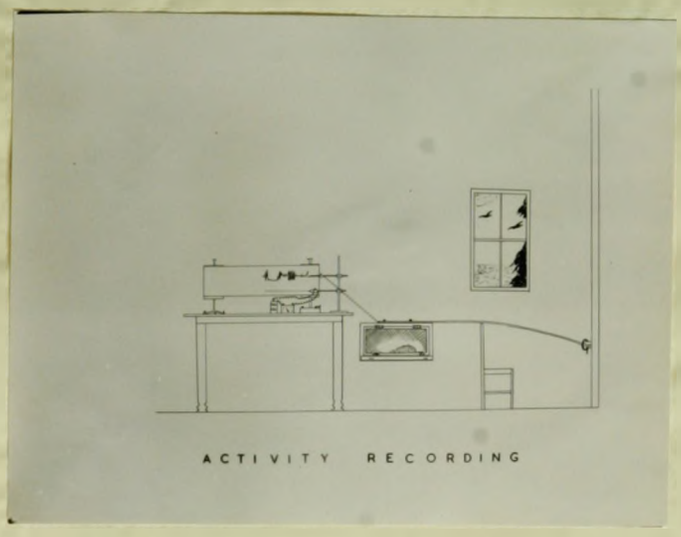

Figure 8 - Sketch of the activity recording apparatus.

By moving the chair nearer to or further away from the cage, the recording sensitivity of the suspended cage could be regulated. The further the chair fulchrum was placed from the cage, the greater was the amplitude of vertical oscillations caused by the movements of the caged animal. Generally oscillations of only two to three inch amplitude were found most satisfactory. Leading from the top center of the cage, a strong thread extended to a pointer lever fastened to a stand.

The pointer enscribed vertical arcs on a slowly moving 4-foot continuous strip of kymograph paper, supported on two kymograph drums. In addition a signal magnet and a timer marked off a time record in intervals of one minute.

Once a 24-hour period of activity had been recorded, the kymograph paper was removed and the hour intervals marked in along with other information on date, experimental conditions, and the animal used. The record was made permanent by immersion in a thin solution of white shellac and then permitted to dry.

The animals were fed and the record paper changed at 9:00 a.m. each day. An endeavour was made to run experiments on consecutive days under same conditions until a similarity of pattern appeared to be exhibited.

For the "controlled" experiments, the room in which the activity recording apparatus was set up was heated. In addition, a large insulated box 6 feet by 4 feet by 4 feet was constructed to house the animal with its suspended cage and part of the recording apparatus. By this means, light, temperature, and humidity could be more readily controlled.

Under the controlled conditions a De Khotinsky thermoregulator was used to operate two blackened light bulbs for heating the large box in which the suspended cage was then enclosed. A wide flat tray containing two large sponges and approximately a gallon of water and placed on the floor of the box to keep a constant high humidity. Temperature read-

ings immediately beside the suspended cage were constantly recorded. The same type and quantity of food was served to the experimental animal throughout the experiments. A goose-neck lamp with a 60 watt bulb and projecting out over the wire mesh top of the cage was used as a constant source of light when such was needed.

DATA ON ACTIVITIES

Feeding

Because of the succulent nature of the food itself, and because of the porcupine's habit of chewing its food well, little of value could be determined concerning the species of vegetation consumed by the porcupine during the summer months from analysis of stomach contents submitted to the National Museum, Ottawa. Actual field observations on feeding porcupine proved to be a more rewarding approach. A list of the species of nematodes and cestodes occurring in abundance in each of the specimens submitted, however, is to be found in the report prepared on the Acadia Station damage survey for the Department of Resources and Development, Ottawa by Radvanyi (1953).

The great diversity of the feeding habits of the porcupine may perhaps be a leading factor in its successful survival. Primarily the feeding habits of the porcupine vary considerably with the region considered, the availability of the natural feeding materials, and the season of the year. During the observational periods in the summer months, feeding was concentrated almost exclusively on vegetation growing at ground level--herbs, leaves, grasses, and various types of water vegetation. During the winter, on the other hand, be-

cause of lack of ground vegetation, feeding is strictly arboreal in nature. It is in this period that most of the damage is caused to the forest trees by porcupines. While snows cover the surface vegetation, the porcupine feeds on the soft underbark and cambium layers of a wide variety of trees--mainly softwoods. Although certain preferences appear to be exhibited, yet almost any tree in the forest is susceptable to attacks. The two keen-edged incisors of both upper and lower jaws cut two clean im prints resulting in long, slanting parallel teeth marks which contrast sharply with the short, rough-edged marks characteristic of rabbits, deer, and mice.

The feeding movements of the porcupine appear almost always to be hurried. Porcupines observed feeding along the shores at Snakeskin Lake were seen at times to move along the shore and hurry out to the drift debris in attempts to reach the areas of succulent water lilies. If no vegetation was to be had, or could not be reached, the animals would hasten back to the shore and try again from another log. The performance may be repeated many times until an area of abundant and easily reached vegetation is found. On two occasions two separate animals were followed by canoe more than a half mile along the shore as they searched for areas of plentiful water lilies. One of these animals, (P_{15}) was first encountered at approximately 8:30 p.m. one evening and was followed for 2¼ hours along the shore at which time a fertile feeding ground was found. At 12:30 a.m. the animal moved off into the

woods. The same animal was found shortly after daybreak the next morning as it moved back toward the point at which it had been originally seen the evening before. During mid-afternoon the animal was seen back at the original point of observation. The travel did not appear to be repeated nightly.

The forest types, and consequently the feeding habits of the porcupine, were different as noted at the Acadia Station and Snakeskin Lake locations. Whereas the prominent tree types at the Acadia Station were red spruce, intolerant hardwoods, black spruce, and pines, dominants at Snakeskin Lake were maple, elm, birch, aspen, pine and alder. Furthermore, the Acadia Station had no extensive bodies of water with the concomittant aquatic vegetation as found at the Snakeskin area.

While the main bulk of the summer feeding at Acadia appeared to be leaves of aspen, clover, and grasses, porcupine at Snakeskin Lake relished the leaves and stems of the white and yellow water lilies (Castalia spp. and Nymphaea spp.) and the arrow-head plants (Pontederia spp.) which bordered the many protected coves of the lake such as shown in Figures 9 and 10. Despite the much greater population of porcupine at Snakeskin, evidence of porcupine attacks on the forest during the winter months was but a fraction of that encountered at the Acadia Station. This lack of damage evidence may have been due to the predominance of the faster healing deciduous types of trees at Snakeskin Lake. On only two regions of

Figure 9 - White and yellow water lilies (*Castalia* spp. and *Nymphaea* spp.) and arrow-head plants (*Pontederia* spp.) growing in the shallow waters along the edge of Snakeskin Lake provide succulent food much sought by the porcupines of the area.

Figure 10 - Porcupine venture out considerable distances on submerged logs in order to acquire rich green water lily pads and arrow-head plants which they relish. The pictured animal continued to feed while the author stood less than five feet away for more than fifteen minutes.

pitch pine (Pinus rigida Mill) was damage by porcupines found to be extensive. That porcupines may return year after year to the same trees was apparent from the difference in colour of exposed sapwood and callus growths. Scar tissue too--perhaps because of its tenderness and high sugar content--is particularly sought by the porcupine. In addition to girdling and gnawing in patches, still another type of attack on trees was noted at the Acadia Station. Attacks here were inflicted on the tips of boughs of spruce and fir. Examination of such coniferous boughs showed that they were but partly eaten and then dropped to the ground, where, it is felt, that they might afford browsing material for deer and rabbits when snow has made other such browse scarce. J.D. Curtis (1941) states that inspection of such coniferous branches noted by him showed "that only the previous year's growth was eaten, sometimes completely, other times only partially. Feeding of this kind is usually confined to the upper part of the crown where the branches are smaller. Presumably the animal can remove a large portion of the branch while bracing itself on the inner part nearest the tree. Furthermore, the succulent foliage is found near the bole high in the crown. Occasionally all of the side branches are pruned close to the bole near the top." An example of the upper region of a fir tree from which the extremities of numerous branches have been clipped by porcupine is seen in Figure 11.

Figure 11 - Porcupine damage to a balsam fir. The main leader had been killed by girdling. In addition, the tips of many of the branches near the top have been clipped by porcupine seeking the more tender portions of bark for food during the winter months when all ground vegetation lies covered by snow.

The intensity of the porcupine attack was found also to vary from one species of trees to the next. This may suggest that the animal possesses a sense of taste and selective abilities. All stages from mere sampling bites of some trees to stripping of bark from base to tip of others were found at the Acadia Station, an example of the latter type being shown in Figure 12.

Figure 12 - An example of recent heavy damage by porcupine feeding on the soft underbark and cambium of red spruce. Approximately 90% of the bark from the main trunk had been removed. Trees so damaged have no chance of survival.

At the Acadia Station the species of trees attacked by porcupines--listed here in descending order of frequency with which such attacks were recorded--were as follows:

Larch (Larix laricina (Du Roi)K Koch.)
Red Spruce (Picea rubens Sarg.)
Black Spruce (Picea mariana (Mill.) B S.P.)
Balsam Fir (Abies balsamea (L.) Mill.)
Wire Birch (Betula populifolia Marsh.)
White Spruce (Picea glauca (Moench) Voss)
White Pine (Pinus Strobus L.)
Eastern Cedar (Thuja occidentalis L.)
Hemlock (Tsuga canadensis (L.) Carr.)
Yellow Birch (Betula lutea Michx. f.)
Trembling Aspen (Populus tremuloides Michx.)

The above species do not occur in the same abundance throughout the Acadia Station. A more lengthy study of the comparative effect of porcupine feeding on the forest trees of the Station appears in the 30 tables of the report prepared during that study--Radvanyi (1953). In this report the frequency of occurrence of trees of different diameter at breast height was taken into consideration and thereby gives a better idea of the preferred tree species.

It is in the porcupine's quest for mineral salt that the animal becomes such a nuisance to mankind. Porcupine have been known to play havoc with deserted cottages--chewing at practically anything which may have been touched by human hands and may have on it the least trace of salt. Floors, rafters, doors and furniture, handles of axes, spades, oars and aluminumware are attacked. Figure 13 shows a portion of an aluminum stake used in marking the corners of working plan survey plots on the Acadia Station. The imprints of the inci-

sor teeth appear clearly on the chewed surfaces and match almost exactly the corresponding teeth of a porcupine's lower jawbone shown at lower right. An electrical hardness test performed on the stake gave a reading of 88-92 Rockwell F or 89-98 Brenel, indicating the metal is one of the strongest aluminum alloys. While at the Snakeskin Lake location, porcupine made repeated attacks on the campsite--chewing at the brass keel strip of the canoe and the tent itself. Preston (1948) describes the glass sides of several catsup bottles chewed through by porcupines.

Figure 13 - A portion of an aluminum stake used in marking forest plots, chewed by salt-seeking porcupine. A lower jaw of a porcupine placed at lower right shows close match between incisor size and teeth imprints on the chewed metal.

Home Range of Porcupine

During the five weeks of study at the Snakeskin Lake location--from June 8, 1953 to July 10, 1953--a total of 45 porcupines were captured, marked, and released. Their re-capture then should afford the basis of certain conclusions concerning the range of movements and hours of activity. Of these marked animals, 20 porcupine--or 44% of all animals marked--were found again and identified at least once. The frequency with which the marked porcupines were found is shown in Table II below.

TABLE II
Frequency of re-identification of marked porcupine at Snakeskin Lake

Number of porcupines	Frequency of re-capture or re-find after marking	Group
8	Once	1
4	Twice	2
1	Three times	3
1	Four times	4
2	Five times	5
3	Six times	6
1	Thirteen times	13
Total 20	64	

The time, location, identification, and activity of all porcupines encountered at Snakeskin Lake were recorded. A total of 223 observations on marked and unmarked porcupines were recorded. This total includes only one observation of any one porcupine per day and the time of observation con-

sidered is at the time of day at which the animal was first seen. Where the possibility existed that repeated counting of unmarked porcupine may be occurring, such observations were not included in the total number of observations. Of the 223 observations, 64 observations, or 37.7% of the total were on marked animals.

In Figure 14 the number of observations of porcupines seen at least once during the field study period is plotted against the half hour intervals of a day. For example the total number of porcupines seen between the hours of 1 p.m. and 1:30 p.m. over the five weeks period was 9; the total between 1:30 p.m. and 2 p.m. was also 9--six animals active and three non-active. The observations have been recorded as both active and non-active. Active porcupine refers to those animals seen either feeding along the shoreline, in the clearing of the abandoned farm, or travelling from one location to another without stopping to feed. These also include porcupine encountered in the immediate vicinity of the camp at practically all hours of the night. Non-active observations refers to those animals found either sleeping or resting up in the trees. Also in Figure 14 I have indicated, by the solid line, the total hours of my observations during the five weeks period, superimposed upon the hours of one day. The broken line indicates what I have chosen to call the "Find Potential". This is a measure of the success with which porcupines were seen, as based on the stated number of observa-

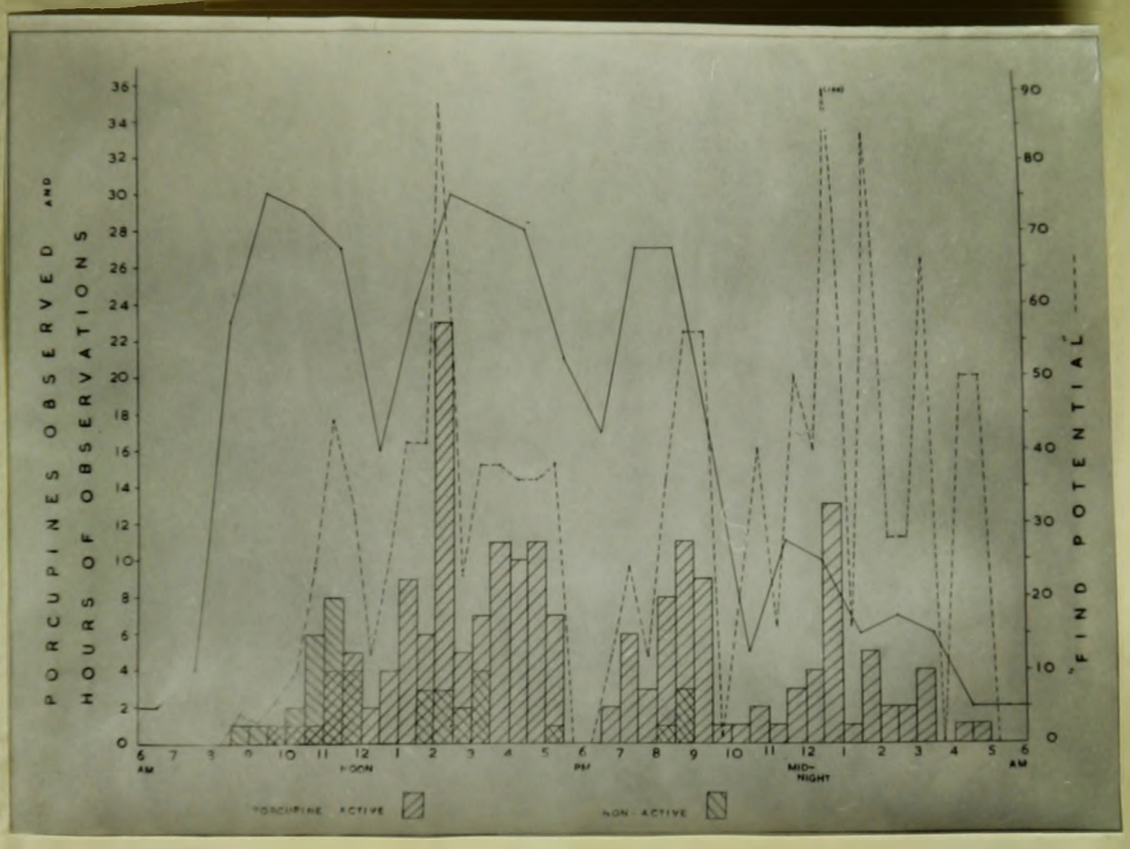

Figure 14 - Graph showing the total number of porcupines encountered at Snakeskin Lake over the five weeks of field study in June and July. The solid line represents total hours of observations. "Find Potential" indicated by the broken line, represents no. of animals seen/ no. of hours of observation.

tions and numbers of animals seen for the first time during the day. The values indicated by the broken line were obtained by the following formula:

$$\frac{\text{number of animals seen}}{\text{number of hours of observation}} \times 100$$

The scale for the "Find Potential" occurs on the right of the graph. During the period 12:30 to 1:00 a.m. more than one animal was seen during each hour of observation at that particular time of day. The potential find value here was 130 and is indicated by a break in the graph and the value

bracketed.

In Figure 15, the date of marking, the date of re-finding, and the distance travelled from the point at which the animal had last been observed, have been summarized in graphic form for the twenty marked porcupine which were found again at least once. For example, P_4, marked on June 11th and released, was not found until June 25th. At this time it was one-half mile from the point at which it had been marked fourteen days earlier. The same animal was found only once more, twelve days later and now one-quarter mile from the point at which it had been noted on June 25th. This third point could be either back toward the first or further away from it.

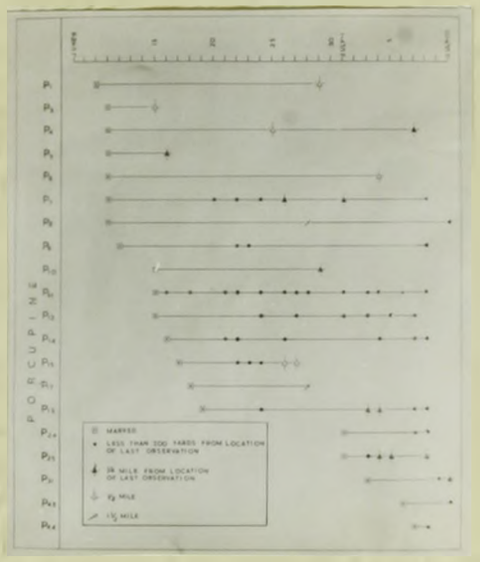

Figure 15 - Graph showing summary of data concerning observations of 20 marked porcupines released and relocated to determine range of movements. Graph shows date of marking and distances travelled by the animals between times of location.

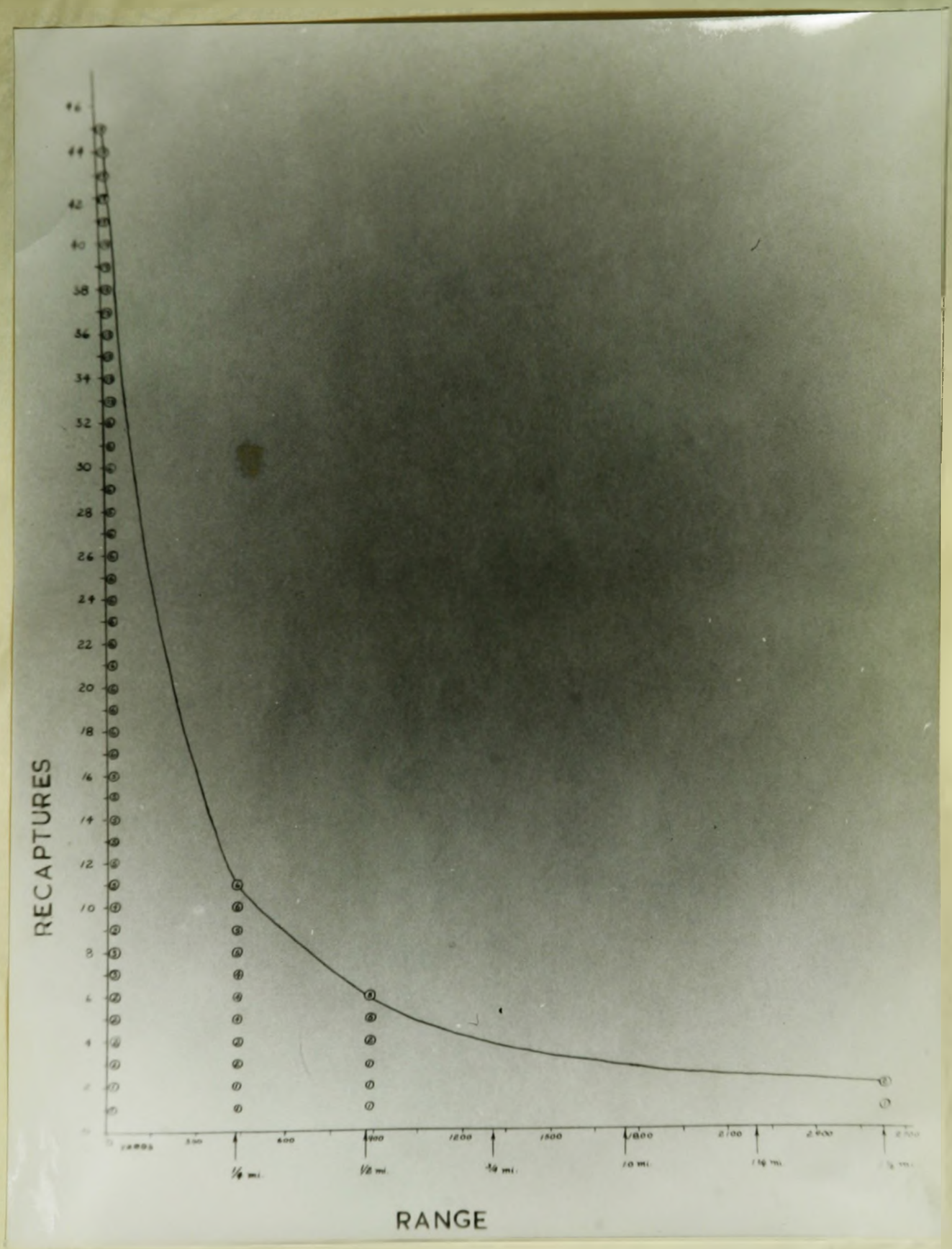

Figure 16 - Graph showing relationship between frequencies of recapture of marked porcupine and distances travelled between times of re-location of the animals. Encircled numbers under the curve line represent number of times observed porcupine were recaptured.

In Figure 16 the 64 re-finds of the twenty marked porcupines have been plotted against the distance between consecutive observations. The encircled numbers below the curve line of the graph indicate to which group of observations the animals belong as outlined in Table II. For example, porcupine which had travelled one-quarter mile between observations include the following: two of the animals which had been re-captured or found but once after having been marked (or one such animal could have travelled the one-quarter mile between observations on two different occasions), two which had been found twice after having been marked, three of the porcupines found four times, two of the ones found five times, and two of the porcupines found six times.

This same means of group distinction is used in Figure 17. On this graph the days between consecutive finds of each of the twenty marked porcupine is plotted against the distance they had travelled during the interval since the last observation. Again the distance travelled has been arranged in the four groups of 0-300 yards, ¼-mile, ½-mile, and 1½-mile. Because the majority of the observations occur within the first group, only in the part of the graph indicating this range has a solid line been included to join the maximum number of observations per unit of day intervals between observations. A summary of the data portrayed in Figure 17 occurs in Table III.

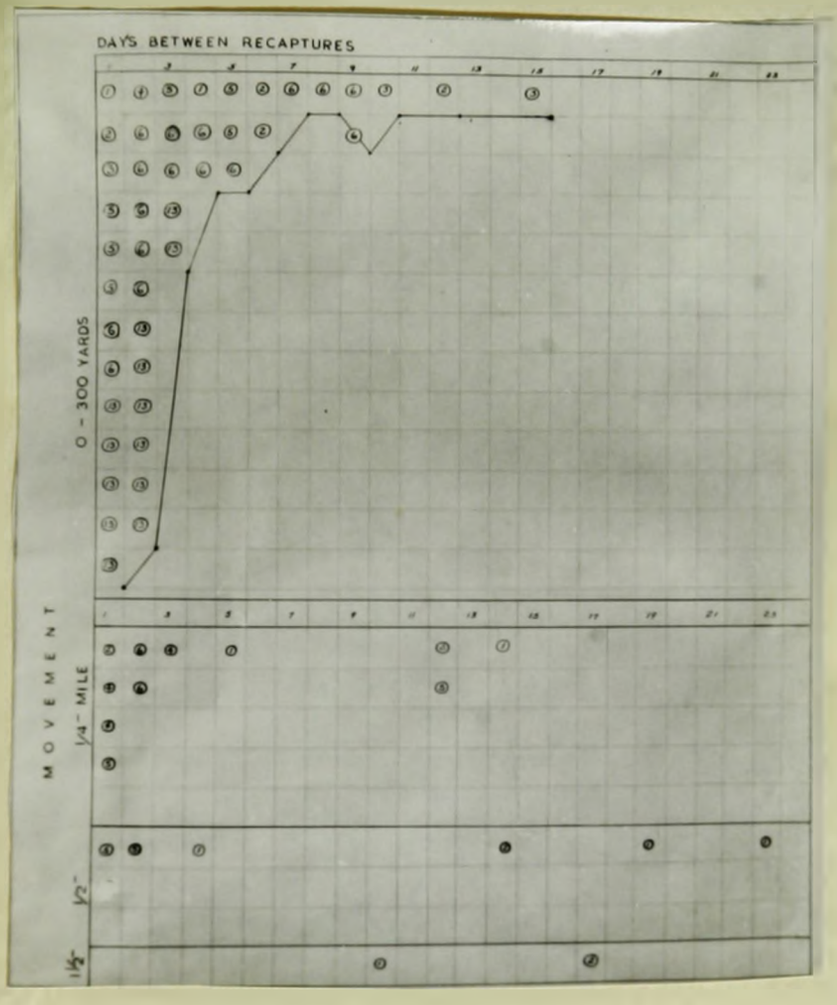

Figure 17 - Graph to show relationship between distances travelled by marked porcupine and the days between recaptures or repeat observation. Data based on observations at Snakeskin Lake.

TABLE III

Days between consecutive observations--Maximum recorded movement relationship, based on porcupine observations at Snakeskin Lake

Movement	Days between consecutive observations 1 - 9	10 - 19	20 - 26	Σ
0-300 yds.	9	1		10
¼-mi.	3	1		4
½-mi.	1	2	1	4
1½-mi.		2		2

Experimental

In the laboratory studies, the activity of both the male and the female porcupine was recorded under various conditions and for varied lengths of time. Because only one set of apparatus was available, the two animals were studied alternately. A greater number of records, however, were made using the larger male animal. The three types of conditions under which activity was recorded were: (1) outside normal, i.e. in the open unheated room, (2) with the animal enclosed in the large box with the light on continuously, and (3) in the same location as (2) but in complete darkness. The male animal was subjected to each of these conditions from four to seven days before activity records were taken. Only whole consecutive days of activity were analyzed for the final analysis. For the male animal--"Uncle Baldwin"--ten days of recording during November and December, under conditions of outside

normal, were made. During April and May eleven days of the same animal were recorded under conditions of constant illumination. Finally during the latter part of May, eight days of activity under conditions of constant darkness were recorded.

Using the female porcupine--"Minnie"--eight days of outside normal activity were recorded during December, and five more during May. After an introductory period, only two days of recording under constant illumination were obtained for this animal during the first week of June. Immediately following this, studies were begun at Snakeskin Lake. Time did not permit recording activity of the female porcupine in constant darkness.

In the analysis of the activity records, the percentage of an hour during which activity had been registered was calculated from the kymograph record sheets. The average for each hour of the day over the experimental series was calculated and plotted in the following figures. In Figure 18 were plotted the hourly averages for the male porcupine under conditions of outside normal, continuous light, and continuous darkness. The activity for the female porcupine under outside normal and continuous light conditions is plotted in Figure 19. A comparison of the activity of the two animals under outside normal conditions is shown in Figure 20. Here the average of the December and May activities of the female are considered as being representative of her movements under

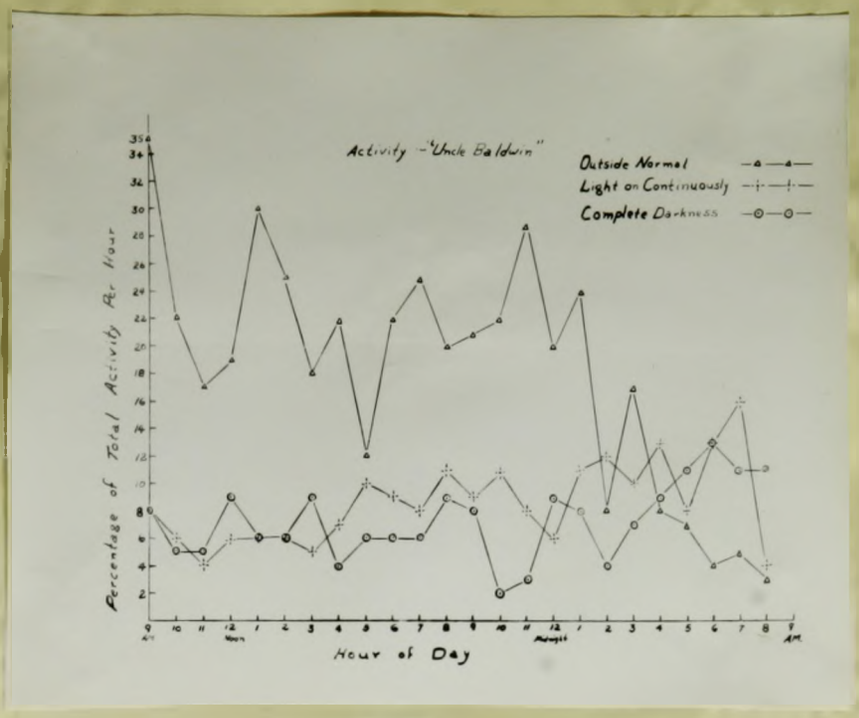

Figure 18 - Activity record of the male porcupine used in laboratory study.

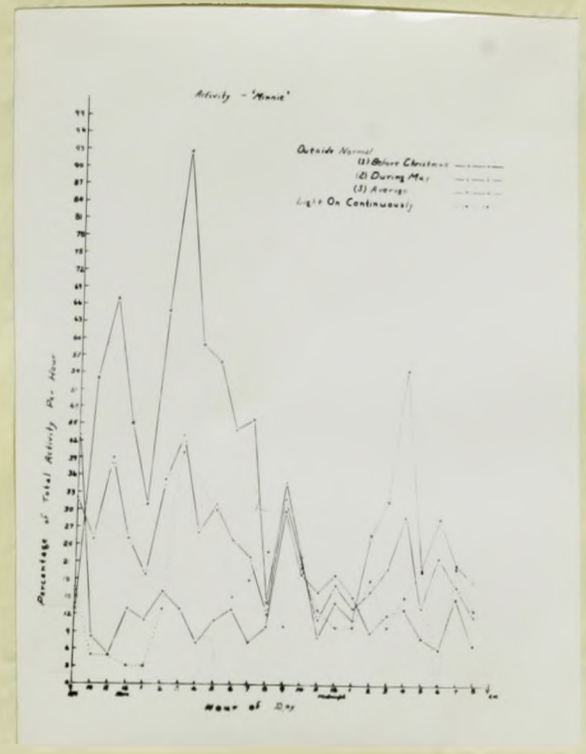

Figure 19 - Activity record of the female porcupine in the laboratory.

outside conditions. Similarly the activity of the two animals under continuous light is shown in Figure 21.

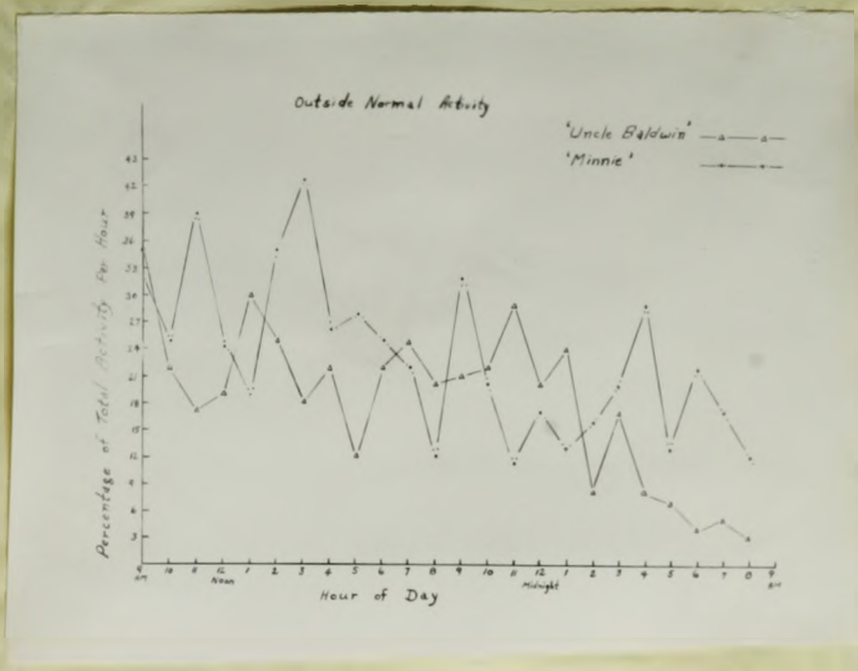

Figure 20 - Comparison of activity of the male and female porcupines under conditions of outside normal.

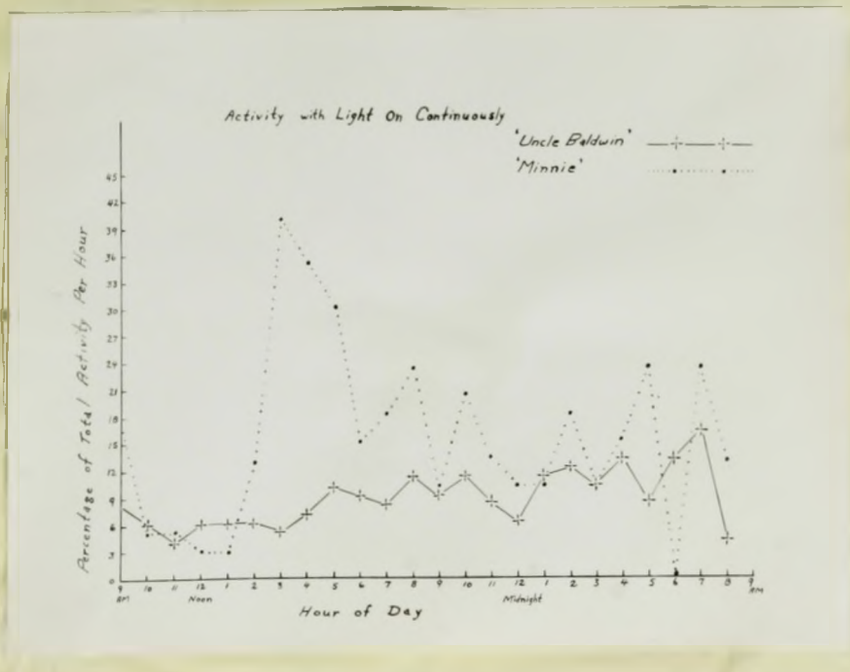

Figure 21 - Comparison of the activity of the male and female porcupines under conditions of constant illumination.

In an attempt to determine whether or not the periodicity of activity in porcupine might not occur over a greater than 24-hour period, hourly activity of the male porcupine over the ten days of continuous recording during December was plotted on one graph. Little or no periodicity could be seen to occur in the graph. The material was then re-analized and five hour running averages of activity then plotted against time. 6 a.m. and 6 p.m. were considered as initial hours of daylight and evening respectively. The smoothed graph appears in Figure 22.

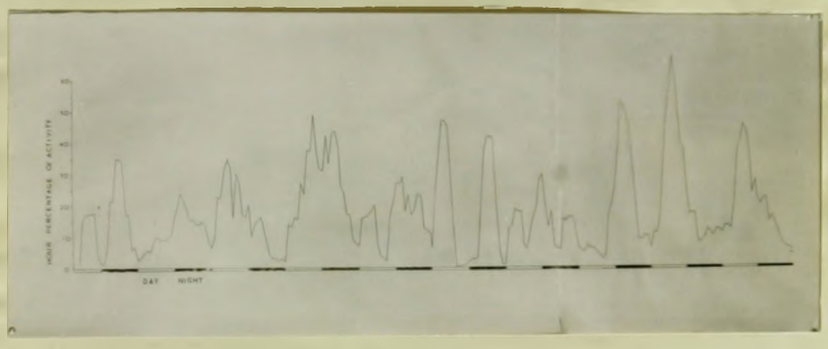

Figure 22 - Continuous activity recording of the male porcupine over a ten day period. Five hour running averages of the original data have been taken to smoothen the curve. Activity is under conditions of outside normal.

DISCUSSION

Field Studies

The Snakeskin Lake area proved to be an ideal location for the study of porcupine ecology. Exhibiting conditions of dense forest, abandoned farmland, swamps, barren outcrops of rock, and shoreline, an excellent opportunity was found to study the animals in a varied series of habitats. Although this field study lasted but five weeks, yet the number of animals present and the methods employed in marking and searching them appear to have provided very usable data.

Spencer (1950) among other authors, maintains that porcupine are nocturnal in habit. In my observations at Snakeskin Lake during the study period here considered, I did not find this to be the case. I feel that such a generalization ought to be considered with reservation. It is realized that this field study is based on but a limited area approximately four miles along the E-W direction of the lake and a mile either north or south of the shoreline. Also the time was limited to only five weeks. Yet because the area studied was sufficient to encompass the greatest range of many of the animals marked and since observations did occur to some degree over the whole twenty-four hours of the day, it must be accepted that although the porcupine may be nocturnal, they are

frequently active during the greater part of the daylight hours as well.

Figure 14 reveals major peaks of porcupine observations occurring at 11 a.m., 2 p.m., 4 p.m., 8:30 p.m., and 12:30 a.m. Although the major peaks in the hours of observations (as indicated by the solid line) occur at almost the same hours of the day, yet the distribution of the numbers of hours of observations was greater than the distribution of the number of porcupines found. Several notable deviations from such a relationship exist.

Puzzled and curious as to why I was unable to locate porcupines during the early hours after sunrise, I had deliberately made several excursions across the lake to search areas near which I had most frequently observed porcupines during other hours of the day. During these early hours a thick fog of 15-20 foot depth lay over the whole lake and surrounding forest. Only the upper reaches of the taller trees extended beyond the limits of the fog blanket. On no occasion, despite such early searches, was I able to locate porcupines between the hours of 5 a.m. and 8:30 a.m. A possible suggestion for this apparent absence of animals may be associated with the possible effect which the ground fog may have in softening the quills of the porcupine. Then, too, the morning period may be a preferred hour for sleeping by the porcupine. Twenty-three of the 35, or 65%, of the porcupine found between the hours immediately after sunrise and

noon were found sleeping or resting in the taller trees of the surrounding forest. The earliest observation after sunrise on active porcupines found feeding either in the clearing or along the lake shore occurred at 10:30 a.m. With three notable exceptions, at 5 a.m. to 8:30 a.m., 5:30 p.m. to 6:30 p.m. and at 3:30 a.m. to 4 a.m., one or more porcupines were observed during each hour of the day over the five weeks period. The greatest peak of activity in the natural habitat (as based on the greatest number of porcupines observed) appeared to occur in the early hours of the afternoon, with lesser peaks during late afternoon and just before sunset. In spite of my attempts to stagger my meal hours and the more than seventeen accumulated hours of search between 5:30 p.m. and 6:30 p.m., yet at this time of the day no porcupine could be located either along the lake shoreline or in the forest. Where the animals disappear at that hour is a mystery. I can but suggest that the porcupine may have retreated to the forest shelter and due to the lengthening of the shadows, failed to be detected. Although unproven in this investigation, it has been suggested by other individuals working on similar ecological problems that the rate of change in atmospheric pressure may influence the animals' behaviour to a considerable degree at certain times of the day--particularly at dawn and dusk. This may account in part for the lack of observations at those hours. On thirteen occasions porcupine were found resting or sleeping during the afternoon.

The majority of the porcupine observed between the hours of 6:30 p.m. and 9:30 p.m. were seen feeding on the aquatic vegetation along the shoreline. Several of these porcupines were observed and followed by canoe from approximately 8:30 p.m. until after midnight. From 10 p.m. through to the following morning, other porcupines observed were encountered within several hundred feet of the camp. These animals invaded the camp area to feed on the aquatic vegetation. They frequently necessitated my arising as often as four times in one night in order to make observations and to prevent repeated attacks by the animals on the canoe and tent. Because of the limitations enforced by the hours of darkness, and because more frequently then than at other hours search was made in response to definite indications that porcupines were present, the find potential curve would lie,, as might be expected, at its greatest peak during the night hours. It obtained a value of 130 between the hours of 12:30 and 1:00 a.m., i.e., 1.3 times as many porcupines were found at that hour than hours during which they were observed. Since I had defined the find potential as the number of animals seen divided by the number of hours of observation, the ratio would naturally have a value of zero during those hours in which I was unable to locate any porcupine.

In figure 15 I have attempted to summarize the data obtained on each of the twenty of the forty-five porcupine which had been marked and found at least once. The maximum

number of times one animal was found repeatedly was thirteen. The animal in question was P_{11}, an animal of about one to two years of age (judging by size alone). On no occasion was this animal found more than 300 yards from what appeared to be the preferred area of West Cove. Eight other porcupine were observed but once after having been marked. Two of these, however, were among the animals painted during my last ten days at Snakeskin Lake, and therefore, should not be considered on equal basis with those painted during the first few weeks of the study.

I should further add that the apparent lack of additional animals being marked between the period of June 20 to 30 was not due primarily to my inability to locate the animals, but rather due to my having used up the supply of marking paint. Additional paint was received on June 30.

While Couch (1932) and Monson (1948) refer to finding of porcupine in desert areas 50 and 120 miles respectively from forested regions, these are exceptional instances. Schoonmaker (1938) makes reference to three observations on the home range of porcupine, based upon repeated investigations by that author to the same general locality. The maximum distance he followed one porcupine during May was ¼ miles. As shown in Figure 16, 56 of the 64 repeated observations on marked porcupine occurred at a range of one quarter mile or less. Forty-five of the 64 marked porcupine observations were on animals which had travelled less than 300 yards

from the point at which they had last been seen. On six occasions porcupine were found to have travelled approximately ½ mile between the time at which I had located them. In only two instances were porcupine found to have travelled more than 1½ miles. Both having been painted along the southern shore of the lake near the farm clearing, P_8 and P_{17} had reached the western extremity of the lake in 17 and 10 days respectively.

Although it is certain that the abundance of aquatic vegetation bordering the lake may have attracted the porcupine to it and thereby influencing the animal's feeding habits, it is, on the other hand, still problematic as to what influence the lake may have had on limiting the travel of the animals. P_4, seen in Figure 23, when first observed was in the process of swimming across the lake. The animal was forced to turn back to the south shore, painted, and then released. Two weeks later the same animal was found several hundred yards beyond the north shore. Because the porcupine was found almost directly across the lake from the point at which it had been marked, and because it had been caught the first time in the very act of swimming across, it was concluded that the animal had repeated the attempt rather than gone around the end of the lake and back to where it was later found. To have gone around the lake would have meant a travelled distance of approximately 2¾ miles, whereas to have swum directly across and move to the point at which it was found involved a minimum

of but a little more than ½ mile. In the majority of the cases, however, the observations at Snakeskin Lake suggest a limited range during the summer months at least.

Figure 23 - P_4, one of several porcupine observed swimming at Snakeskin Lake. The pictured animal was captured, marked, and then released. Fourteen days later, the same animal was found 500 yards beyond the far shore of the lake.

Porcupines which had travelled one-half mile between consecutive observations included P_1, P_3, P_4, P_6, and P_{15}. Of these only one repeat observation had been made on P_1, P_3, and P_6. No further information was obtained on these particular animals to determine whether further travel would have been of an additive or a back-tracking nature. Between the time that P_4 had been marked and the time at which it was again located, the animal had travelled slightly more than one-half mile--in this case, presumably across the lake. On the next occasion, which was also the last the animal was observed, it had again

moved another quarter mile. This however, was in addition to its former range. The animal was now three-quarters of a mile from where it had originally been marked. P_{15} on the other hand, after having been marked, was seen on three occasions within a few hundred feet of the original point of observation. On the fourth occasion, the animal was followed by canoe as it travelled more than a half mile along the shoreline. The observation lasted from 8:30 p.m. until well after midnight at which time the animal entered the forest and was lost from view. The same animal was found the next morning making its way back along the same path followed the night before. By mid afternoon it had returned to the point from which the travel had originated. This was, therefore, an example of travel in which the distance covered between observations was not of an additive type.

From Figure 17, there does not appear to exist any clear-cut correlation between the number of days between consecutive observations on marked animals on the one hand and the distance travelled by these animals on the other hand. The maximum time between consecutive observations on animals which had apparently travelled less than 300 yards was 15 days. It was realized, however, that this cannot be taken to indicate that such animals had not travelled greater distances. They could very readily have done so and returned to within the 300 yard range before the next observation. A minimum of one day and a maximum of fourteen days interval was seen to occur among porcupine found within a range of one-quarter of a mile.

One might expect greater intervals of time to be required for these slow moving creatures to traverse greater distances. Here, however, individuality becomes a factor of increasing importance. Whereas on 13 occasions (not 13 animals) a range of less than 300 yards had been exhibited in unit time, yet on four occasions ¼ mile and on one occasion ½ mile had been traversed in the same period of time. On the other hand, 23 days of searching passed between the time of marking and locating of P_6 at one-half mile distant. Much would depend upon the inclinations of the animals themselves, the nature of the immediate environment in which the animal had been marked, and upon the frequency with which these particular areas of the forest were searched. Although an attempt was made to alternate the areas in which search was to be made each day, nevertheless, the observation on P_6 is significant in that it occurred within an area which was searched with as much frequency as any other location.

Because the forty-five porcupine had not been marked at the same time, it was felt that the Lincoln Index could not be used to calculate the porcupine population in the study area at Snakeskin Lake. Basing my calculations on a known total number of animals encountered for the first time each day over the five weeks period, and on the number of porcupines marked, I would estimate that between 80 and 100 animals inhabited the eight square miles studied.

Although it had been anticipated that information of

value concerning the hourly activities of individual porcupine would have aided in a better understanding of the ecology of the animals, yet the preparation of such "porcupine minutes" was soon found to be quite impractical. Dense vegetation too readily accorded concealment to the animals as soon as they entered the woods. Nor did the author possess binoculars at the time of the field study to be used in observing from a greater distance.

In summary it may be stated that from the information based on the methods employed during the five weeks of study during mid summer at Snakeskin Lake, the majority of the porcupines appear to exhibit a home range of ¼ mile or less.

Experimental Studies

In the experimental studies, the percentages of hourly activity of the male porcupine under the three laboratory conditions was plotted against the hours of a day. This is shown in Figure 18. Under each of the conditions employed there does not appear to be any precise regularity in the number of hours between the major peaks of activity. Several reasons may be suggested which might in part account for this seeming lack of a more exacting periodicity. First, the periodicity, if present, may have been influenced by factors which themselves are divorced from the 24-hour cycles. Secondly, several factors inherent in the procedures followed may have been of a more influential nature than had been anticipated

at the time of the study. Of major consequence among these was the necessitated procedure of feeding the animal and changing the record sheets at 9:00 a.m. each day. It is felt, therefore, that the peaks of activity occurring immediately after this period would display only feeding movements. Also it is uncertain as to what degree this enforced feeding hour influenced the activity of the remainder of the day. A fresh quantity of apples and soda biscuits were given to the animals each day at this time. These were generally consumed by noon. A continuous supply of dog checkers, upon which the porcupine fed with little less appetites, was maintained by means of a self-feeding apparatus within the cage.

The male animal appeared to exhibit major peaks of activity near noon and midnight, with a major decline midway between the peaks. Unlike the activity periods of laboratory mice, however, which gradually build up to a peak and then decline rapidly, the activity of the porcupine was found to reach its peak quickly and then diminish at a much slower rate. From midnight to dawn activity declines rapidly. Under conditions of continuous light and darkness the activity was greatly reduced and was not only out of phase with one another but also out of phase with the outside activity. A more consistent level of activity, however, was maintained over the whole day.

A much closer correlation appears to exist when the outside activity here recorded in the laboratory is compared with observations recorded on activity of porcupine in the

field. Compare Figure 14 and 18. With variations of one to two hours, the major peaks of the field observations--occurring at 11 a.m., 2 p.m., 4 p.m., 8:30 p.m., and 2:30 a.m.--are matched by those found to occur in the laboratory under conditions here described as "outside normal". With certain possible limitations, therefore, it would appear that the basic activity of the animal had not been greatly changed by restrictions imposed by the laboratory methods.

The same type of field-laboratory correlation appears to exist in the activity of the female porcupine shown in Figure 14 and 19. Here again the major peaks at 11 a.m., 3 p.m., 5 p.m., and 9 p.m. each occur within one hour of the corresponding field observation. As with the male animal, peaks of activity vary in occurrence from two to four hours. Also here too, the activity under conditions of constant illumination are much reduced. Another field-laboratory correlation may be suggested from the activity recorded of the female porcupine. Just as an increase of activity in the spring of the year might be expected in the field, so also the activity under outside normal conditions in the laboratory during May showed a great increase over corresponding activity recorded during December. In the comparison of the results obtained in the laboratory, the major peaks of activity during these two separated months appear to correspond more closely to one another during the late afternoon and night hours than they do during the morning and early afternoon.

The comparison of the outside normal activity of the male and the female porcupines is shown in Figure 20 while a similar comparison under conditions of constant illumination occurs in Figure 21. At first glance it would appear that the activity of the male is surpassed by that of the female and that the major peaks of activity do not occur at the same hours for the two animals. The activity of the female porcupine represented here is the average of the activity recorded during December and May. To have taken such a value as being representative may perhaps have been unfortunate. A striking similarity in activity is seen, however, if the whole pattern exhibited by the male were to be shifted two hours to the left on the graph, i.e., should the peaks for the male occur two hours earlier. In doing so, five of the six major peaks of activity of the male animal are found to occur at the same intervals as do those of the female. This, however, because of the small number of records obtained, ought to be attributed to coincidence--at least until a greater number of statistically significant records are obtained. On the other hand, a shift of activity curve may be justifiable to compensate for the earlier hours of darkness during the period over which experimentation using the male animal had been carried out.

That a periodicity of activity, irregular though it be, does exist in the porcupine is seen when the hourly activity over several days is considered. The ten days of recorded outside normal activity of the male porcupine was plotted in

a continuous series and smoothed by taking five hour running averages. The result is shown in Figure 22. The conditions of night and day appear below the activity curve. While one or more major peaks of activity appear to occur during the day and during the night, these peaks are not consistently higher in one or the other of these two major periods. Nor does there appear any consistency in the time at which the peaks occur during the day or night.

SUMMARY

From the result of the studies on the porcupine at the Acadia Station, at Snakeskin Lake, and the experimental studies at McMaster University, several points of interest were evident. First, there appears to be considerable correlation between the activity data obtained in the field studies and those obtained in the laboratory. Within one to two hour limits, the major peaks of activity were found generally to occur at the same hours of the day--the greatest peak at 2 p.m. and lesser peaks at 11 a.m., 4-5 p.m., 7-9 p.m., and near midnight.

Several limitations regarding methods employed should also be considered. In the field studies at Snakeskin Lake, the majority of the animals were found to exhibit ranges of a quarter mile or less. This value appears to be reliable and agrees with the work of other authors stated. It must be remembered, however, that this study was made at the edge of a lake, and although considerable portion of the approximately eight square miles surrounding the campsite, yet the very presence of the lake with its concommitant aquatic vegetation would very likely have served to attract porcupine and thereby limits somewhat the summer range. On the other hand, proof that such is the case, is also lacking. It can but be

suggested that the actual range of the animal would be influenced to a degree by the terrain, availability of preferred foods, and other habitants of the study area or any other study area. For completeness, it is felt that similar studies should be made at different seasons of the year within the same locality and in areas which differ in respect to vegetation and terrain.

Another factor which would be of great interest to determine is a method of marking porcupines, or other comparable animals, in a manner such as that used in this study but which would be retained over several years, thus enabling a range study over a greater period of time. The rapid molting of the caged animals in the spring cast doubt as to whether the marking methods used at Snakeskin Lake could be applicable in an extended study over several years. The use of paint rather than ear tags has the advantage of enabling identification of the animal without necessitating actual recapture.

Within the time of the field study, no close correlation could be found to exist between the distance a porcupine had travelled and the number of days which had lapsed since the animal had been last seen. Within fifteen days, marked animals had been found at locations revealing variations from less than 300 yards to those which had travelled more than 1.5 miles. No marked animal was found to have travelled a distance greater than 1.5 miles during the period of the study. The observer, on the other hand, had made repeated searching trips of five to six miles per day.

Several inevitable factors were encountered in the experimental aspect of the activity study; it is realized that some of these may have had undetermined influences upon the final results. For a more extensive study, more than two animals should have been used. Also the records ought to have been simultaneous rather than alternating for the different animals used. The number of days of consecutive recordings under conditions of constant illumination and constant darkness were not as great as those during which activity was recorded under outside normal conditions. More records under these two circumstances might have served to give a more equitable comparison. The results obtained do show a marked decrease of activity under both the conditions of constant illumination and constant darkness. As with outside normal, the three to four hour interval between peaks of activity is maintained but with less regularity. The greatest peaks of activity generally occur once during the day and once during the night, but the exact hour at which these occur varies considerably. In other words, although a periodicity does exist in the activity of the porcupine, information gained from the experimental studies suggests that the periodicity may be governed by factors other than light and temperature. One such factor may be that of a normal mathematical cycle inherent in numbers themselves. Such factors may become more clearly defined with the completion of much more extensive studies now begun on experimental studies of the behaviour of porcupines.

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