SEASONAL ASPECTS OF THE ECOLOGY AND MICROENVIRONMENT OF BEAVER (*CASTOR CANADENSIS* KUHL) IN NEW YORK

by John J. Bascietto

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approval of advisor
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INTRODUCTION

Species notes

The genus Castor contains the only living representatives of the family Castoridae : C. canadensis Kuhl , 1820 of North America ; and C. fiber Linnaeus , 1758 of Europe and Asia . Castor is found from the Pliocene to Recent of North America, Europe, and Asia (Simpson, 1945).

Except for the capybara of South America, the beaver is the largest member of the Order Rodentia. The largest specimens weigh up to 70 pounds with most adults of three or more years weighing between 30 and 60 pounds (Palmer ,1954). Specimens captured in Maine and New York had the following measurements: total length, 1170 mm.; tail, 412 mm.; hind foot, 175 mm. (Hamilton, 1943).

The external form is highly adapted for aquatic life, thickset and compact, with short legs. The broad, horizontally flattened tail resembles a paddle, and is covered with scales from which a few hairs protrude. The caudal vertebrae are dorso-ventrally flattened. The pentadactyl hind feet posess toes which are broadly webbed. The second digit is a double-clefted claw, acting as an effective comb for removing ectoparasites.

As a herbivore feeding mainly on the bark and cambium of deciduous trees, the teeth of a beaver are of extreme importance to its survival. The incisors are strongly developed and quite large with (orange) pigmented enamel. The cheek teeth are not constantly growing as are the incisors, but are excessively hypsodont, with a heptamerous pattern which changes little with age and rarely wears out. The dental formula is:

$$\frac{1 - 0 - 1 - 3}{1 - 0 - 1 - 3}$$

(Hall and Kelson, 1959).

The life history and ecology of this animal has been the subject of a vast literature. European accounts of the life of beaver (presumably C. fiber) date to at least the end of the 12th century A.D. . Giraldus Cambrensis, writing c. 1190, gives a description of beaver colonies in Wales and Scotland (Cambrensis, 1908). The long quest for beaver pelts was probably the major factor in the exploration of the North American continent (Palmer, 1954).

Regarding C. canadensis, scientific publications prior to 1955 may be consulted for an extensive treatment of beaver ecology, natural history, beaver culture, and management (Bailey, 1927; Bradt, 1938 and 1940; Cook, 1943; Grasse and Putnam, 1950; Hodgdon and Hunt, 1953; Leighton, 1933 and 1935; Osborn, 1955; Soper, 1937; and Tevis, 1950). However, for the most part, these works are particularly lacking in quantitative data.

Recent ecological studies are few, but more quantitative in nature. Osborn (1953) treats age classes, reproduction, and sex ratios. Hall (1960) reports on qualitative and quantitative aspects of beaver food species. Aleksiuk and Cowan (1969 a,b) are concerned with the physiological ecology of Arctic populations while Novakowski (1967) treats the winter bioenergetics of sub-Arctic Canadian beaver.

Early quantitative physiological data was obtained by Irving (1937, 1939) and Irving and Orr (1935) concerning the beaver's diving and respiratory abilities. The functional anatomy of the tail been treated by Steen and Steen (1965) and Aleksiuk (1970). The former work shows that the tail has a major thermoregulatory function while the latter work shows that fat is deposited in the tail during periods of low energy expenditure and mobilized during periods of high energy expenditure, conforming to the function of other known fat depots.

The winter metabolic depression

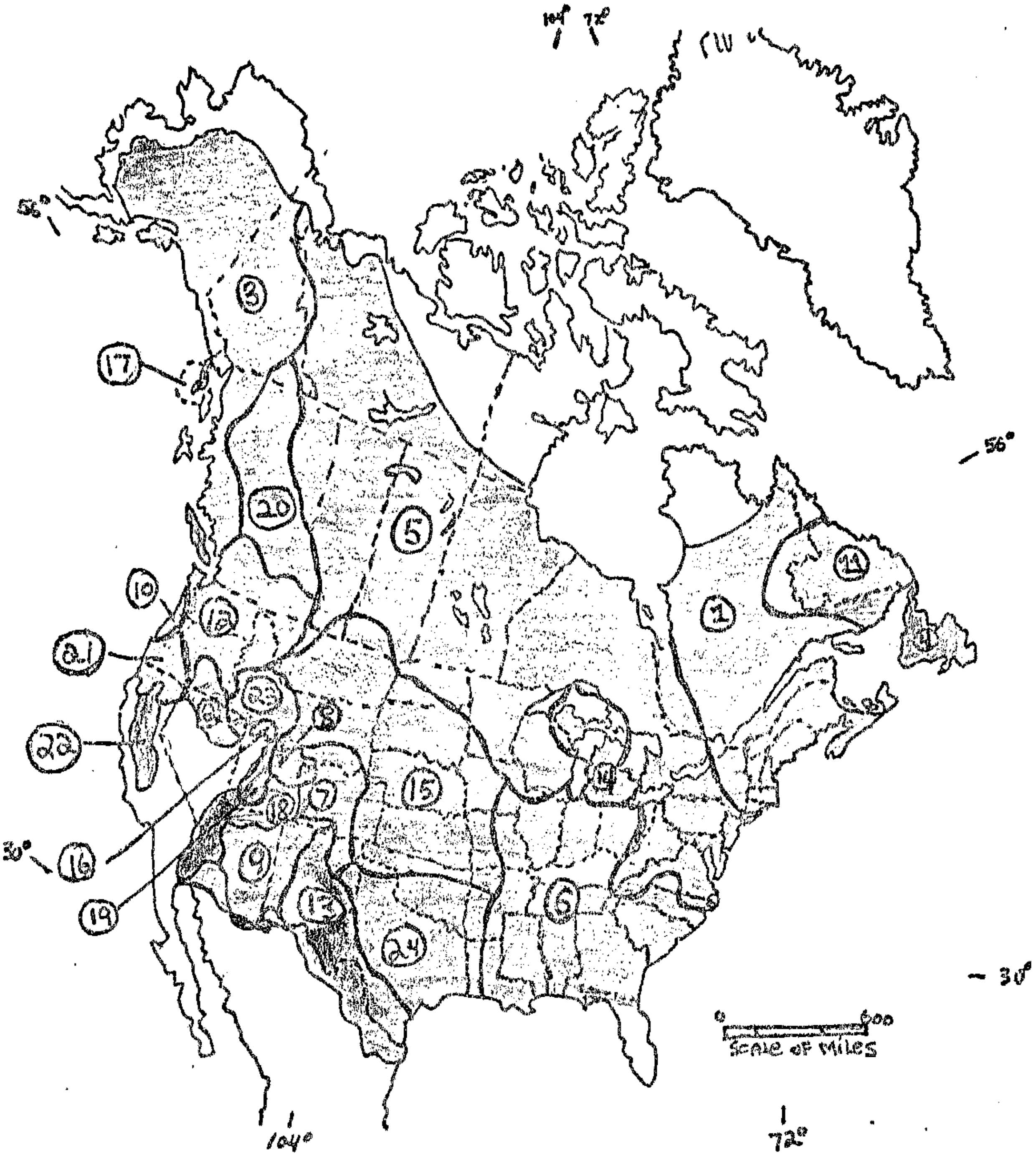
At the northern limit of their distribution in the Mackenzie Delta, Northwest Territories (Map 1.), beavers are subject to a fluctuating energy regimen. In summer (lasting 4 months) the animals have access to an abundant food supply, i.e., the growing plant material. In winter (8 months) the animals are effectively isolated in a microenvironment consisting of the lodge and a small area immediately in front of it (below the ice of ponds). Their food supply is limited to a cache of twigs and saplings stored under the ice of ponds, surrounding the lodge or adjacent to it.

These Arctic populations undergo what has been described as a "winter metabolic depression". Aleksiuk and Cowan (1969a), who first described this aspect of the beaver's physiological ecology, show that (in the field) growth is rapid in summer and absent in winter. In adults, fat was deposited in autumn , maintained in the winter, and mobilized in spring. A winter weight loss characterized immature animals. Thyroid gland weights were found to be greater in summer than in winter. It was concluded from these data that metabolic energy expenditure is greater in summer and depressed during the excessive climatic conditions of the Arctic winter.

In controlled laboratory experiments (Aleksiuk and Cowan, 1969b) Arctic beaver and animals from northern California were kept under Vancouver, B.C. climatic conditions with a constant food ration avail-

MAP 1. RANGE AND DISTRIBUTION OF NORTH AMERICAN BEAVER
CASTOR _CANADENSIS_ KUHL

(after Hall and Kelson, 1959)



1. C. c. acadicus
2. C. c. baileyi
3. C. c. belugae
4. C. c. caecator
5. C. c. canadensis
6. C. c. carolinensis
7. C. c. concisor
8. C. c. duchesnei
9. C. c. frondator
10. C. c. idoneus
11. C. c. labradorensis
12. C. c. leucodontus
13. C. c. mexicanus
14. C. c. michiganensis
15. C. c. missouriensis
16. C. c. pallidus
17. C. c. phaeus
18. C. c. repentinus
19. C. c. rostralis
20. C. c. sagittatus
21. C. c. shastensis
22. C. c. subauratus
23. C. c. taylori
24. C. c. texensis

able *ad libitum*. Arctic beaver exhibited the following during winter: a growth cessation; a 40% reduction in food intake; and a depression of the protein-bound ^{131}Iodine conversion ratio, demonstrating a depressed thyroid activity. No major seasonal variation in these data were observed in beaver from northern California.

In the same study decreasing photoperiod was shown to induce the reduction in food intake, weight loss, and a muscular paralysis (which was not understood by the authors). Exposure to constant light, after 24 days of darkness, completely eliminated all of the above effects. Variation of photoperiod had no effects on California beaver.

These data were offered as evidence to support their hypotheses that: A) a winter metabolic depression exists in populations of Arctic beaver; B) the adaptive significance of this pattern is that metabolic energy expenditure is regulated by environmental energy availability; and C) this annual pattern is an inherent characteristic of northern beaver and is induced by decresing light intensity in the autumn.

Winter adaptations, thermoregulation and the microenvironment

According to Aleksiuk and Cowan the winter metabolic depression is highly significant since a pronounced seasonal pattern of energy expenditure, as exhibited by Arctic beaver, had not been previously observed in non-hibernating mammals[1]. However, the woodchuck , *Marmota monax*, although usually a hibernator, shows seasonal metabolic decreases when

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[1] No evidence of hibernation by beaver has ever been observed (Aleksiuk and Cowan, 1969 a,b).

prevented from entering torpor experimentally (Bailey, 1965). Additionally , woodchucks normally show seasonal cyclic food consumption (Fall, 1971). Davis (1967 a,b) suggests that in M. monax, "endogenous circadian rhythms" are apparently independent of external and internal feedback mechanisms. Seasonal fluctuations in growth patterns have been observed in black tailed deer, Odocoileus hemionus (Wood et al, 1962) and the racoon, Procyon lotor (Mech et al, 1968).

If we are to understand the climatic adaptations of mammals, such as the "winter metabolic depression" of beaver, we must have a knowledge of environmental temperatures encountered by these animals, and moreover, we must know how these temperatures affect activity and behavior patterns. This is particularly important in the case of the beaver. Formazov (1946) shows how many mammals and birds develop similar adaptations to winter habitats, when food is scarce and nutritional value reduced. Major physiological adaptations apparently exist in Arctic populations of these rodents. The adaptations of more southerly populations of C. canadensis may only be behavioral.

In a study involving beaver from Wood Buffalo National Park, Alberta, Canada, where the icebound period is 164 days, Novakowski (1967) shows that,except for an increase in winter weights of kits and yearlings, methods of energy conservation were strictly behavioral. These included reduced activity, huddling, lodge construction, and a curious reference to periods of "dormancy" [2]. These findings conflict somewhat

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[2] Kill records, using a Conibear trap in the plunge hole of the lodge, indicated an average movement of one animal from each lodge every two weeks. Novakowski (1967) is unclear as to whether these data were used to describe "reduced activity" or "dormancy" , which are referred to separately.

with the results of Aleksiuk and Cowan (1969 a) who found that kits and yearlings lost weight in a longer icebound period.

Other than the studies on Arctic and sub-Arctic Canadian animals already mentioned, no quantitative data have been obtained on seasonal adaptations of beaver. Negative results have been obtained for physiological adaptation in beaver from northern California. Stephenson (1969) has obtained quantitative data on the specific role of temperature in the ecology of sub-Arctic Canadian beaver , however, only data from January and February, 1965, were reported and behavioral analysis was only marginal. Seasonal comparison was therefore, impossible. This kind of data is essential to an understanding of the thermoregulatory problems of animals under seasonal stress.

Consider the winter weight loss of kits and yearlings which may or may not occur (conflicting reports). Kleiber (1961) states that weight loss may approach 34% of initial body weight before thermoregulation breaks down. This, therefore, is probably not a problem for kits and yearlings losing weight in winter (Aleksiuk and Cowan, 1969 a) nor for adults with a winter weight loss (Novakowski, 1967) , as weight loss from these reports does not approach 34 per cent of initial body weight.

In order to maintain a constant body temperature an animal must regulate heat loss and heat gain. Considering that endotherms use 80-90 per cent of their oxidative energy doing this (Vaughan, 1972) it seems likely that a good deal of their adaptive strategies will serve to minimize the cost (in terms of oxidative energy) of thermoregulation. This metabolic cost is also called "thermal conductance" . By definition, (Vaughan, 1972), "thermal conductance" may be reduced by reducing ΔT

in the equation,

$$\Delta T = T_{\text{ambient}} - T_{\text{body}} \qquad (T = \text{temperature, } ^{\circ}\text{C}).$$

Metabolic economy (adaptation) is thus achieved by minimizing ΔT.

Many mammals decrease ΔT through the construction of lodges or burrows (Hayward, 1965; Stephenson, 1969; Novakowski, 1967), which may be considered as a behavioral adaptation, especially when energy availability is reduced. Stephenson (1969) has shown that the internal chamber of a beaver's lodge provides a relatively constant environmental temperature and, moreover, it is a high temperature relative to outside , air temperatures in winter. The data from January and February, 1965 (in Ontario, Canada) showed that daily minimum internal temperatures ranged from +2°C to -3°C while outside temperatures got as low as -37°C ! Lodge temperatures remained quite stable with only 0.8°C separating average minimum and maximum values. Daily ambient temperatures varied as much as 30°C, placing unprotected mammals under severe thermal stress.

In the Canadian study, changes in lodge temperatures were caused by a combination of extreme cold periods and reduced snow cover. However, it was noted that beaver activity (in the form of entrances and exits to and from the lodge) would also cause fluctuations in the internal temperature values obtained hourly, reflecting body heat produced by the animals. Only average values were reported and the actual temperature record was not used as a measure of activity. It was noted that when internal lodge temperature dropped below 0°C there followed a period of relative inactivity.

The present study looks at temperature as a factor in the ecology of beaver from relatively southern latitudes. Specifically, internal lodge temperature is determined on a day to day basis (throughout one year) and used as a measure of activity. This is a particularly productive method since activity levels and patterns are not only defined by changes in the temperature record but, at the same time, can be directly compared and correlated with it.

Seasonal variation in these data replaces standard physiological parameters in determining whether New York beaver undergo any form of winter adaptive strategy. Additionally, a better understanding of the thermoregulatory problems faced by southern beaver (and the solutions to these problems) will be gained. Seasonal temperature variation also helps to elucidate the complex physical mechanisms involved in lodge thermodynamics.

STUDY AREA AND EXPERIMENTAL POPULATION

This study was performed at the Harvard Black Rock Forest which is about 3,600 acres in extent, lying just west of the Hudson River in the towns of Cornwall and Highland, Orange county, New York. The Forest lies in the area known as the Hudson Highlands, which is a belt of rocky hills extending northeast and southwest across the Hudson River about fifty miles north of New York City.

Elevations in the Forest are from about 450 ft. above sea level at its northern edge, 500 - 1200 ft. on the northern slopes of the Highlands, and 1200 - 1350 ft. in an elevated plateau-like region in the southern portion of the Forest. Denny (1938) provides a topographical reference map of the Forest prepared by the U. S. Geological Survey. The center of the study area lies at 41° 24' N , 74° 01' W.

Due to the long quest for beaver pelts, no wild beaver remained in this area by the end of the 19th century. In an effort to restore these rodents to their former range, New York State conservationists imported twenty-five Canadian beaver (*C. c. canadensis*) in 1901 - 1906 and fourteen animals from Yellowstone National Park (*C. c. missouriensis*) in 1901 (Buckley, 1955). As a result the subspecific status of the present population is uncertain [3].

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[3] Data from previous studies (Aleksiuk and Cowan, 1969 a,b; Stephenson, 1969) were obtained on animals from the following taxonomic categories and localities:
C. c. canadensis, Mackenzie Delta, 68° N, 135° W.
C. c. shastensis, northern California, 42° N, 123-124° W.
C. c. canadensis, Ontario, Canada, 45° 35' N, 78° 27' W.

MATERIALS AND METHODS

Access to the lodge chamber and probe assembly

The anatomy of a beaver lodge is a primary consideration if an accurate internal temperature is to be obtained. If the lodge were of the "island type" described by Hodgdon and Hunt (1953), access to the internal chamber was easily obtained by drilling a 2 inch diameter hole at any point adjacent to the apex (Fig. 1). If the lodge is of the bank type or "domed half-lodge" described by Soper (1937), the location of the internal chamber must first be determined. This was accomplished by inserting 3 metal rods into the lodge as shown in Fig. 2 . If the rods touched when moved about, the internal chamber had been tentatively located. Proof of the effectiveness of this method comes only after beaver vocalizations have been recorded in this chamber (as described below).

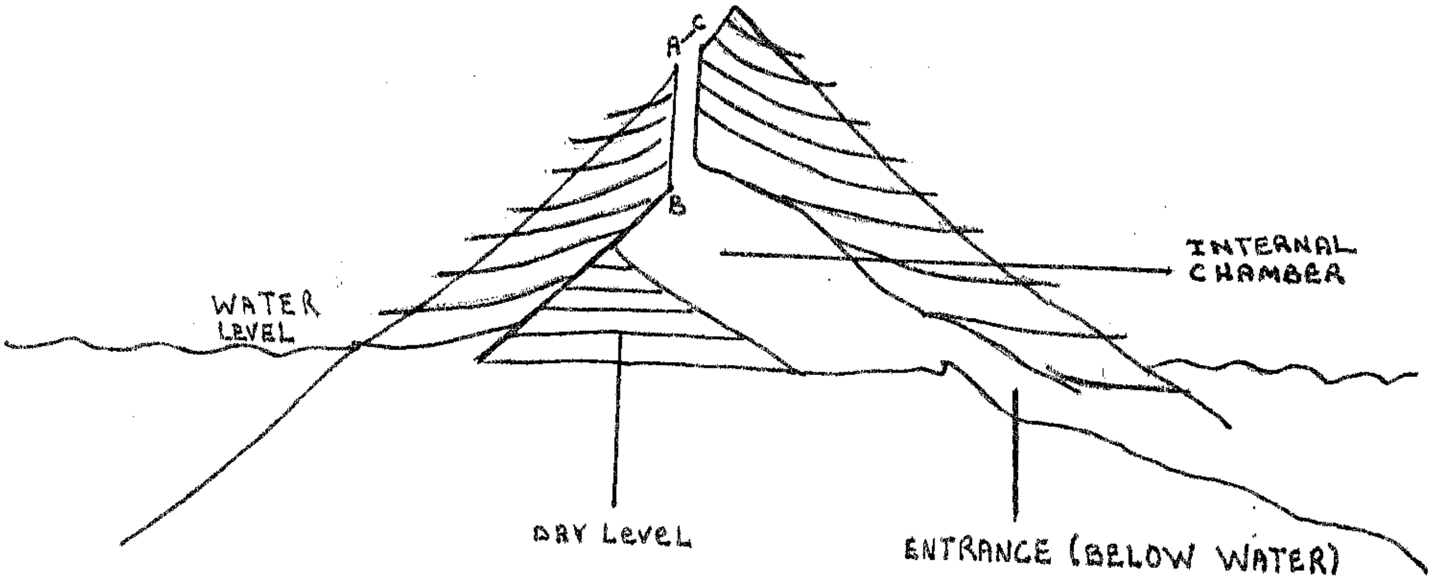
Drilling was accomplished with a hand brace and expandable drill bit. Bit extenders were used for thick lodge walls. A long, thin hand saw was useful in removing twigs and branches missed in drilling. Drilling was quite easy in the spring but very difficult in winter. Indeed, the strength of the combination of materials used in lodge construction has been compared to "reinforced concrete" once hardened (Anonymous, 1977).

A 2 inch (O.D.) polyvinyl chloride (PVC) pipe, fitted with a collar, was inserted into each hole drilled. This outer pipe was filled with a snugly fitting 1 inch (O.D.) PVC inner pipe which contained fiberglass insulation and recording probes (Fig. 3).

It seemed prudent to place the recording end of the pipe as close

FIGURE 1. AN IDEAL CROSS SECTION THROUGH AN "ISLAND" LODGE

(Line A-B shows location of pipe containing recording probes. Line A-C shows the outer diameter of pipe)



A – B = 2 FEET
A – C = 2 INCHES

FIGURE 2. AN IDEAL CROSS SECTION THROUGH A "BANK" LODGE

(Technique for locating internal chamber is illustrated.)

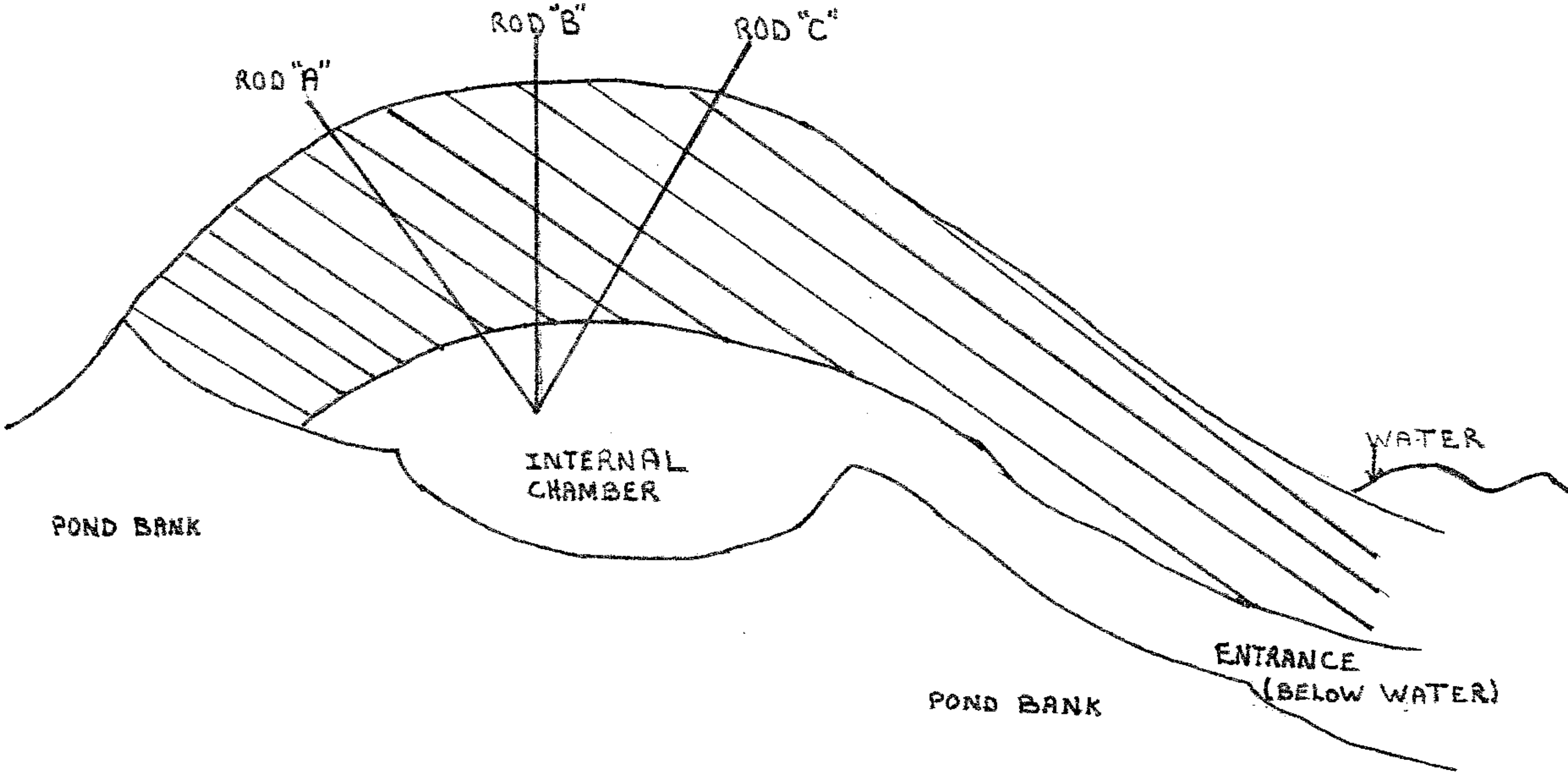
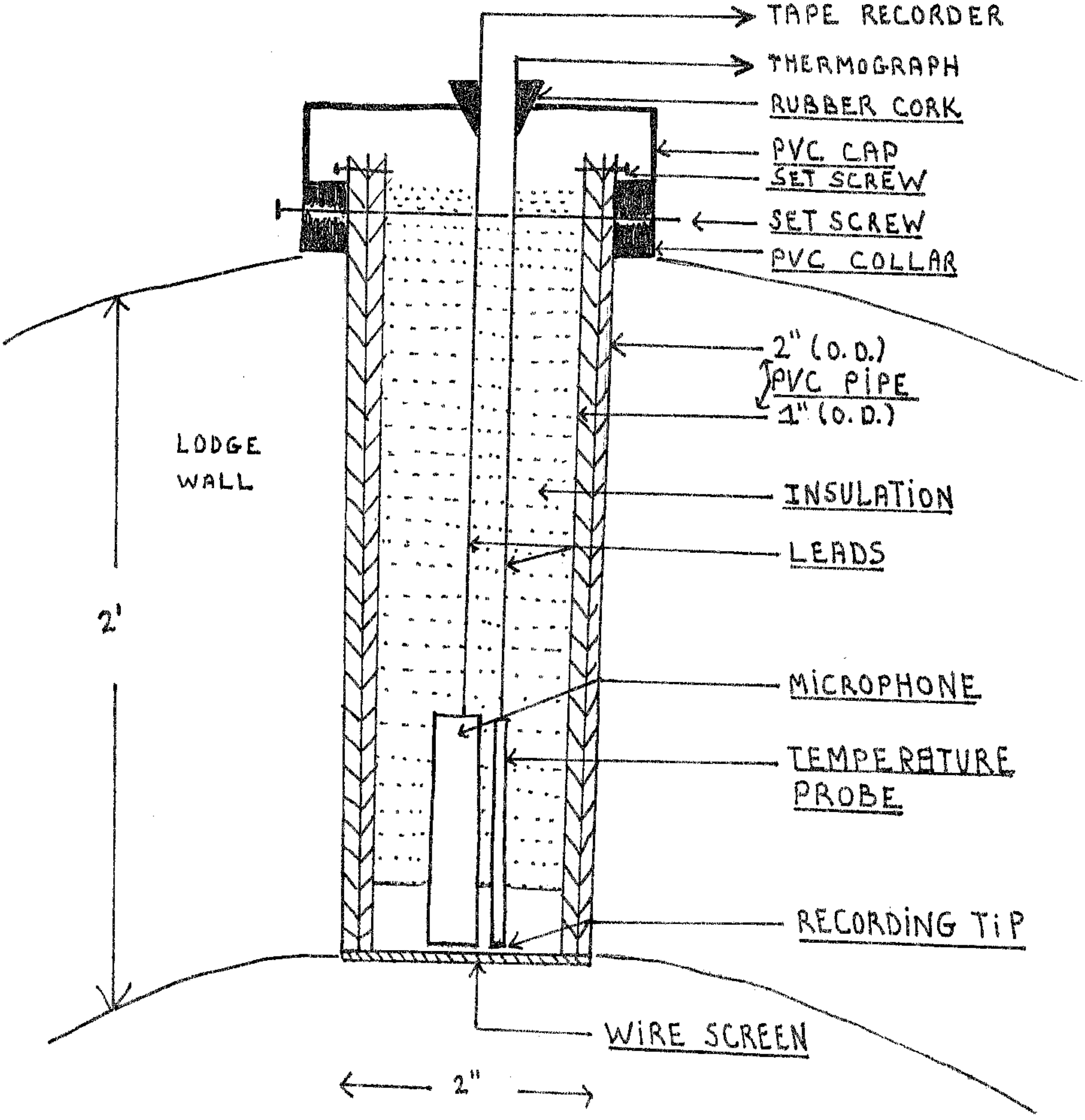

ROD "A"
ROD "B"
ROD "C"
WATER
INTERNAL CHAMBER
POND BANK
ENTRANCE (BELOW WATER)
POND BANK

FIGURE 3. CROSS SECTION THROUGH LODGE WALL SHOWING PROBE APPARATUS INSTALLED



INTERNAL CHAMBER

as possible to the entrance of the drilled hole to the internal chamber, without actually entering the chamber, so as not to disturb its occupants. This was accomplished by measuring the thickness of lodge walls around the drilled area with a hooked metal rod. The rod is placed into the hole and slowly drawn out. When the hooked end catches the lodge wall the distance to the top of the lodge is measured. PVC pipes are then custom cut with a saw. All lodge walls were approximately 2 feet thick.

Collars are adjusted to the proper height and serve to support the entire assembly against the lodge walls. The recording end of the pipe is fitted with a wire mesh screen as a further precaution. Beavers never tried to plug up the recording end of the pipe, but this is always a potential problem.

Meyer (1973) points out that grave errors may result if recording equipment is exposed to excessive humidity. This is a particular problem in the aquatic surroundings of a beaver lodge. Accordingly the entire assembly was capped with a PVC cap (2 inch I.D.) containing necessary holes for lead wires. All exposed portions of the apparatus as well as internal junction points were sealed with modeling clay and liberally wrapped with waterproof PVC tape. These precautions proved sufficient to keep all moisture out.

Measurement of the internal lodge temperature

Internal lodge temperature (T_i) was continuously recorded by a Rustrak Nickel Wire Probe (Resistance bulb) thermograph (Gulton Industries). Utility probes (nickel wire) were fitted as shown in Fig. 3. Temperature span was -45^0C to $+55^0C$. The accuracy of the machine is rated at ± 2.5 per cent of the span (100 centigrade degrees), with a stability rating of ± 0.5 per cent of span. Chart record could be read out to 0.5 centigrade degrees. The chart drive was a 12 VDC special inverter motor compensating for millivolt fluctuation. Power supply to the recorder was a 12V (14 amp-hour) rechargeable motorcycle storage battery (Yuasa Co.). Recorder drew 25 mA per hour. Both recorder and battery were kept in an insulated, steel, weatherproof field locker with appropriate holes for lead wires. Pressure sensitive chart paper eliminated the need for ink refills. The apparatus could be left unattended for as long as three weeks.

Measurement of air temperature

The air temperature outside the lodge (T_a) was continuously and simultaneously recorded on the same thermograph described above. By installing an additional probe to the thermograph (fitted with a special "time sharing feature" - Gulton Indus.) T_i and T_a records are superimposed on the same chart. The two records could never be confused as the "time sharing feature" allows a broken line for one record and a solid line for the other. As suggested by Meyer (1973) lead wires were color coded so as never to be confused. Probes for T_a were placed above the lodge and shaded from direct sunlight. Records for precipitation and other weather data were obtained from the National Oceanographic and Atmospheric Administration (NOAA) weather monitoring station at West Point, New York (about 2 miles SE of the study area).

Calibration

The machine was originally calibrated by the manufacturer. Before thermograph and probes were installed in the field calibration was checked against known accurate mercury thermometers. Standards used in these tests included the freezing point of water, air temperature in a room, air temperature in the field, and human oral temperature. In the field calibration was checked against the same mercury thermometers before and after installation, and at various points during the course of the project (see "Results", Table 1).

Recording of sounds within the lodge

The apparatus in Fig. 3 was modified by adding a highly sensitive microphone (Sennheiser Co.) to the pipe. Lead wires connected the microphone to a high fidelity, portable tape recorder (Uher 4000 Report-L, Martel Co.). Tape used was long playing magnetic tape (BASF) running at 7.5 inches/sec. .

RESULTS

Calibration tests

Table 1 shows data collected during various tests to check the calibration of the Rustrak thermograph against a known accurate mercury thermometer. Various temperature standards and test conditions were used. The thermograph was found to be accurate within the manufacturer's limits, particularly during the first 8 months of the study (Feb. - Sept., 1977). Tests before installation revealed both absolute and relative accuracy as well as stability. After about 6 months in the field the machine was again tested for relative and absolute accuracy, and proved satisfactory.

In the last months of the study the thermograph registered 1.5 - 2^{o}C below the mercury thermometer. Data collected during this period was corrected by adding 2^{o}C to each observation.

Calibration tests were performed with 3 interchangeable probes using both thermograph inputs randomly. Except for normal machine variance all probes and inputs gave the same results. In the field, however, the same inputs, probes and leads were always used for T_i and T_a respectively. The third "back-up" probe had to be installed in Sept., '77 due to probe damage (before testing).

Time record accuracy was checked at the time tests were performed and always after the retrieval of each data sheet. The record could be read at 1 minute intervals. In short term testing (up to 24 hours) the machine was always exact. With long term use (3 weeks) 3-5 "extra" hours of data were usually added. Time of day was then approxi-

TABLE 1. RESULTS OF CALIBRATION TESTS

(control instrument = a known accurate mercury thermometer; T_{Hg} = temperature record of mercury thermometer; T_{Rus} = temperature record of Rustrak thermograph; figures in parentheses indicate plus or minus degrees Centigrade.)

DATE	TEST STANDARD	T_{Hg} (°C)	T_{Rus} (°C)	CONDITIONS
25 Feb. 77	Air (room)	+24(±1)	+24(±0.5)	Before installation; 2 hour test.
	Human Oral	+37.5	+37.0(±1)	two 10 minute tests.
	H_2O (ice)	0.0	0.0	2 hour test.
26 Feb. 77	Air	+11	+11	Before installation; in sun; 1100 hrs.
	Air	+8.5	+8.0	Before installation; shaded ; 1200 hrs.
	H_2O (pond)	+1	+1.5	1200 hrs.
	Air	+4.9	+5.5	After installation; 1730 hrs.
10 Mar. 77	Air	+12(±2)	+13(±1.5)	one hour test; 1215
12 Mar. 77	Air	+14(±2)	+13(±1.5)	one hour test; 1420
	H_2O (pond)	+8	+7.5	1500 hrs.
3 Apr. 77	Air	+12(±2)	+13(±1.5)	one hour test; 1215
15 Apr. 77	Air	+20(±1)	+20(±0.5)	one hour test; in sun; 1530 hrs.
30 Apr. 77	Air	+15(±2)	+15(±1.5)	one hour test.
20 May 77	Air	+34(±3)	+35(±2)	one hour test; in sun.
9 Jun. 77	Air	+9	+10	Heavy Rain; 10 minute test.
18 Sep. 77	Air (room)	+16(±2)	+16(±1)	air conditioned room; 3 hour test; before installation
	Air (field)	+21	+22	one hour test; before installation

DATE	TEST STANDARD	T_{Hg} (°C)	T_{Rus} (°C)	CONDITIONS
18 Sep. 77	H_2O (ice)	0.0	0.0	one hour test.
	Human Oral	+36.5	+37	two 10 minute tests.
	Plant (leaf)	+21(±2)	+21(±1)	2 hour test in air conditioned room at 16°C.
13 Oct. 77	Air	+7(±0.5)	+5(±0.5)	After installation; one-half hour test; shaded; 1600 hours.
1 Nov. 77	Air	+7(±1)	+5(±0.5)	one-half hour test; shaded; 1100 hrs.

mated by dividing the "extra" data over the time period involved. In one case 15 "extra" hours had been added over 3 weeks (unknown cause).

THE TEMPERATURE ECOLOGY OF BEAVER

Seasonal profile of internal lodge temperature (T_i)

Stephenson (1969) showed that the T_i of a beaver lodge in Canada was stable in winter and that changes in T_i were associated with low air temperautres combined with a lack of snow cover, and beaver activity. Present results document a limited degree of stability for a winter season in New York and expand the record to include a seasonal overview. Figures 4, 5, 6, and 7 show the seasonal records of mean daily internal lodge temperature ($\overline{T_i}$) and mean daily air temperatures ($\overline{T_a}$) (based on 24 observations of each record, each day). The periods shown are somewhat arbitrary in the sense that they conform, generally, to traditional solar seasons, but deviate slightly from these traditional seasons because they were chosen on the basis of mean periodical air temperatures which were determined to be "different" by t-tests for significant difference of means (Table 2.)[4]. Seasonal data analysis is thus performed on these 4 periods or, in some cases, on seasonal sub-divisions obtained from these periods.

An examination of daily $\overline{T_i}$ and $\overline{T_a}$ records immediately reveals two important points. First, changes in daily $\overline{T_i}$ are not only associated

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[4] Since a probe for measuring T_a was not available untill April 15th, 1977, NOAA climate data was used for calculating mean T_a in winter.

FIGURE 4. RECORD OF MEAN DAILY INTERNAL LODGE TEMPERATURE AND MEAN DAILY AIR TEMPERATURE FOR WINTER,(1976-1977).

(Solid line indicates mean daily internal lodge temperature. Broken line indicates mean daily air temperature.)

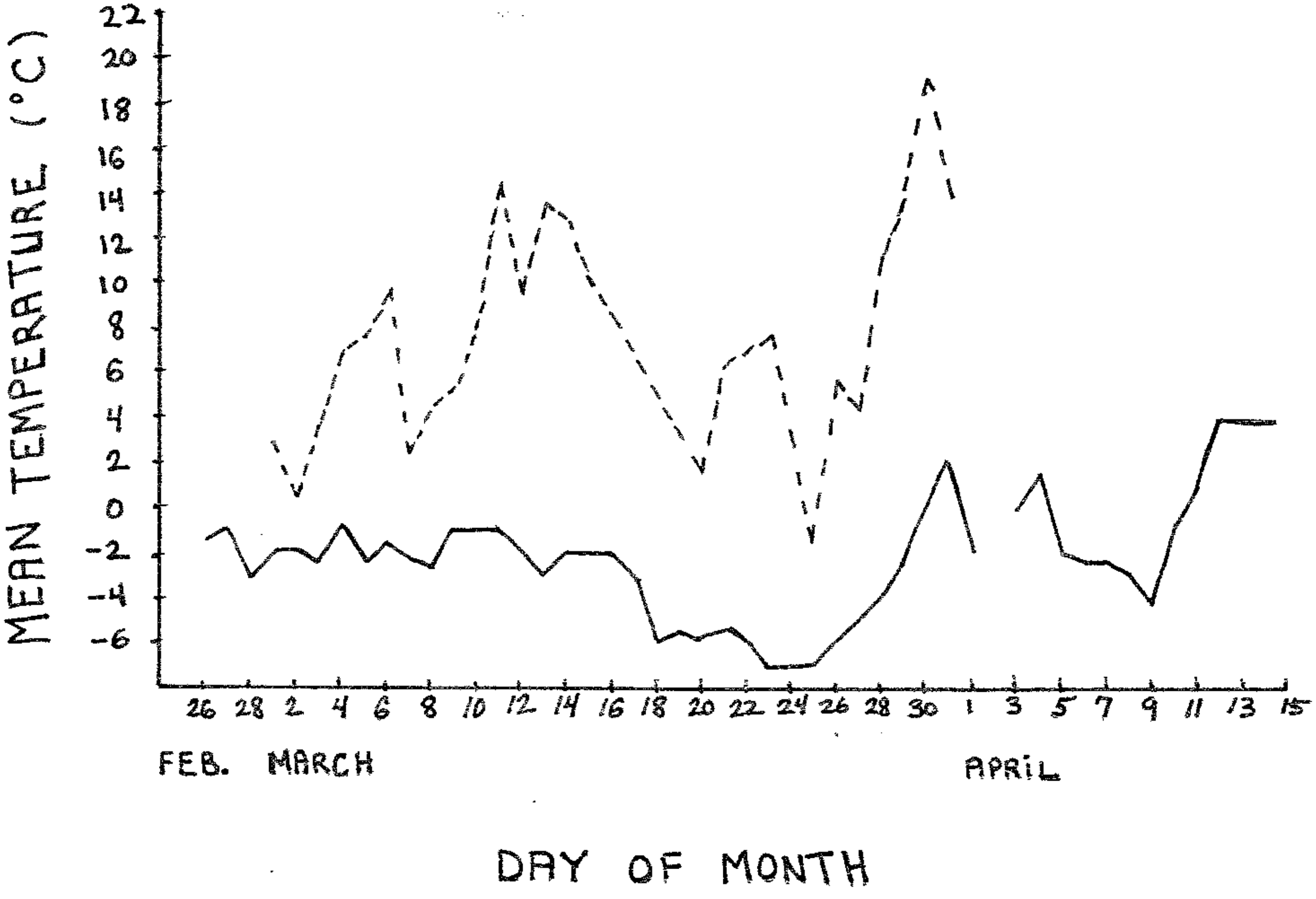MEAN TEMPERATURE (°C)
22
20
18
16
14
12
10
8
6
4
2
0
-2
-4
-6
26
28
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
1
3
5
7
9
11
13
15
FEB.
MARCH
APRIL
DAY OF MONTH

FIGURE 5. RECORD OF MEAN DAILY INTERNAL LODGE TEMPERATURE AND MEAN DAILY AIR TEMPERATURE FOR SPRING, 1977.

(Solid line indicates mean daily internal lodge temperature. Broken line indicates mean daily air temperature.)

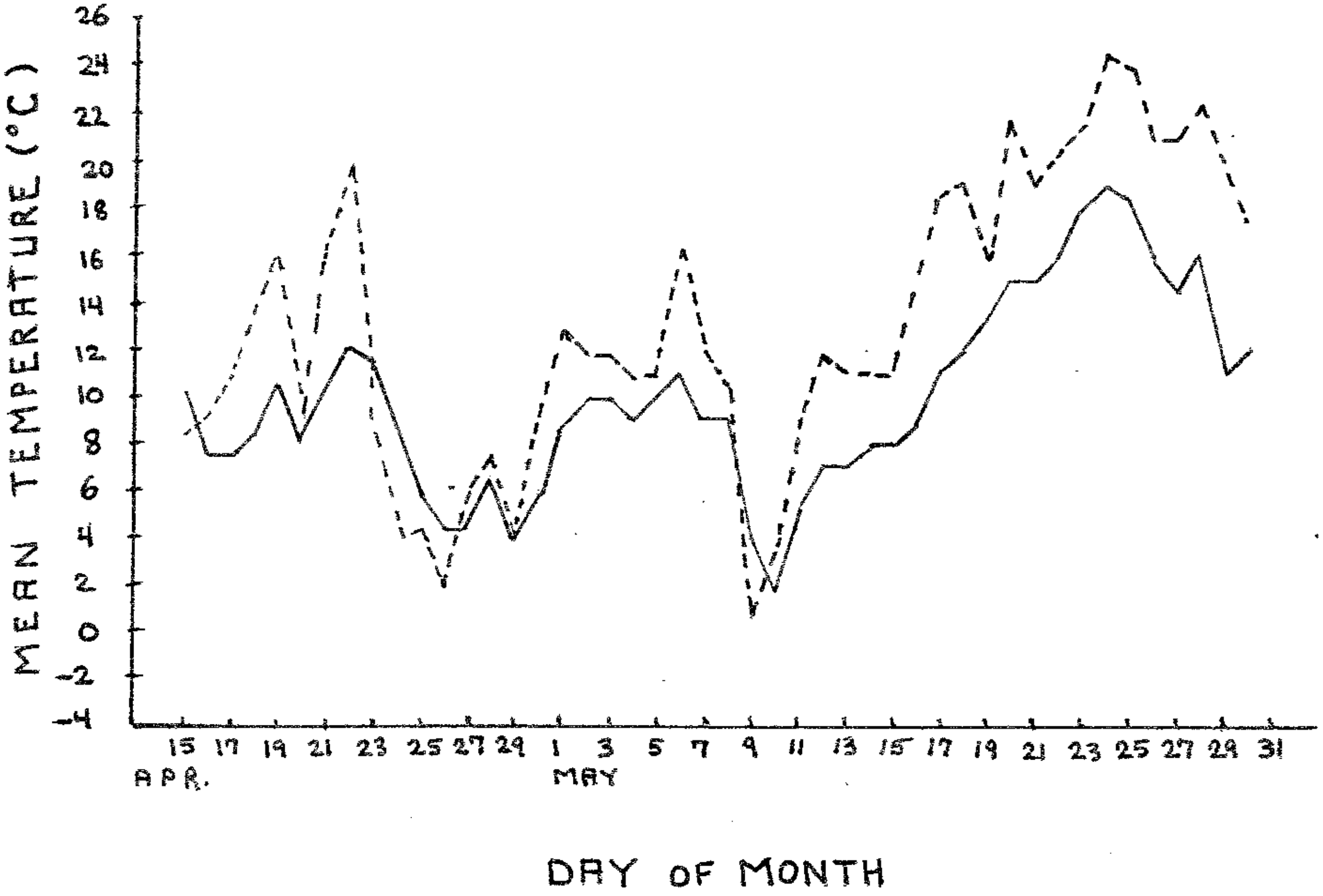
MEAN TEMPERATURE (°C)
26
24
22
20
18
16
14
12
10
8
6
4
2
0
-2
-4
15 17 19 21 23 25 27 29 1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31
APR.
MAY
DAY OF MONTH

FIGURE 6. RECORD OF MEAN DAILY INTERNAL LODGE TEMPERATURE AND MEAN DAILY AIR TEMPERATURE FOR LATE SUMMER, 1977.

(Solid line indicates mean daily internal lodge temperature. Broken line indicates mean daily air temperature.)

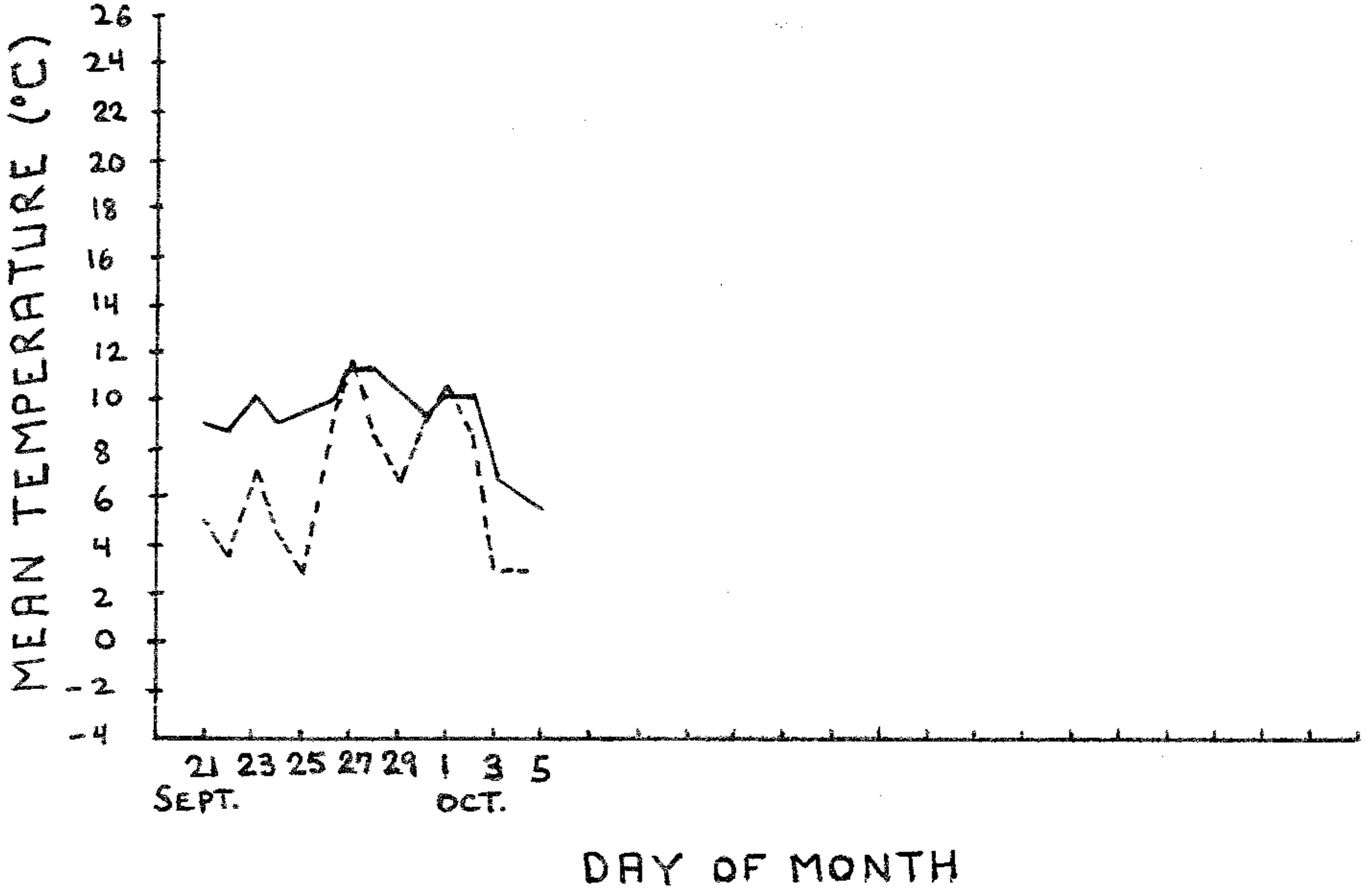
MEAN TEMPERATURE (°C)
26
24
22
20
18
16
14
12
10
8
6
4
2
0
-2
-4
21
23
25
27
29
1
3
5
SEPT.
OCT.
DAY OF MONTH

FIGURE 7. RECORD OF MEAN DAILY INTERNAL LODGE TEMPERATURE AND MEAN DAILY AIR TEMPERATURE FOR AUTUMN, 1977.

(Solid line indicates mean daily internal lodge temperature. Broken line indicates mean daily air temperature.)

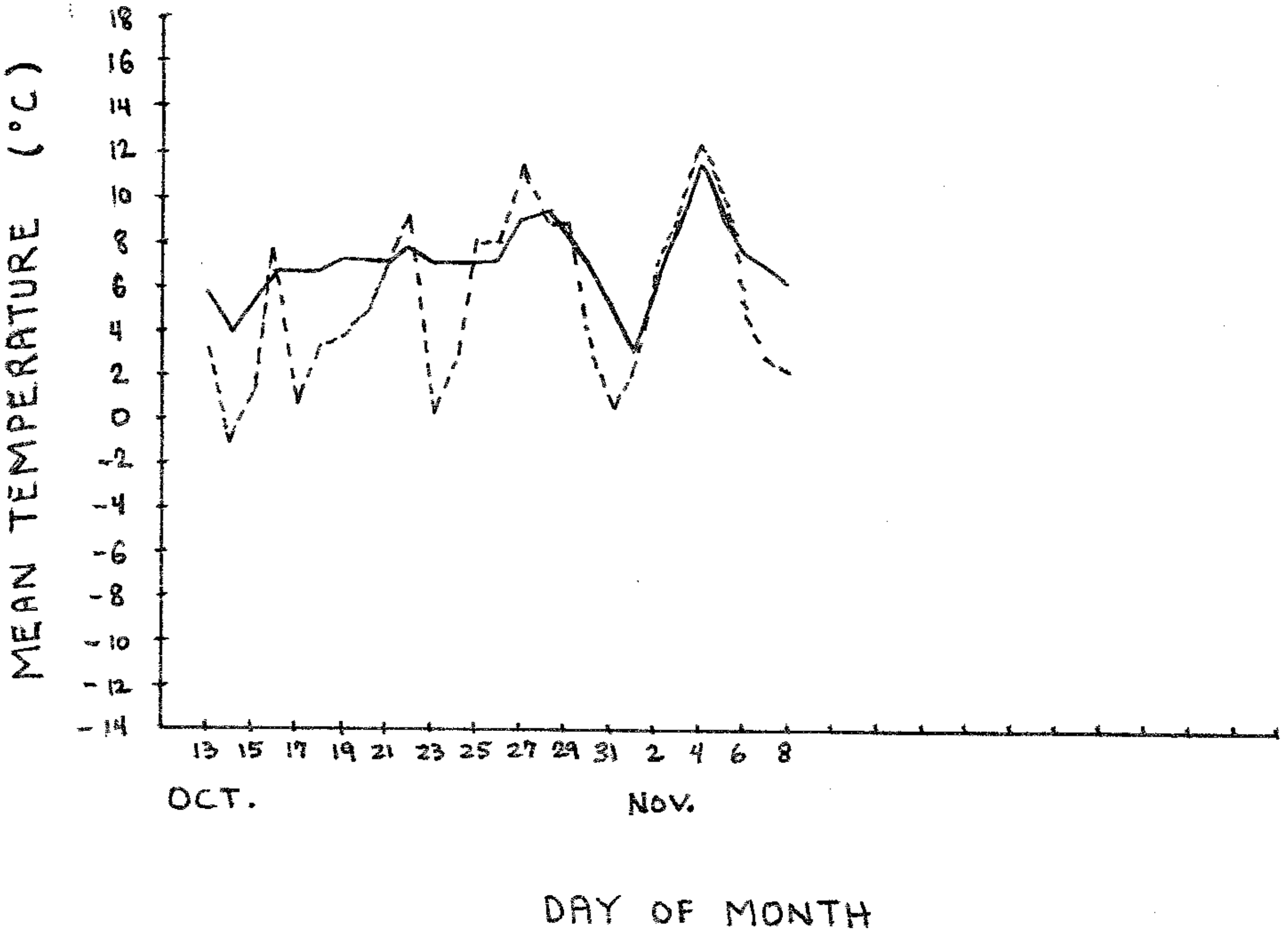
MEAN TEMPERATURE (°C)
18
16
14
12
10
8
6
4
2
0
-2
-4
-6
-8
-10
-12
-14
13
15
17
19
21
23
25
27
29
31
2
4
6
8
OCT.
NOV.
DAY OF MONTH

TABLE 2. CLIMATIC AND STATISTICAL DATA FOR SEASONAL PERIODS

(Figures in parentheses are standard deviations)

SEASON	$\overline{T}_i$ (^{o}C)	$\overline{T}_a$ (^{o}C)	N (days)	p ($\overline{T}_a$)*
Winter (Mar.-Apr.)	-2.0 (± 2.7)	+7.2 (± 5.0)	48	.001
Spring (Apr.-Jun.)	+9.9 (± 4.0)	+13.0 (± 6.0)	46	
Spring (Apr.-Jun.)	+9.9 (± 4.0)	+13.0 (± 6.0)	46	.001
Summer (Sept.-Oct.)	+9.4 (± 1.6)	+6.7 (± 3.1)	14	
Summer (Sept.-Oct.)	+9.4 (± 1.6)	+6.7 (± 3.1)	14	.001
Autumn (Oct.-Nov.)	+6.4 (± 1.6)	+4.5 (± 3.3)	27	

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[*] Confidence levels indicating that $\overline{T}_a$ for the two periods are significantly different (by t-tests).

with low mean daily T_a but, except for the winter season [5], all changes in $\overline{T}_i$ parallel changes in $\overline{T}_a$. In other words a correlation seems to exist. Second, mean daily T_i is indeed quite variable although the lodge always has some insulatory properties, even in winter, despite the lack of snow cover.

The relationship between T_a and T_i

In order to fully show the correlation between T_a and T_i a scatter diagram was constructed in Fig. 8, with the dependent variable, $\overline{T}_i$ plotted as a function of the independent variable, $\overline{T}_a$. Considering only that portion of the graph above $\overline{T}_i = 0^\circ C$, a regression line can be fitted to the values obtained ("Least Squares" method). The line shows theoretical $\overline{T}_i$ as a function of $\overline{T}_a$. From the difference between theoretical and observed values, the coefficient of correlation (r) is obtained. The correlation is shown to be quite strong ($r = 0.962$). The section of Fig. 8 below $\overline{T}_i = 0^\circ C$ corresponds to values obtained in March, 1977. Thus the correlation completely breaks down with $\overline{T}_i$ independent of $\overline{T}_a$ for values of T_i less than, or equal to $0^\circ C$. It happens that for all points not conforming to the established correlation (March 1st. - 27th), the mud of the lodge walls was frozen. As the lodge began to thaw out (March 28th through spring) the points corresponding to consecutive days approach regression line values.

However, when the correlation does exist (approximately April 15th through the next lodge "freeze - out") the line of regression takes the

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[5] During the winter period shown the lodge in question (a bank lodge) had little, if any, snow cover. Snowfall occurred only 3 times during the period (March 4th - 20 cm.; March 18th - 10 cm.; and March 23rd - 2.5 cm.). Snowfall was always followed by mild temperatures and rain which essentially destroyed the snow cover on the lodge.

form of,

$$Y = mX + b$$

(where m is the slope and b is the Y intercept). Values for m and b are calculated by the "Least Squares" method and the formula for estimating $\overline{T}_i$ becomes,

$$\overline{T}_i = 0.62\ \overline{T}_a + 2.8^{\circ}C.$$

The same method was used to show the somewhat weaker correlation ($r = 0.730$) between minimum T_i (T_i min.) and minimum T_a (T_a min.) . The results are shown in Fig. 9 with the same "winter effect" - i.e., the values below T_i min. = $0^{\circ}C$ do not have any correlation with values for T_a min., but again these are the points plotted for March 1st - 27th, with points for the "thawing-out" period approaching the line of regression on consecutive days. The formula for estimating T_i min. becomes,

$$T_i \text{ min.} = 0.54\ T_a \text{ min.} + 5.2^{\circ}C.$$

Points plotted in a similar fashion for T_a max. vs. T_i max. have a very weak correlation ($r = 0.4$). It is assumed that even this weak correlation would disappear during the lodge's frozen period.

The lack of any temperature correlations during the lodge's frozen period has been tentatively termed the "winter lodge buffer effect" and has thus far only been observed in a frozen winter lodge lacking the benefit of adequate snow cover. Figures 8 and 9 show that the "buffer effect" limits the internal lodge temperature to $T_i < 0^{\circ}C$, regardless of the air temperature.

Figure 9 shows that the minimum T_i can drop as low as $-8^{\circ}C$! Values for minimum T_i between $-6^{\circ}C$ and $-8^{\circ}C$ correspond to days when beaver were

FIGURE 8. MEAN DAILY INTERNAL LODGE TEMPERATURE AS A FUNCTION OF MEAN DAILY AIR TEMPERATURE.

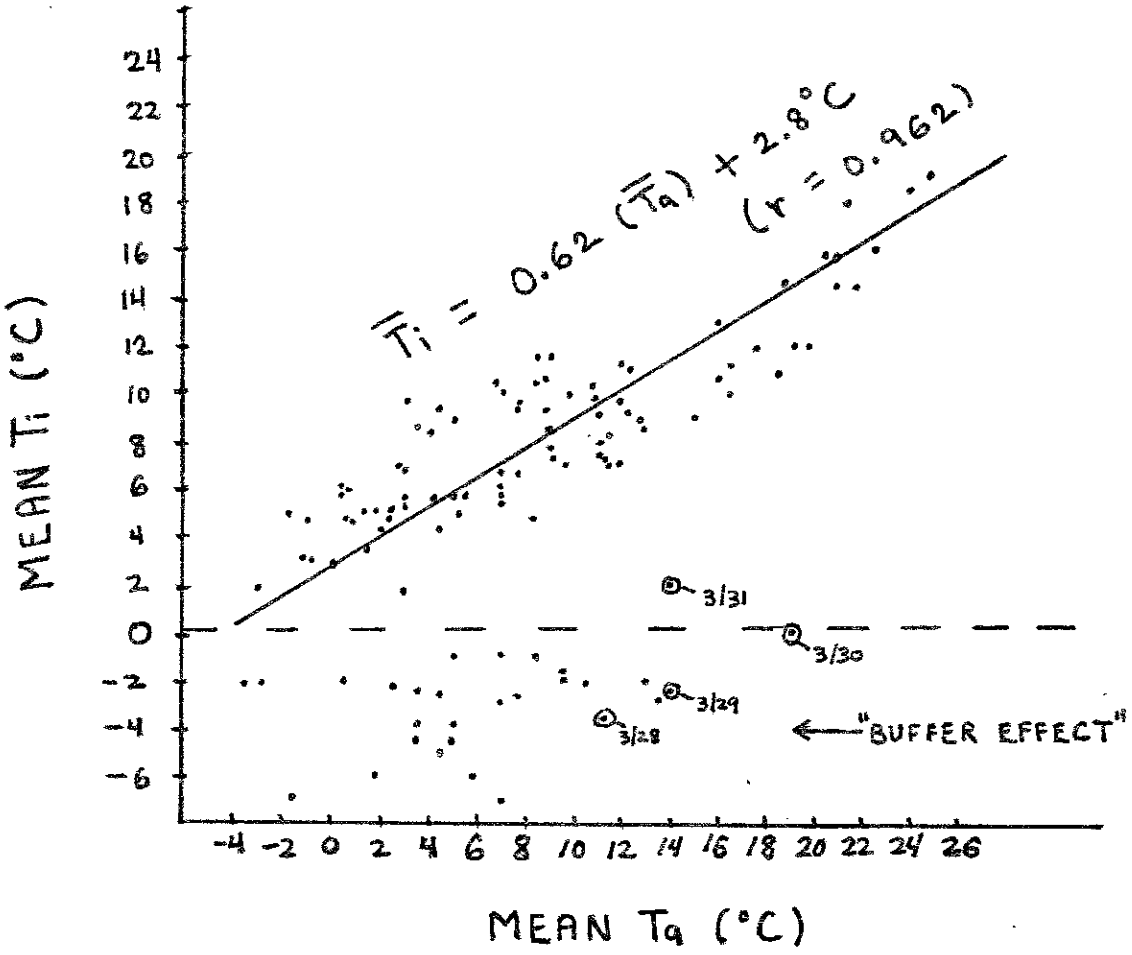
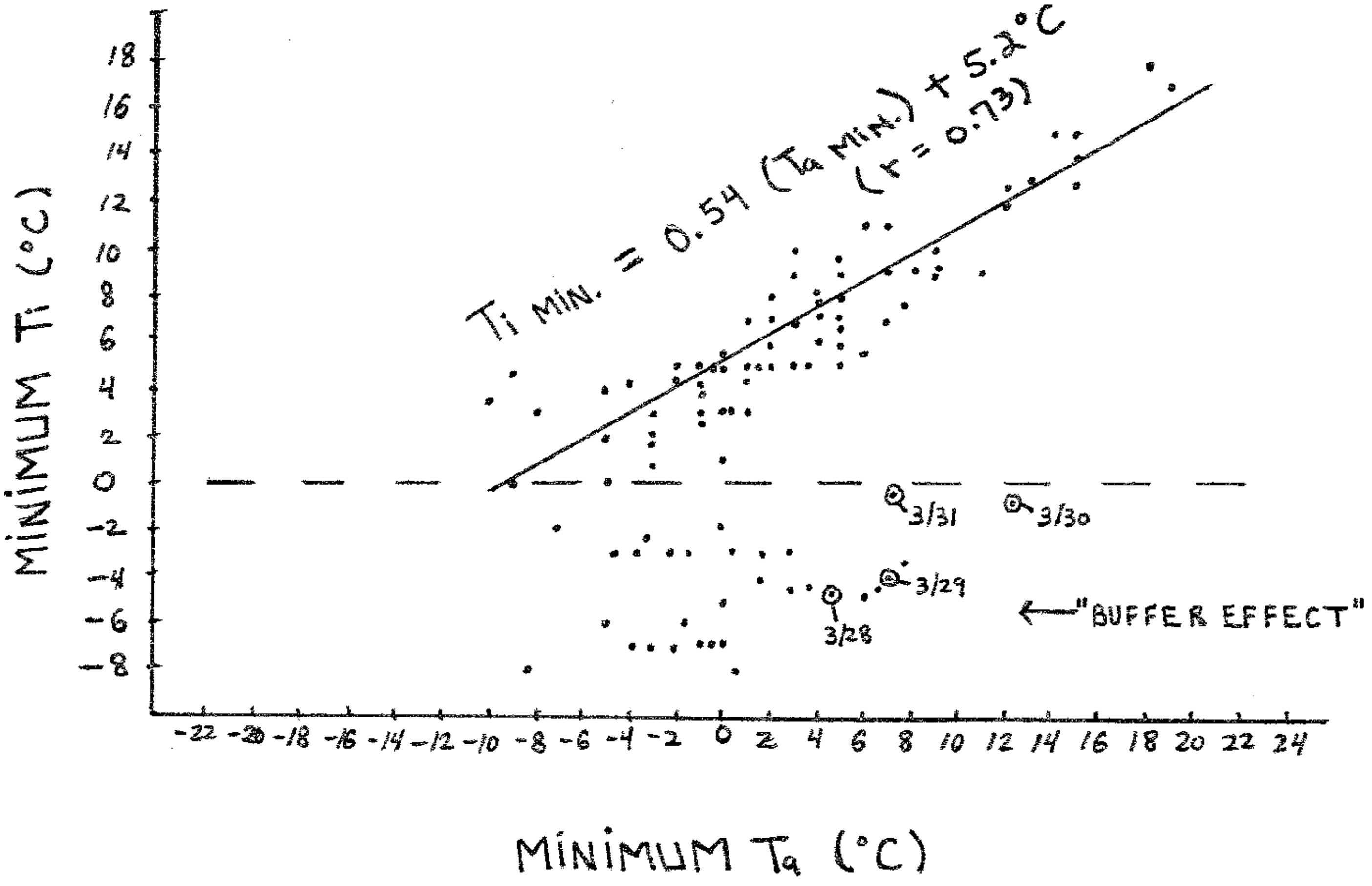

$\overline{T_i} = 0.62\,(\overline{T_a}) + 2.8°C$
$(r = 0.962)$
MEAN Ti (°C)
24
22
20
18
16
14
12
10
8
6
4
2
0
-2
-4
-6
3/31
3/30
3/29
3/28
"BUFFER EFFECT"
-4
-2
0
2
4
6
8
10
12
14
16
18
20
22
24
26
MEAN Ta (°C)

FIGURE 9. MINIMUM DAILY INTERNAL LODGE TEMPERATURE AS A FUNCTION OF MINIMUM DAILY AIR TEMPERATURE.


Ti MIN. = 0.54 (Ta MIN.) + 5.2°C
(r = 0.73)
3/31
3/30
3/29
3/28
←"BUFFER EFFECT"
MINIMUM Ti (°C)
18
16
14
12
10
8
6
4
2
0
-2
-4
-6
-8
-22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10 12 14 16 18 20 22 24
MINIMUM Ta (°C)

absent from the lodge for extended periods[6].

Seasonal variation of the internal lodge temperature

The "buffer effect" has been shown to limit the mean daily T_i to less than 0^oC in frozen lodges without snow cover, with mean daily T_i falling as low as -7^oC on some occasions. Stephenson (1969) has shown that mean daily T_i can rise above 0^oC (to a maximum of $+2^oC$) when the lodge has adequate snow cover. Snow cover enabled T_i to remain above -3^oC in all cases. The insulatory properties of snow are thus apparent. Accordingly, it is desirable to know how T_i varies when snow is lacking.

Figure 10 shows daily coefficients of variation as a measure of daily T_i variability. Note that T_i is quite variable (within each day) in "late winter - early spring". Variation is at a minimum during winter and late summer with a slight increase of the coefficient of variation (CV) in fall. What are the factors responsible for the seasonal maxima and minima observed ? Why does T_i vary more in some seasons and less during others ?

In general the responsible factors will effect the flow of heat in or out of the lodge and will consist of heat sources, heat "sinks", and regulators of heat flow. Since data obtained consists only of T_i, T_a, ΔT_i, and ΔT_a, empirical analysis requires that the factors in question be expressed as functions of these data. Table 3 has been constructed for this purpose. In Table 3 $\overline{CV_i}$ expresses the observed results of

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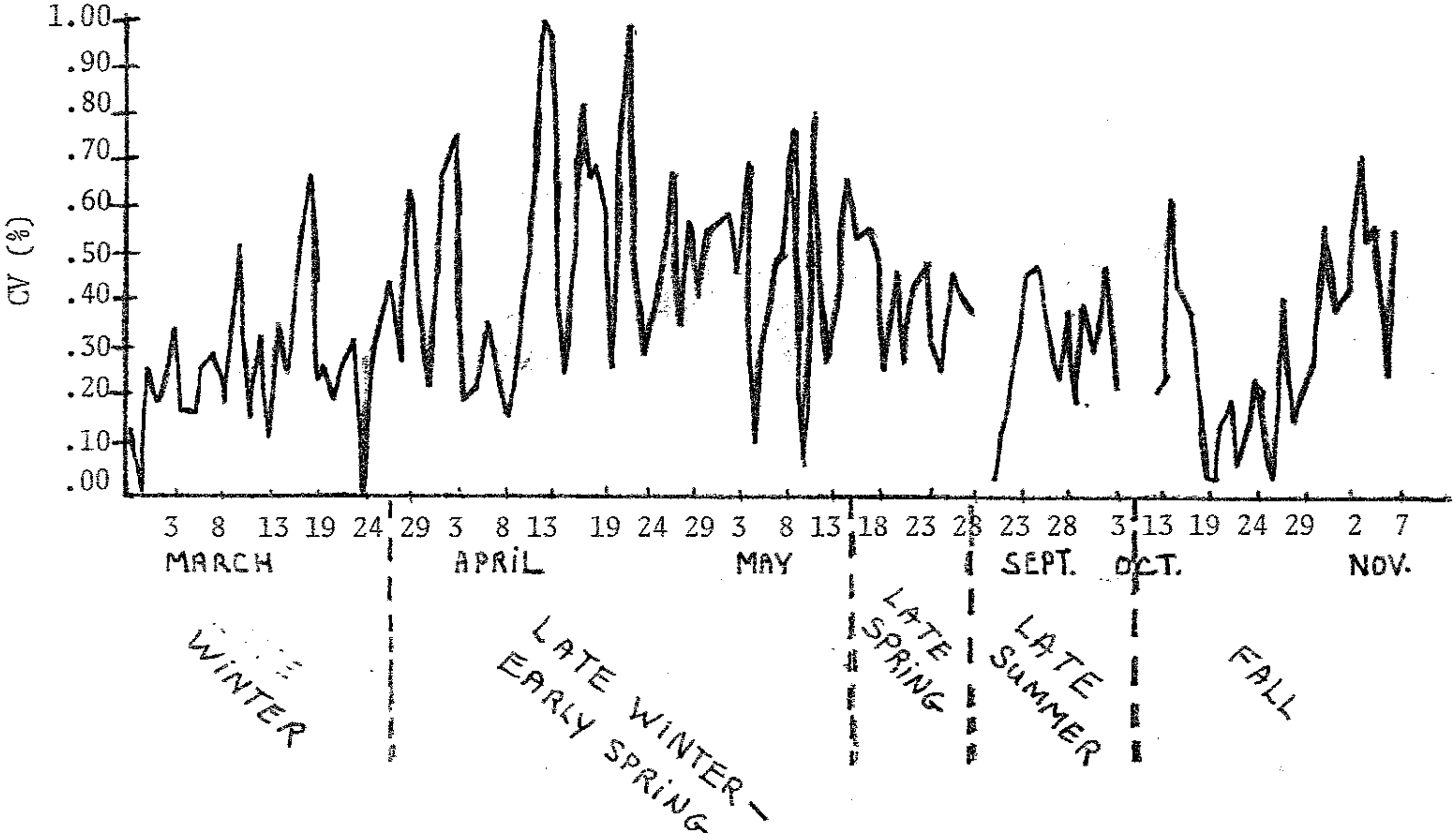
[6] See "Seasonal Activity Analysis" for a discussion of how this is determined. Since beaver maintained secondary lodges without food beds, it is assumed that they visited these lodges from time to time. Stephenson (1969) also observed that the lowest T_i was recorded when beaver were absent from the lodge for extended periods.

FIGURE 10. DAILY COEFFICIENTS OF VARIATION (CV) OF THE INTERNAL LODGE TEMPERATURE.

$$(\; CV = \frac{\text{daily standard deviation of } T_i \quad X\ 100}{\text{daily mean } T_i \ (^{o}K)} \; .$$

The coefficients of variation are computed after converting temperature data to Kelvin degrees to avoid the zero point of winter mean temperatures. CV cannot be computed for a mean temperature of $0^{o}C$, but can be computed for mean temperature of $+273^{o}K$ (= $0^{o}C$).


CV (%)
1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
.00
3
8
13
19
24
29
3
8
13
19
24
29
3
8
13
18
23
28
23
28
3
13
19
24
29
2
7
MARCH
APRIL
MAY
SEPT.
OCT.
NOV.
WINTER
LATE WINTER-
EARLY SPRING
LATE
SPRING
LATE
SUMMER
FALL

different rates of heat flow through the lodge (i.e., the sub-seasonal mean T_i variability). Heat sources consist of solar energy (T_a) and beaver body heat. The solar energy available to the lodge is, of course, also variable and is thus expressed as sub-seasonal $\overline{CV_a}$. Beaver body heat produced was only measured as "instantaneous" ΔT_i on the temperature record where

$$\text{instantaneous } \Delta T_i = T_i \pm \text{body heat produced.}$$

Instantaneous ΔT_i is strictly a function of the number of times beaver enter or exit a lodge. The body heat source is therefore expressed as the "Index of Activity" (I_A), a behavioral factor where

$$I_A = \text{instantaneous } \Delta T_i/\text{day}$$

(for "entrances" only[7]).

The remaining thermodynamic factors, i.e., heat sinks and regulators of heat flow, could not be directly measured by the available data. Accordingly, the primary heat sink is considered as the air surrounding the lodge because most of the surface area for heat loss occurrs at the lodge-air interface. Water, lodge walls, and lodge floor are secondary heat sinks. For purposes of seasonal comparison the effects of heat sinks are indirectly expressed as whether or not temperature correlations are established due to net heat flow. Finally, the regulator of heat flow is generally considered as the lodge itself. Because the lodge

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[7] The reasons for using only entrances in the computation of I_A and its associated value, F_e are discussed under "Seasonal Activity Analysis". Because I_A does not take into account the number of animals contributing to its magnitude, it cannot be used to compare seasonal activity. Seasonal data may be obtained from different lodges with different numbers of animals in residence. However, sub-seasonal I_A, in Table 3, is a useful comparative measure since the variation of T_i is being considered as a function of the number of times an entrance occurs per day, regardless of the number of animals contributing to it.

causes different thermodynamic effects in different seasons (e.g., the "buffer effect", temperature correlations) its sub-seasonal physical state is considered as an indicator of its regulatory ability[8].

From Table 3, it is clear that in winter the low degree of T_i variation is partly the result of the regulation of heat flow through a "frozen" lodge. This cancels the effects of large variation in the amounts of available solar energy ($\overline{CV}$ = 0.77 per cent), as evidenced by the lack of temperature correlations (r values). Thus, in winter, $\overline{CV}_a$ is not a factor in $\overline{CV}_i$ variation. However, the Index of Activity is relatively high during this period ($I_A = 3.3$), implicating behavioral factors in the variation of T_i.

In "late winter - early spring", when lodges thaw, T_i variation is at a maximum ($\overline{CV}_i$ = 0.50 per cent). Because of the thaw, temperature correlations have been established allowing high solar energy variation to directly affect T_i variability ($\overline{CV}_a$ = 1.9 per cent). The increase of I_A from winter values is three fold, while $\overline{CV}_i$ rises sharply from 0.27 to 0.50 per cent. Thus it would appear that behavioral factors are again implicated in $\overline{CV}_i$ variation.

In late spring through summer's end the internal temperature becomes increasingly stable ($\overline{CV}_i$ falling from 0.50 to 0.36 per cent

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[8] Stephenson (1969) shows this with respect to snow cover. If a frozen lodge exists without snow cover, the "Heat of Fusion" of ice in the frozen walls is an extremely important factor to consider in heat flow regulation. Additionally, the presence of ice in the walls causes other subtle thermodynamic effects. Many important physical variables involved in seasonal lodge thermodynamics could not be measured in this study. However, because of its importance to thermoregulation, the topic of lodge thermodynamics is treated more thoroughly in the "Discussion".

TABLE 3. SUB-SEASONAL ANALYSIS OF THE VARIATION OF THE INTERNAL LODGE TEMPERATURE (T_i) AND OF FACTORS CONTRIBUTING TO THE VARIATION OF T_i WHEN LODGES LACK SNOW COVER.

(CV_i is the coefficient of variation of T_i. CV_a is the coefficient of variation of T_a. I_A is the "Index of Activity".)

DATES	SUB-SEASON	$\overline{CV_i}$ (%)	$\overline{CV_a}$ (%)	LODGE STATE	TEMP. CORRELATIONS (r)			I_A	FACTORS CONTRIBUTING
					$\overline{X}$	Min.	Max.		
26 Feb. - 27 Mar.	Winter	0.27	0.77	Frozen	0.0	0.0	0.0	3.3	Physical, behavior
28 Mar. - 17 May	Late winter - Early spring	0.50	1.95	Thawed	0.9	0.7	0.4	9.9	Physical, thermodynamic, behavior
18 May - 30 May	Late spring	0.36	1.15	Thawed	0.9	0.7	0.4	3.0	Physical, thermodynamic, behavior
21 Sept. - 4 Oct.	Late summer	0.28	1.10	Thawed	0.9	0.7	0.4	1.0	Physical, behavior
13 Oct. - 8 Nov.	Autumn	0.30	1.20	Thawed	0.9	0.7	0.4	1.7	Physical, thermodynamic, behavior

in late spring, then to 0.28 per cent in late summer). Temperature correlations still apply but available solar energy is most stable at this time ($\overline{CV}_a$ = 1.1 per cent for late spring and late summer). The Indices of Activity drop sharply from early spring values while $\overline{CV}_i$ continues to decrease slightly after the initial large decrease from early spring. Thus, behavioral and thermodynamic factors seem to be implicated in T_i variation in late spring. However, behavioral factors alone seem to control T_i variation in late summer because the stability of $\overline{CV}_a$ during late spring and late summer is not reflected by the changing $\overline{CV}_i$ during these periods.

The differences observed during the transition from late summer to autumn seem to be correlated with both increasing $\overline{CV}_a$ and increasing I_A . The increase in $\overline{CV}_i$ is 0.02 per cent. The increase in $\overline{CV}_a$ is 0.01 per cent while I_A also increases slightly. The variation of T_i seems, therefore, to be an intermediate result, due to both increasing $\overline{CV}_a$ and I_A.

In summary, Table 3 shows that during winter and late summer T_i variation is the result of behavioral factors. In all other seasons both behavioral and thermodynamic factors may contribute to the variation of T_i. In all seasons the physical state of the lodge (heat flow regulator) must be considered.

SEASONAL ACTIVITY ANALYSIS

Both Novakowski (1967) and Stephenson (1969) have reported a reduction in beaver activity during cold stress. Aleksiuk and Cowan (1969 a,b) show that Arctic populations not only reduce their activity in winter but are also subject to a "winter metabolic depression". The present study has characterized the temperature ecology of animals in New York. A special measure of beaver activity, the Index of Activity, may or may not be a factor in the thermal stress faced by beaver (depending on the season). It is therefore necessary to quantify beaver activity in order to make geographic comparisons and demonstrate seasonal variation in New York.

Determining activity from the temperature record

The basic data used in this analysis are the instantaneous changes in the internal lodge temperature (ΔT_i) due to the presence or absence of beaver body heat. This phenomenon was first described by Stephenson (1969) (however he did not quantify activity), and has been previously described in this study.

A number of problems arise when using instantaneous ΔT_i as a measure of activity. These include: 1) establishment of criteria for "true" ΔT_i as opposed to that caused by limited thermograph stability; 2) variation of the established criteria due to seasonal lodge thermodynamics; and 3) the effects of different numbers of animals in different behavioral and demographic circumstances when a ΔT_i is recorded.

Due to thermograph specifications an instantaneous ΔT_i less than 0.5°C/minute was considered as a machine error, and ignored. Because of the insulatory properties of the lodge, (-) ΔT_i (i.e., "exit" activity) is not well defined on the temperature record. In other words, since heat is lost slowly when the beaver "heat source" is removed, (-) ΔT_i occurs over 10 - 15 minutes. However, with the lodge as an insulator, "entrance" activity [(+) ΔT_i] occurs over 1 - 5 minutes and appears as an abrupt, visible change on the continuous record. Accordingly, only (+) ΔT_i is useful as an instantaneous ΔT_i.

Table 4 shows the seasonal criteria for "true" (+) ΔT_i. It is based on 20 observations of beaver as they entered the lodge, and on 28 observations of beaver when "entrance" or "exit" was not observed. From Table 4 it is clear that the magnitude of (+) ΔT_i cannot be used as an indicator of the number of animals contributing to it (unless a specific case is observed). Accordingly, any (+) $\Delta T_i = 1.0 - 3.0^{\circ}C$ per minute can simply be considered as an indicator of "entrance" activity (in winter and spring). In summer and autumn two problems arose in determining "true" (+) ΔT_i. First, the magnitude of (+) ΔT_i decreased for the same number of animals contributing to it. Second, two false indications of (+) ΔT_i activity were observed on the record [i.e., (+) $\Delta T_i > 0.5^{\circ}C$ per minute occurred when "entrances" were not observed].

To offset these difficulties "entrance" activity will be defined by

$$(+)\ \Delta T_i \geq 1^{\circ}C/\text{minute}$$

in winter and spring. "Entrance" activity in summer and fall will be defined by

$$(+)\ \Delta T_i \geq 0.5^{\circ}C/\text{minute}.$$

(Speculative explanations for the observed differences in the magnitude of (+) ΔT_i are given in the "Discussion").

TABLE 4. DATA USED IN DETERMINING SEASONAL CRITERIA FOR "TRUE" (+) ΔT_i DUE TO ENTRANCE ACTIVITY.

("True" [+] ΔT_i is indicated when entrances are actually observed in the field.)

SEASON	NUMBER OF BEAVER OBSERVED	RATE OF (+)ΔT_i (^{o}C/MINUTE)	
		(Entrance observed)	(No entrance observed)
Winter	2	1.0-2.0 (n = 3)*	-
	2	2.0-3.0 (n = 1)	-
	0	-	0.5 (n = 5)**
	0	-	$>$0.5 (n = 0)
Spring	1	0.5-1.0 (n = 1)	-
	2	1.0-2.0 (n = 2)	-
	2	2.0-3.0 (n = 1)	-
	3	2.0-3.0 (n = 1)	-
	0	-	0.5 (n = 5)
	0	-	$>$0.5 (n = 0)
Summer	1	0.5-1.0 (n = 2)	-
	2	0.5-1.0 (n = 3)	-
	0	-	0.5 (n = 8)
	0	-	$>$0.5 (n = 1)
Autumn	1	0.5 (n = 1)**	-
	1	0.5-1.0 (n = 3)	-
	2	0.5-1.0 (n = 2)	-
	0	-	0.5 (n = 10)
	0	-	$>$0.5 (n = 1)

* (n) = the number of cases observed on the temperature record

**$\Delta T_i < \pm 0.5C^o$ cannot be detected on the temperature record.

The above criteria have the following limitations: 1) a small amount of "true entrance" activity may be excluded from the data for winter and spring; 2) a small amount of "false entrance" activity may be included in the data for summer and fall. Although these criteria are limited, they allow for the most conservative estimates of activity without excluding the large amount of summer and autumn activity which would be missed if $(+)\Delta T_i \gtrsim 1^oC$ per minute is used throughout.

The seasonal "Index of Activity" and "Frequency of entrance"

Earlier reference was made to the "Index of Activity" and its role in the temperature ecology of beaver. The Index of Activity (I_A) for any period of time may be defined as,

$$I_A = \Sigma[(+)\ \Delta T_i]/\text{day}.$$

Thus, the daily I_A is the number of times $(+)\Delta T_i$ occurs per day and periodical I_A is the number of times $(+)\Delta T_i$ occurs in a period, divided by the number of days in the period. The periodical I_A is thus a daily comparative measure of $(+)\Delta T_i$, independent of the number of animals at a lodge.

If the relative activity of each animal is to compared, the number of animals resident at a lodge must be known. In this case, the frequency of activity, or more accurately, the "frequency of entrance activity" (F_e) is the number of times $(+)\Delta T_i$ occurs per day, per beaver, or

$$F_e = I_A/\ \text{number of resident animals}.$$

Daily F_e may be computed but, for purposes of seasonal comparison, mean periodical F_e was computed by

$$\overline{F}_e = \Sigma I_A\ (\text{daily})/\text{number of resident animals}$$

which is also

$\overline{F_e} = [\Sigma\,(+)\Delta T_i$ (period)/days in period]/number of resident animals.

F_e is simply a measure of the number of times "entrances" occur at a given lodge, per animal, but it does not measure activity as such. How does one know whether the ΔT_i used in computing I_A and F_e lasted one minute, ten minutes, or ten days ? Of what importance is F_e without this knowledge ?

Seasonal activity levels and patterns

In order to use F_e as meaningful data, one must know the appoximate amount of time beaver spend in or out of the lodge. To know this, $(-)\Delta T_i$ must be know. $(-)\Delta T_i$ can be computed from the temperature record but the point at which beaver actually left the lodge can only be approximated. The approximation should not be more than 15 minutes off since $(-)\Delta T_i$ has occurred by that time (see above). Thus, time spent in the lodge is the time interval from $(+)\Delta T_i$ (an exact moment) to $(-)\Delta T_i$ (an approximate moment). Time spent out of the lodge is, therefore, 24 hours minus the time interval involved (on a daily basis). However, this result does not give the number of beaver out of the lodge, since ΔT_i cannot be used as an indicator of the number of animals contributing to it.

Table 5 shows the sub-seasonal comparison of activity levels and patterns found by computing I_A, $\overline{Fe}$, and the approximate amount of time spent out of the lodge, per day with corresponding percentages. The data is taken from three lodges having different numbers of animals. Sub-seasonal $\overline{F_e}$ is computed on the basis of the number of animals at the appropriate lodge. Note particularly, I_A and $\overline{F_e}$ values for two different

TABLE 5. SUB-SEASONAL LODGE DATA, "INDICES OF ACTIVITY" (I_A), "FREQUENCIES OF ENTRANCE" (F_e), AND APPROXIMATE AMOUNT OF TIME BEAVER SPEND OUT OF THEIR LODGES.

(Time spent out of the lodge is computed on the basis of time spent inside of the lodge. Time spent inside is computed on the basis of $(+)\Delta T_i$ and $(-)\Delta T_i$. $(-)\Delta T_i$ was considered to have been completed when T_i reached levels equal to those prior to $(+)\Delta T_i$.)

PERIOD		LODGE	I_A	BEAVER PRESENT	F_e	APPROX. HRS. OUT PER DAY	APPROX. % OF TIME SPENT OUT OF LODGE
2/26 - 3/27	Winter	A	3.51	2	1.76	1.9	8.1
3/28 - 4/14	Late winter-Early spring	A	7.1	2	3.50	3.4	14.3
4/15 - 5/17	Late winter-Early spring	B	11.0	3	3.60	5.6	23.7
5/18- 5/30	Late spring	B	3.0	3	1.00	10.3	43.0
9/21 - 1o/4	Late summer	C	1.0	2	0.5	11.7	49.0
10/13 - 10/31	Early autumn	C	1.1	2	0.5	11.8	49.5
11/1 - 11/8	Autumn	C	3.0	2	1.5	11.2	46.8

lodges, "A" and "B", in the same sub-season (late winter-early spring). I_A is greater at "B" because the number of animals there is greater. However, $\overline{F_e}$ remains constant within the period, from lodge "A" ($\overline{F_e}$ = 3.5) to lodge "B" ($\overline{F_e}$ = 3.6), even though the number of beaver at "A" and "B" are unequal.

If general activity is defined by the amount of time spent out of the lodge, then Table 5 indicates that beaver are fairly inactive in winter, entering the lodge approximately twice a day but spending only about two hours out of the lodge. Activity levels rise in "late winter-early spring" , with beaver spending progressively more time out of the lodge as the season progresses, and entering the lodge more frequently. In "late spring" beaver enter the lodge approximately once each day (in the morning) but spend more than 40% of their day out of the lodge. In "late summer" and "early fall" beaver enter the lodge about once each day ($\overline{F_e}$ = 0.5 because two beaver may enter the lodge at approximately the same time, in the morning, or are absent from the lodge on certain days, presumably visiting secondary lodges). During this period they spend about 50% of their day in activity (swimming, eating, etc.). As autumn progresses, beaver spend less time in activity and enter the lodge more frequently. Presumably, this trend continues untill only 8% of the day is spent in activity in "late winter". Although no temperature data is available for "late fall - early winter"[9], visual observations during this period in 1976 indicate that beaver enter and exit

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[9] Due to extremely heavy rains on Nov. 7th, 8th, and 9th, 1977, streams supplying the study pond (a man-made reservoir) caused very high water levels in the pond, and flooding of the study lodge.

the lodge as they feed, so that $\overline{F_e}$ may be high at this time (e.g., $\overline{F_e} = 4$) while the amount of time spent out of the lodge continually decreases (e.g., from 46% in early November to 15% in late December).

DISCUSSION

THE ADAPTIVE SIGNIFICANCE OF THE INTERNAL LODGE TEMPERATURE

Since the "winter metabolic depression" is caused by the drastic reduction of photoperiod accompanying the Arctic winter, and since beaver from northern California did not respond physiologically to this same reduction of photoperiod, and are at similar latitudes to the present study population, it is unlikely that New York State animals undergo a "metabolic depression" in cold stress. However, in winter, these beaver, like the Arctic populations, are restricted to a limited microenvironment consisting of a lodge and a small area under ice. During this time (3.5 - 4 months) their food supply is limited to a cache of twigs and saplings accumulated in the autumn. However, they have been observed to leave their microenvironment, occasionally, to feed on land. During mild spells, and if snow cover is reduced, beaver can leave via a small hole in the ice which they maintain for this purpose (personal observations).

It is apparent that during the "iced - in" period, southern populations are subject to extremely cold ambient temperatures of air and water, but spend most of their time (about 90%) inside their lodges where mean microenvironmental temperatures remain between $+2^{o}C$ and $-2^{o}C$.

Consider "Newton's law of cooling" as presented by McNab (1966):

$$M = C\ (T_b - T_a)$$

where M is the rate of heat production (metabolism) and C is the rate of heat loss (conductance) at a given ambient temperature (T_a), and T_b

is body temperature [10]. The adaptive significance of behavioral or physiological strategies becomes clear (in terms of energy conservation) when M is minimized by reducing either $\Delta T = T_b - T_a$, C, or both. Minimization of M is clearly desirable in the somewhat restricted energy regimen of temperate winters. Southern beaver accomplish the above reductions partly by reducing ΔT for 90% of their day.

The data obtained in this study seem to indicate a maladaptive T_i in March when $\overline{T}_a$ remains above $\overline{T}_i$. However, this is deceptive because of the peculiar circumstance of a winter lodge lacking snow cover. Additionally, $\overline{T}_a$ in January and February (NOAA data) remained well below any recorded $\overline{T}_i$. Stephenson (1969) showed that $\overline{T}_i$ in January and February, 1965, remained well above $\overline{T}_a$, averaging at about -1°C. This was caused by snow insulation. T_i is adaptive in the results of the present study, because winter lodges retained snow cover (about 15 cm.) in January and February, 1977. The seemingly "maladaptive" T_i in March is due to a lack of snow cover in southern New York. In this circumstance the "winter lodge buffer effect" causes the "maladaptive" T_i.

Upon closer examination the "buffer effect" reveals two aspects. First, a "suppression" aspect in which T_i is kept low (below 0°C) when T_a may be quite mild (maladaptive). Second, a "stabilizing" aspect, in which T_i is kept at levels between 0°C and -5°C, when T_a is exceptionally low. In other words, if T_a happens to be severe (e.g., -15°C), T_i is stabilized between 0°C and -5°C. This is indeed quite adaptive for

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[10] Aleksiuk and Cowan (1969 b) found that for twelve normal beaver, $T_b = 36.7°C \pm 1.0°C$. "Metabolic depression" caused T_b to drop as low as 34°C in two animals, with the average T_b of all "depressed" animals being 36°C.

animals living in winter lodges which may lack snow cover, particularly if the circumstance occurrs in northern New York or southern Canada. Thus, T_i is only adaptive in winter if snow is present or if T_a is very low when snow is lacking. Mild spells at temperate latitudes frequently destroy snow cover, but may also preceed extremely harsh environmental temperatures, necessitating the "stabilizing" aspect of the "buffer effect". The "suppression" aspect of the "buffer effect" remains maladaptive but is only applicable when mild spells do not preceed severe temperatures.

The circumstances outlined above apply only to frozen winter lodges with or without snow cover. In spring, when lodges thaw, temperature correlations are established between $\overline{T}_a$ and $\overline{T}_i$ and between T_a min. and T_i min. . Correlations are strong enough to permit prediction of T_i based on T_a (positive linear correlation). This situation persists throughout summer and autumn and presumably untill the lodge freezes again in "late fall - early winter". Thermodynamic properties of frozen and thawed lodges presumably cause all of the above effects (see "Thermoregulation and Thermodynamics").

The overall consequence of lodge construction plus temperature correlations is to allow beaver ambient temperatures to remain adaptive throughout the "thaw" period. $\overline{T}_i$, in the "thaw" period, is about $10^{o}C$, while $\overline{T}_a$ may fluctuate well above and below this level. Temperature correlations may be used to illustrate the adaptive nature of T_i. In an extreme case, if $\overline{T}_a = 45^{o}C$, $\overline{T}_i$ is expected to be only $30.7^{o}C$. At $\overline{T}_a = 50^{o}C$, $\overline{T}_i$ would be a "cool" $33.8^{o}C$. These examples have never been observed, but serve to illustrate the potential significance of the lodge. The limiting factor in the southern distribution of <u>C. canadensis</u> (Map 1) is probably $\overline{T}_i$ (which will be a function of $\overline{T}_a$).

In very warm weather beaver find favorable water temperatures to which they can escape (and often do), if T_i rises much above the "comfortable" levels of 10^o - 15^o C. As will be seen later, other important behavioral strategies may exist for thermoregulation in warm weather. Thus T_i is adaptive for beaver in exactly the same way mean burrow temperature is for *Peromyscus*, where the burrow was much more important as a refuge from temperature extremes in winter than in summer (Hayward, 1965). Mean burrow temperature for *Peromyscus* was 10^oC in summer and 0^oC in winter (for six geographic races in six different environments). These levels seem surprisingly similar to the respective seasonal $\overline{T}_i$ for *Castor*, a much larger animal. However, it is not surprising to note that the least stable burrow temperatures found by Hayward (1965) were those recorded in the Nevada desert, a habitat which lacks both forest and snow cover.

Stephenson (1969) has shown that T_i variability is positively correlated with lack of snow and with beaver activity in winter. The present study confirms these winter observations, but shows that T_i variability is correlated only with behavioral factors in winter and summer, taking on a slight correlation with thermodynamic factors at other times. Behavioral factors completely control T_i variability in a frozen lodge, when snow is lacking and temperature correlations do not apply. The cyclic nature of T_i variability is thus apparent and can result from: the adaptive nature of T_i; behavior; or the thermodynamics of the respective seasonal lodge. Thus, the nature of T_i stability bears only marginal similarity to the nature of burrow temperature stability for *Peromyscus*.

THE ADAPTIVE SIGNIFICANCE OF SEASONAL ACTIVITY PATTERNS

Aleksiuk and Cowan (1969 a,b) and Novakowski (1967) have already demonstrated the adaptive significance of metabolism and activity patterns in Arctic and sub-Arctic populations of Castor. Adaptation in southerly populations seems mostly behavioral. A thickening of fur does, however, occur in southern Canadian beaver (Stephenson, 1969) but no data is available on seasonal fat content and distribution in southern beaver. Since the southern energy regimen does not fall to the levels observed for Arctic and sub-Arctic populations, it is assumed that autumn fat is not deposited in southern populations to the extent it is in the north.

A pronounced pattern of seasonal activity is, however, observed in southern beaver and can represent behavioral adaptation in these populations. In winter, beaver spend much less time out of the lodge (in activity) and enter the lodge more frequently (reducing $\Delta T = T_{body} - T_{ambient}$) in colder air - water temperatures. The cyclic nature of their activity levels and patterns is apparent - i.e., the colder the environmental temperatures, the less time they spend out of the lodge, and the more frequent are the entrances to the lodge.

With respect to winter adaptation, Scholander, et al, (1950) showed that thermal conductance is greater through beaver fur (at $0^{o}C$) in water than in air. Stephenson (1969) suggested that beaver probably face a greater thermoregulatory problem while swimming. Clearly then, the reduction of swimming activity demonstrated in colder environmental temperatures is a behavioral adaptation since both C and ΔT are reduced in the equation, $M = C\ (T_{body} - T_{ambient})$, in winter.

THERMOREGULATION AND THERMODYNAMICS

Thermoregulatory considerations

Scholander, et al (1950) has shown that beaver can extend their zone of thermoneutrality below 0°C by an increase in the thickness of fur insulation. Therefore in winter, T_i, although averaging between -2°C and +2°C, remains adaptive.

In summer, beaver could easily thermoregulate within the lodge. Since minute blood vessels permeate the entire tail and a countercurrent heat exchange system is present at its base (Aleksiuk, 1970), a beaver could merely dip its tail into the water at the "wet level" of the lodge to quickly lose heat. Steen and Steen (1965) have shown that up to 20% of heat loss occurrs via the tail of beaver. McNab (1966) has clearly demonstrated a similar strategy for fossorial rodents lacking tail fur. In an extreme case, the naked mole-rat, *Heterocephalus glaber*, uses its entire (hairless) body for conductive heat loss. This animal has the lowest T_b and is the poorest known mammalian thermoregulator - even less effective than the monotreme, *Tachyglossus aculeatus*[11].

"Tail - dipping" behavior within the lodge has not been observed, however it almost certainly must occur because heat loss by convection is greatly reduced in an enclosed atmosphere (McNab, 1966) and emergency heat loss by evaporative cooling is not effective in beaver. Structural specializations of the lips and tongue, and an internarial epiglottis

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[11] Compare data of McNab (1966) for *H. glaber* with that of Schmidt-Nielsen, et al (1965) for *T. aculeatus*.

do not allow "panting" . These specializations do, however, allow them to gnaw underwater without the danger of taking water into the lungs (Cole, 1970). "Tail - dipping" behavior was frequently observed when beaver sat on the edge of a pond, usually to feed (personal observations).

Model thermodynamics

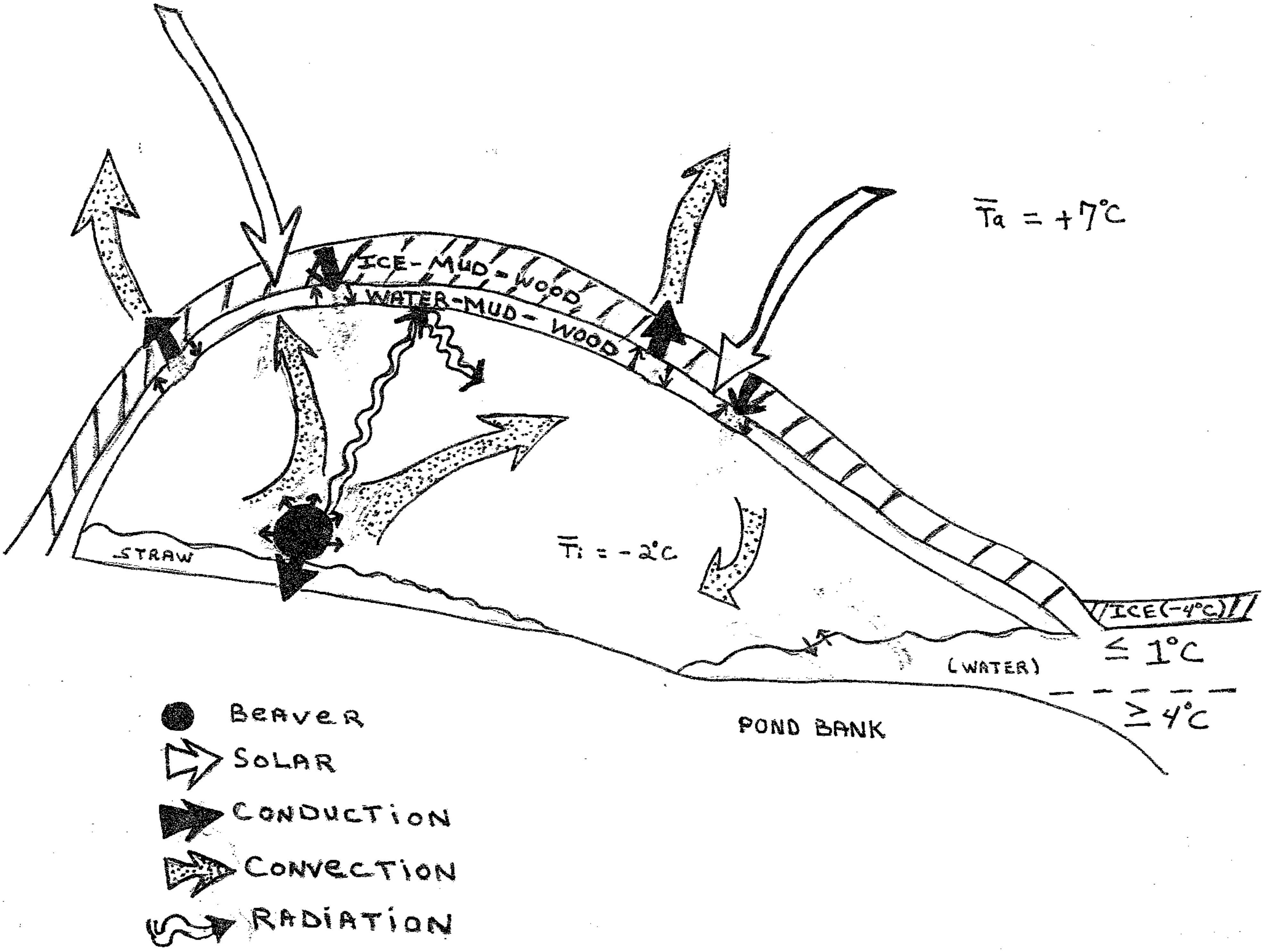
Much has been said about the thermodynamics of a seasonal lodge and its adaptive consequences. Accordingly, models for frozen and thawed lodges, showing seasonal heat sources, heat sinks, and regulators of heat flow, are desirable. An attempt to construct these models was made in Figures 11 and 12.

In Figure 11 a frozen lodge exists without snow cover. The relative amounts of heat flow are indicated by the thickness of the arrows. Dashed arrows indicate that solar energy is available only during daylight hours. Heat sources include solar energy, beaver body heat, and, to a limited extent, the water at the wet level of the lodge (plunge hole). Heat sinks include air, water, lodge walls, and floor. A large amount of heat is lost through the plunge hole to water at about $+1^{\circ}C$. Due to the presence of ice sheets in the upper layers of the lodge walls, a large amount of external and internal heat (80 calories/gram) is absorbed in the transition from ice to water (heat of fusion) (Sears and Zemansky, 1970). Dissection of a frozen lodge showed that the lower layers of the walls (adjacent to the internal chamber) contained water (mud) at $0^{\circ}C$ (personal observations). The thermal conductivity (k) of the ice sheets of the upper layers is

$$k = 0.004 \text{ cal. } s^{-1} \text{ cm.}^{-1} (C^{\circ})^{-1}$$

FIGURE 11. THERMODYNAMIC MODEL OF A FROZEN LODGE LACKING SNOW COVER.

(Arrows indicate the direction of heat flow and their thickness indicates the relative amounts of heat flow. Legends show heat sources and types of heat loss.)


T̄a = +7°C
ICE-MUD-WOOD
WATER-MUD-WOOD
T̄i = -2°C
STRAW
/ICE(-4°C)/
≤ 1°C
(WATER)
≥ 4°C
POND BANK
● Beaver
Solar
Conduction
Convection
Radiation

(Sears and Zemansky, 1970), while the thermal conductivity of water (mud) at $0^{o}C$, of the inner layers is

$$k = 0.001 \text{ cal. } s^{-1} \text{ cm.}^{-1} (C^{o})^{-1}$$

(Weast, 1969). Thus, both external and internal heat flow less readily through the inner lodge wall layers containing no ice, thereby allowing internal heat to be retained longer.

The lodge floor is a relatively small heat sink since it is insulated by dried vegetation placed there by beaver (personal observations , and Hodgdon & Hunt,1953). If this insulation did not exist, heat loss via the foot pads would, of course, be much greater.

Radiative heat loss is in the form of infra-red electromagnetic radiation at the relatively cool beaver body temperature of $36.7^{o}C$ (Sears and Zemansky, 1970). A very small amount of radiative heat will be reflected back into the chamber by the lodge walls and water. Lodge walls will, of course, produce their own radiative heat. Radiative heat energy is proportional to the fourth power of the temperature of the radiating body ("black body radiation"), however, this applies only to "freely radiating" bodies (Sears and Zemansky, 1970). Thus, radiative heat loss (and reflection) is probably negligible compared to conductive heat loss (already discussed).

Convective heat loss has been shown to be a negligible factor in the enclosed atmospheres of fossorial forms (McNab, 1966). However, in a lodge, convective heat loss will be greater than in burrows, and certainly greater in a thawed lodge than a frozen lodge, since the thawed lodge has more air flow.

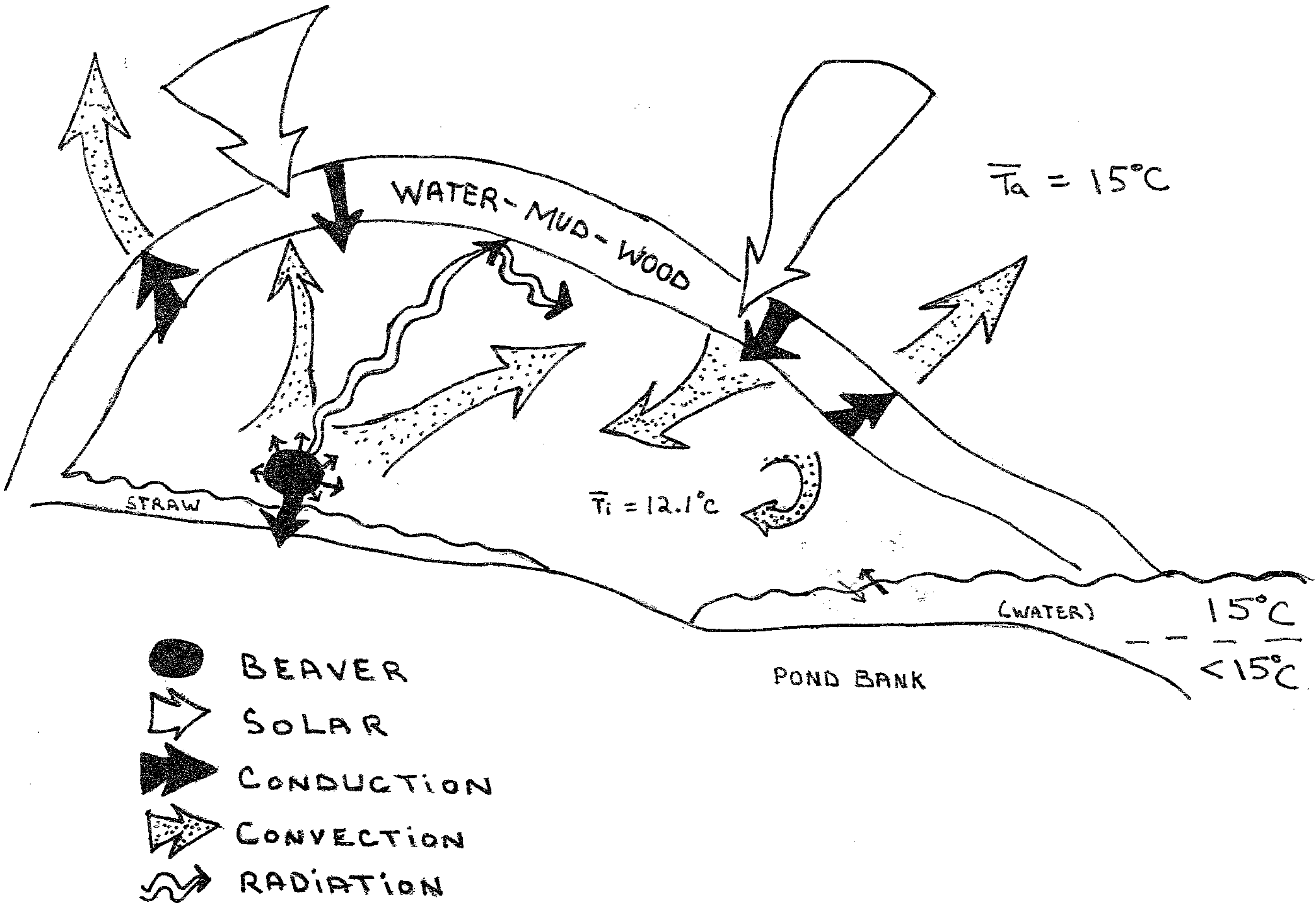
A small amount of solar heat may be lost by reflection from the upper layer ice sheet.

In Figure 12 a thawed lodge is shown to have similar thermodynamic properties, but the effects of ice no longer apply. Heat is therefore lost and gained more readily through the lodge walls, with air acting as the major heat sink. Warmer water temperatures reduce heat loss to the water. Conductive, radiative, and convective heat loss occurrs as in the frozen lodge, minus the effects of ice on heat flow rates for conduction and convection.

If these models accurately reflect reality then two observed thermodynamic effects of the frozen lodge may be explained. First, the "winter lodge buffer effect" and lack of temperature correlations are observed because of the greater absorbtion of heat by the upper lodge wall layers (absorbed by the heat of fusion of ice), resulting in a deficiency of available solar energy inside the lodge chamber. Second, larger values for (+) ΔT_i were observed in winter and spring when T_i values were generally "low". $\Delta T = T_{body} - T_{ambient}$ is thus greater in cooler microenvironmental temperatures ("ambient") and results in more convective and conductive heat loss. Hence, (+) ΔT_i due to "entrances" is larger in the cooler "ambient" temperatures of winter and spring.

FIGURE 12. THERMODYNAMIC MODEL OF A SPRING, SUMMER, AND EARLY AUTUMN LODGE (THAWED).

(Arrows indicate the direction of heat flow and their thickness indicates the relative amounts of heat flow. Legends show heat sources and types of heat loss.)


WATER-MUD-WOOD
$\overline{T_a} = 15°C$
$\overline{T_i} = 12.1°C$
STRAW
(WATER)
15°C
<15°C
POND BANK
BEAVER
SOLAR
CONDUCTION
CONVECTION
RADIATION

activity levels are intermediate. The "Frequency of entrance" increases in cold air - water temperatures and decreases in warmer air - water temperatures, seasonally. This is clearly adaptive as it allows beaver to reduce the metabolic cost of thermoregulation in the slightly reduced energy regimen of winters at temperate latitudes.

Special thermoregulatory mechanisms during heat stress consist of swimming and retreating to the "cool" microenvironment of the lodge. An additional mechanism, i.e., "tail - dipping" behavior, would be useful as an emergency thermoregulatory measure within the lodge, but has only been observed for beaver feeding on pond banks. Mechanisms such as evaporative and convective cooling are not effective because of anatomical specializations and lodge atmospheric conditions. The ineffectiveness of such mechanisms indicates that "tail - dipping" behavior is likely to occur at the wet level of the lodge.

Like _Peromyscus_ burrows, beaver lodges provide an average winter internal temperature of about 0°C, while average summer internal temperature is about 10°C. Both _Peromyscus_ burrows and beaver lodges are more important as refuges from winter ambient temperatures rather than from summer ambient temperatures.

Three major seasonal aspects of the internal lodge temperature have been observed. These include: the "winter lodge buffer effect"; the establishment of air-lodge temperature correlations in thawed lodges; and differences in the magnitude of instantaneous changes of the internal lodge temperature due to "entrance" activity. These special seasonal aspects of beaver lodges can help elucidate the complex physical mechanisms involved in seasonal lodge thermodynamics.

CONCLUSIONS

The microenvironmental temperatures faced by beaver at southern latitudes vary according to activity levels in winter but are independent of behavior in warm weather, varying with outside ambient temperatures according to the following linear relationships:

$$\bar{T}_i = 0.62\ \bar{T}_a + 2.8^{\circ}C\ (r = 0.9);$$

and

$$T_i\ \text{min.} = 0.54\ T_a\ \text{min.} + 5.2^{\circ}C\ (r = 0.7).$$

Internal lodge temperatures are most stable in late spring through late summer when available solar energy is most stable.

Snow cover is an integral factor in the winter thermal ecology of beaver, having an insulatory and stabilizing effect on microenvironmental temperatures, and allowing them to remain at about $0^{\circ}C$. Variation in mean daily T_i, in winter, is correlated with lack of snow cover and a high degree of "entrance - exit" activity (F_e). Frozen winter lodges, lacking snow insulation, exhibit a thermal "buffer effect" which is adaptive in severe cold stress or if mild periods preceed severe cold. However, this effect is temporarily maladaptive if air temperatures remain mild.

T_i is adaptive in winter because a thickening of the winter pelage allows beaver to extend their zone of thermoneutrality below $0^{\circ}C$. Internal lodge temperatures are also adaptive in warm weather as T_i remains between 10° - $15^{\circ}C$ while outside temperatures may reach $37^{\circ}C$ or more.

Beaver activity exhibits a cyclic seasonal pattern ranging from 10% of the day in winter, to 50% of the day in summer. Spring and autumn

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