

THE UNIVERSITY OF MANITOBA

BEHAVIORAL AND PHYSIOLOGICAL ASPECTS OF TEMPERATURE  
REGULATION IN THE MUSKRAT  
(Ondatra zibethicus)

BY

ROBERT ALLAN MACARTHUR

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## ABSTRACT

Behavioral and physiological adaptations for thermoregulation were examined in relation to season in the muskrat, Ondatra zibethicus. Avoidance of macroclimatic stress was attributed primarily to the construction and selective use of multiple shelters. Between November, 1973, and July, 1975, air temperatures in Delta Marsh ranged from  $-39$  to  $34^{\circ}\text{C}$ , whereas temperatures recorded from within lodges, burrows, and pushups varied from  $-9$  to  $30^{\circ}\text{C}$ . The range of mean temperatures ( $3$  to  $25^{\circ}\text{C}$ ) recorded from within occupied lodges and burrows during this period approximated the thermoneutral zone of this species. In winter, group occupation of lodges resulted in nest chamber temperatures that averaged  $20^{\circ}\text{C}$  (range =  $11$  to  $35^{\circ}\text{C}$ ) higher than external air temperature. In summer, high lodge temperatures appeared to favor the alternate use of open nests and burrows.

Most activity took place within a  $15$  to  $25$  m radius of a lodge or burrow. Although muskrats were predominantly nocturnal, intermittent activity occurred throughout the day, with a mean periodicity of  $5.8$  hours in summer, and  $6.2$  hours in winter. Pronounced inter- and intra-individual variability in daily activity ensured continuous, or nearly continuous occupation of winter lodges by a variable number of muskrats, and hence facilitated microclimate

stability. Daily variation in activity and weather were weakly correlated during both summer and winter.

Field studies indicated little seasonal variation in either level or daily amplitude of body (abdominal) temperature. In juveniles during summer, and in adults during winter, body cooling accompanied foraging activity, and was retarded by periodic withdrawal from water. Net body temperature decline during winter foraging seldom exceeded  $2^{\circ}\text{C}$ , and was relatively independent of foraging time for excursions exceeding 40 min duration. In addition to periodic rewarming within feeding lodges and pushups, muskrats appeared to avoid hypothermia during winter foraging by elevating body temperature prior to entering water. This elevation was related to foraging time, being maximal (mean increase =  $1.2^{\circ}\text{C}$ ) for excursions exceeding 40 min duration. Comparable increases were not observed in summer.

In the laboratory, no significant seasonal differences were observed in resting metabolic rate over an air temperature range of  $-15$  to  $30^{\circ}\text{C}$ . During winter, huddling by three muskrats resulted in a 33 percent reduction in the slope of thermal conductance at air temperatures between  $-17$  and  $10^{\circ}\text{C}$ . Body temperature was independent of air temperature between  $-20^{\circ}\text{C}$  and  $30^{\circ}\text{C}$ , but body cooling in water occurred at all temperatures below  $30^{\circ}\text{C}$  in summer, and  $25^{\circ}\text{C}$  in winter. Cooling rates in summer exceeded those in winter ( $P < .01$ ) at all water temperatures tested ( $6$  to  $30^{\circ}\text{C}$ ).



Abdominal cooling of muskrats swimming in water at 2°C during winter was accompanied by an increase in the temperature of interscapular brown adipose tissue, implying an active role of non-shivering thermogenesis in retarding hypothermia.

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## GENERAL INTRODUCTION

Thermal homeostasis in small mammals is often viewed as a compromise between behavioral evasion of climatic extremes, and physiological responses to "unavoidable" environmental stress (Hayward 1965; Brown 1968; Muul 1968; Hart 1971). Of particular interest are those species of non-hibernators which have dispersed over broad geographic ranges with markedly different macroclimates. One such mammal is the muskrat, Ondatra zibethicus (Link). This semi-aquatic rodent is endemic to North America, where its range extends from Louisiana coastal marshes in the south, to the arctic tundra regions of northern Canada and Alaska (Errington 1963). Following introduction into Czechoslovakia in 1905, O. zibethicus spread rapidly through continental Europe (Storer 1937), and its present range in Eurasia includes Scandinavia and Russia (Errington 1963).

Although the general ecology of this species has been extensively studied (Dozier 1948; Bellrose 1950; Fuller 1951; Stevens 1953; Sather 1958), knowledge of thermoregulatory capabilities was, prior to this study, limited to laboratory investigations (Hart 1962; Johansen 1962; Shcheglova 1965; McEwan et al. 1974). Before thermoregulation in the muskrat can be adequately described, intensive field research is required. A need exists for detailed studies of the microenvironment in nature, and the extent to which the



muskrat modifies its microclimate from season to season. In-depth analysis of activity and body temperature patterns should provide additional insight into the role of behavior in temperature regulation in this species. Aside from behavioral adaptations, it is desirable to know what basic physiological adjustments the muskrat undergoes during seasonal acclimatization.

It is the aim of the present study to overcome some of these deficiencies in our knowledge through the adoption of a broad, field-oriented approach to temperature regulation in O. zibethicus. This subject is examined in relation to season, with major emphasis on adaptations to cold in winter. The thesis is comprised of three major parts with supporting appendices. In consecutive order, these parts deal with: (1) structural and thermal aspects of the micro-environment, (2) activity and body temperature patterns of free-ranging animals, and (3) thermoregulatory capabilities of seasonally-acclimatized muskrats in the laboratory. The third part is followed by a note on winter movements and home range in the muskrat. This note comprises data which is ancillary to the central theme, and its inclusion in the thesis is motivated by the paucity of existing data on winter home range in this species.

PART I

Summer and Winter Microenvironments of the  
Muskrat (Ondatra zibethicus) in a Prairie  
Marsh

## INTRODUCTION

Knowledge of the structural and thermal features of microenvironments is fundamental to studies of homeotherm energetics. In the past, microclimate studies have tended to emphasize the thermal buffering role of either subterranean (Kennerly 1964; Hayward 1965; Breyen et al. 1973) or subnivean (Pruitt 1957; Coulianos and Johnels 1962; Fuller et al. 1969) microhabitats. In many of these studies, problems of accessibility have precluded measurement of nest conditions directly. Such information is available for only a few genera, including Microtus (Stark 1963), Neotoma (Brown 1968), Spermophilus (Wang 1972), and Castor (Stephenson 1968).

One species for which the microenvironment is readily accessible to investigation in summer and winter is the muskrat, Ondatra zibethicus. Basically a burrowing rodent, this semi-aquatic microtine normally excavates a bank burrow along bodies of water bounded by abrupt shorelines. Where shoreline relief is gradual, O. zibethicus instead erects conspicuous mounds of emergent vegetation into which it burrows and excavates one or more resting chambers and associated passageways (Johnson 1925; Seton 1929; Warwick 1940; Bellrose 1950; Errington 1963).

To date, much of the impetus for study of the microhabitat of this species has stemmed from economic damage

to earthen embankments (Warwick 1940; Beshears and Haugen 1953), as well as from management practices associated with fur harvesting (Dozier 1948; Bellrose 1950; Fuller 1951; Stevens 1953). Consequently, little attention has been given to the potential significance of these shelters in temperature regulation. In view of the broad distribution and year-round activity of O. zibethicus (Errington 1963), shelter construction may constitute a vital thermoregulatory adaptation in this species.

It is the objective of the present study to examine the physical microenvironment of O. zibethicus inhabiting a prairie marsh ecosystem. Particular attention is given to seasonal modification of microclimate resulting from the construction and occupation of various types of shelters.

## MATERIALS AND METHODS

### Study Area

Field studies were conducted in the western sector of Delta Marsh, located on the southern shore of Lake Manitoba, Canada (50°11'N; 98°23'W). The marsh comprises a heterogeneous series of shallow bays and interconnecting channels and creeks, which are generally less than 1 m deep, and never exceed 3 m (Walker 1965). The principal emergents bordering the bays and channels are cattail, Typha latifolia, and bulrush, Scirpus spp., whereas higher, seasonally-flooded areas are dominated by common reed, Phragmites communis, and sprangle-top, Scholochloa festucacea. The predominant submergents are the pondweeds, Potamogeton spp. and Myriophyllum spp. A detailed account of the vegetation of Delta Marsh is given by Walker (1965).

The climate is characterized by high summer and low winter temperatures with annual variation often approaching 70 to 75°C (Monthly Record, Meteorological Observations in Canada, Environment Canada). Mean monthly temperatures are generally below 0°C from November to March, and above 10°C from May to September.

### Microhabitat Physiognomy

External and internal configurations and dimensions were recorded from 1 burrow system and 39 dwelling lodges

in summer (June and July, 1974, 1975), and from 27 dwelling lodges, 23 feeding lodges (feeders), and 19 pushups in winter (November through March, 1973-74, 1974-75). Winter shelter definitions followed Dozier (1948) and Fuller (1951).

Various external features of shelters were examined, including composition, distance to open water, length, width, and height above water surface, and water depth. In winter, ice thickness, snow depth, and distances between associated shelters were also measured. Internal configuration was determined by dissection. The number and relationships of nest chambers and plungeholes were recorded, as were maximum wall thickness, chamber dimensions (length, width, ceiling height), plungehole diameter, and floor-to-water distance. Measurements were made with a meter stick and steel tape, except for distances exceeding 5 m, which were determined by pacing (estimated accuracy:  $\pm 4$  percent). At the conclusion of observations, every effort was made to reconstruct lodges, and in winter, to restore a heavy mantle of snow.

#### Ambient Temperature

Ambient temperature ( $T_a$ ) recordings were obtained with a battery-powered, 9-channel Grant Miniature Temperature Recorder equipped with Type C (small) thermistor probes (Grant Instruments [Developments] Ltd.). This instrument provided automatic recordings at hourly or half-hourly

intervals from coaxial thermistor leads ranging in length from 6 to 100 m. Allowing for maximum error from all potential sources; Bocock (1973) has estimated the accuracy of this temperature recorder to be within  $\pm 2.5^{\circ}\text{C}$ . However, a calibration check of nine thermistor probes immersed in a stirred, alcohol-water bath indicated that the instrument used during most of this study was accurate to within  $\pm 0.5^{\circ}\text{C}$  over a  $T_a$  range of  $-7.5$  to  $35^{\circ}\text{C}$ .

The temperature recorder was housed in a weather-proofed, styrofoam-lined, plywood box (90 x 60 x 60 cm) that required heating in winter. In 1973-74, heating was accomplished by placing the box in a prefabricated metal shed (192 x 145 x 192 cm), and venting warm air from a catalytic tent heater (Coleman Inc.) into the box via a furnace elbow duct mounted in the latter. In the winter of 1974-75, the above weather box was located approximately 180 m from a University of Manitoba Field Station building from which an electric cord extended to the box. A goose-neck lamp (100 watt bulb) wired to a household wall thermostat (Honeywell Inc.) provided a reliable, silent mode of heating.

To avoid damage by muskrats and other rodents, thermistor leads were suspended above ground and water wherever possible, and probes were encased in copper or aluminum tubing (0.6 cm diam) for water and lodge, pushup, and burrow chamber measurements. For shelter instrumentation, the tubing was cut to a length approximating

wall thickness, and was crimped at one end. This end was inserted into the wall until it protruded 3 to 7 cm inside, and a thermistor lead was threaded into the tube as far as the crimp and taped in position. In burrows and winter lodges it was necessary to drive a sharpened steel rod (0.6 cm diam) through the soil or frozen wall before inserting a tube. At the completion of all observations, each structure was carefully dissected to determine the precise location of the thermistor. Automated  $T_a$  recordings were obtained from a total of four lodges and three bank burrows in summer, and from eight lodges and four pushups in winter. Burrow temperatures were recorded from two shallow chambers located 7 to 20 cm beneath the soil surface, and from a single deep chamber situated at a depth of 45 cm in the soil.

Efforts to encase thermistor probes in plastic rather than metal shielding invariably resulted in the destruction of the leads by muskrats, and metallic protection was deemed essential, despite potential error due to thermal conductivity. A comparison of metal- and plastic-shielded probes fixed in an "artificial lodge" during summer, however, failed to reveal any detectable differences in  $T_a$ .

Owing to scale limitations of the temperature recorder in use during the winter of 1973-74, no ambient air temperatures were recorded at that time. However, daily maximum-minimum air temperatures were available throughout



this study from the University of Manitoba Field Station situated within 2.5 km of all observation sites. In the summer of 1974, air  $T_a$  was measured with a thermistor probe shielded by an aluminum foil cylinder (0.6 cm diam) suspended 46 cm above the water in a stand of T. latifolia. In the following winter and during the summer of 1975, air  $T_a$  was measured with a probe housed in a Stevenson Screen 75 cm above ground level in a mixed stand of P. communis and T. latifolia. Shallow (3 to 20 cm) and deep (30 to 50 cm) water temperatures were recorded from probes fastened to a stake driven into the marsh bottom. The variability in water depth at each of the latter two recording sites resulted from fluctuating water levels in the marsh.

#### Use of Radio Telemetry

With the exception of Lodge Nos. 3 and 4, all burrows, lodges, and pushups instrumented for recording  $T_a$  were situated within the home ranges of transmitter-equipped muskrats. Telemetry observations assisted in the verification of the occupied/abandoned status of these shelters. In addition, the "radio-tagging" of all muskrats occupying Lodge No. 5 during winter, 1974-75, permitted comparison between lodge  $T_a$  changes and the presence or absence of the resident animals.

The FM transmitter used in this study has been described extensively by Wang (1972). Each transmitter

was surgically implanted into the abdominal cavity, and the continuous tone that it emitted was received on the FM band of a transistor radio (Sony AM/FM Cassette-Recorder, Model CF-350 and CF-400). Details concerning telemetry instrumentation and monitoring techniques are provided in Part II.

## RESULTS

### Summer Microhabitat

#### Bank Burrows

The use of bank burrows in Delta Marsh was restricted mainly to dykes and natural embankments flanking channels, ditches, and occasionally sloughs. Dissection of one burrow system revealed a complex labyrinth of chambers and passageways located at various depths in the soil profile (Fig. 1, Table 1). Probing with a steel rod indicated vertical stratification of chambers in other burrow complexes. Surface chambers were frequently identified by the presence of fresh vegetation-mud "plastering" on the bank exterior. The extent of burrow systems was revealed further by telemetry observations indicating underground animals as much as 3 to 6 m inland along dyke embankments. Burrow entrances were always submerged, and shallow trenches were sometimes observed leading to deeper water. Evidence of trenching was also present along the shoreline opposite some summer lodges, and at three sites located in June, 1974, these gave way to shallow inland burrows, all within 15 m of respective lodges.

#### Lodges

The most conspicuous shelter encountered in Delta

Figure 1. Three-dimensional configuration of a single burrow system (No. 1) located in a shallow ditch in Delta Marsh. The sketch illustrates resting chambers (a through l), interconnecting passageways, and external entrances. Dimensions and depths of resting chambers are presented in Table 1. A thermistor probe was situated in chamber a. This complex was occupied by a transmitter-equipped adult male, as well as an adult female and at least one litter of young in June and July, 1974. It was dissected in October of the same year, after water had receded and the burrow was abandoned.

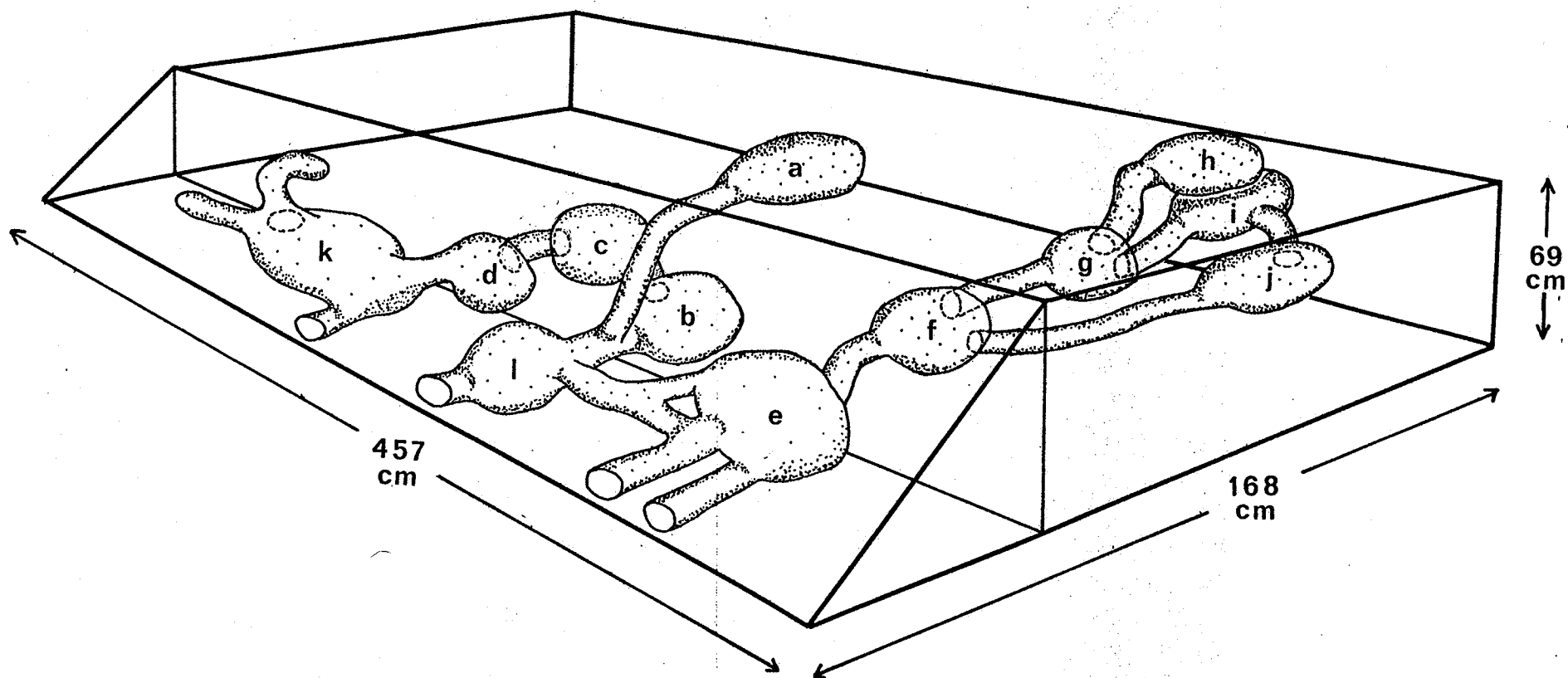


Table 1. Chamber measurements of Burrow System No. 1

Chamber	Soil Depth (cm)	Length (cm)	Width (cm)	Height (cm)
a	8	36	20	20
b	52	30	23	24
c	53	36	27	24
d	52	25	23	24
e	20	36	29	23
f	15	—	—	—
g	13	36	23	20
h	9	28	24	19
i	29	62	28	28
j	41	28	31	31
k	30	33	16	16
l	—	—	—	—
$\bar{x}$	29.2	35	24.4	22.9

Marsh was the dome- or conical-shaped lodge. Though semi-floating, these structures usually extended to the bottom substrate, and were often anchored to surrounding emergent vegetation. The mean distance from a lodge to the edge of the emergent zone bordering on open water was 5.3 m (range = 0 to 24 m; n = 14), and the mean water depth at the lodge site was 42 cm (range = 10 to 71 cm; n = 74).

Lodges were usually composed of the dominant emergent vegetation in the area, interspersed with Potamogeton spp. and bottom detritus. The majority of lodges were located in stands of T. latifolia. Thus, of 41 lodges examined, 37 consisted principally of T. latifolia, and the remaining 4 of either P. communis or Scirpus spp. The only evidence of preferential selection occurred in stands of P. communis, where T. latifolia represented 50 percent or more of the construction material (n = 5 lodges).


Each lodge contained one or more spherical or ellipsoid nest chambers lined with compacted, longitudinally-shredded T. latifolia or Scirpus spp. Where more than one nest chamber was present, they tended to be horizontally displaced, and were often interconnected (Fig. 2A). Entrances were submerged in all lodges examined. External and internal dimensions are summarized in Table 2.

#### Open Nests and Feeding Platforms

In summer, muskrats sometimes constructed open nests which resembled the lodge nest chamber described above, but

Figure 2. Internal configuration of representative summer and winter shelters used by O. zibethicus (lateral view).

- A - Summer lodge
- B - Occupied winter dwelling lodge
- C - Abandoned winter dwelling lodge
- D - Winter feeding lodge
- E,F,G,H - Winter pushup types

 - Structure composed of vegetation

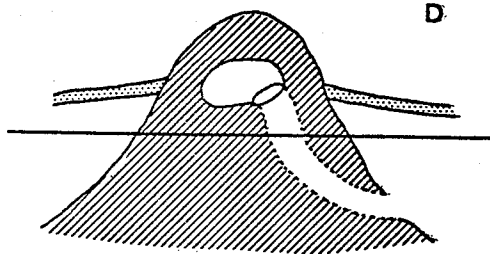
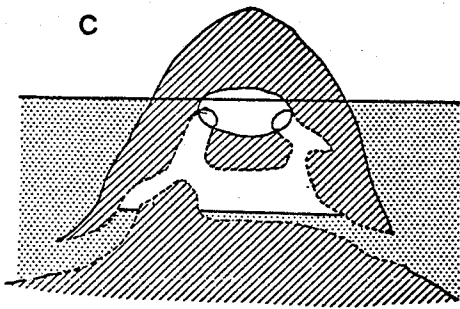
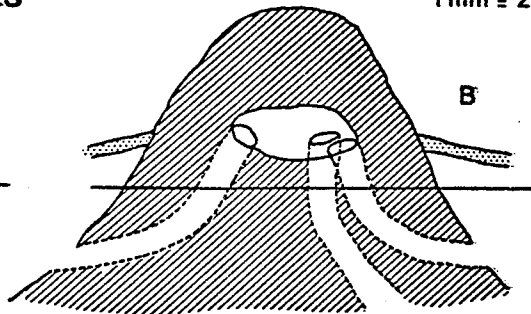
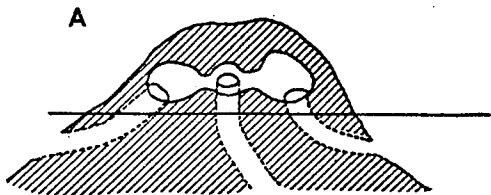
 - Ice

Solid horizontal line - Water surface



# LODGES

1 mm = 2.5 cm



# PUSHUPS

1 mm = 0.5 cm

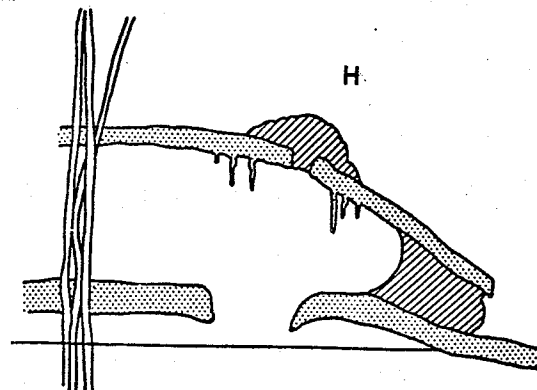
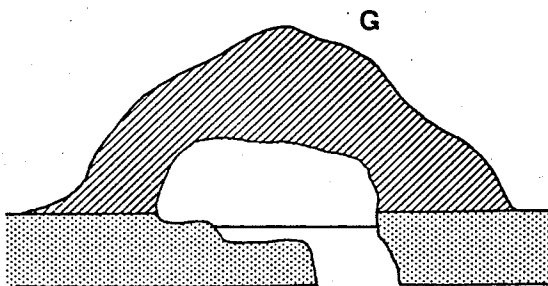
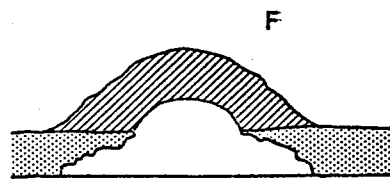
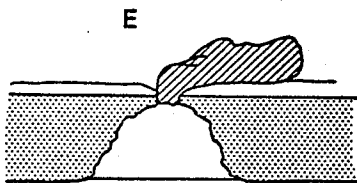


Table 2. Summer and winter lodge measurements <sup>a</sup>

Variable	Summer Dwelling Lodges	Winter Dwelling Lodges	Winter Feeders
<u>External</u>			
Length	145(6.6) <sup>b</sup> 81-244 39	164(7.1) 107-254 27	80(3.3) 53-112 23
Width	121(5.9) 48-203 39	147(6.8) 84-244 27	62(3.2) 30-94 23
Height	48(1.8) 33-81 38	70(2.5) 44-104 27	36(1.9) 20-58 21
<u>Internal</u>			
Wall thickness	23(0.9) 11-38 46	46(1.9) 28-78 30	18(1.5) 8-37 24
No. plunge holes per chamber	1.5(0.1) 1-3 56	2.2(0.1) 1-3 20	1.5(0.1) 1-2 24
Plunge hole diam.	12(0.9) 8-15 7	16(2.5) 9-23 5	18(1.4) 11-25 12
No. chambers	1.9(0.2) 1-7 34	1.2(0.1) 1-3 20	1.1(0.1) 1-2 24
Chamber length	25(0.5) 15-38 60	49(3.6) 23-89 23	33(1.9) 23-66 25
Chamber width	23(0.4) 15-29 60	37(2.6) 15-72 23	25(1.4) 18-53 24
Chamber height	15(0.2) 10-20 58	22(1.1) 14-34 23	22(1.4) 13-46 25
Floor-water distance	12(0.8) 0-22 41	24(2.4) 5-47 15	9(2.3) 0-25 16

<sup>a</sup> Summer measurements made June 1-July 1, 1974, 1975; winter measurements made Nov. 26-April 13, 1974-75; all dimensions in cm.

<sup>b</sup> Mean (standard error)  
Range  
Sample size

without a ceiling. These open nests were often located beneath over-hanging emergent vegetation, and were usually clustered within a 50 m radius of a dwelling lodge.

During the period of open water, muskrats also made extensive use of feeding platforms. These were simply floating, or semi-floating mats of rejected food items (mainly T. latifolia and Scirpus spp.) upon which animals rested while feeding. Feeding platforms were always situated within the emergent zone, and again, tended to be clustered about a central lodge or burrow system.

#### Winter Microhabitat

##### Bank Burrows

No data are available concerning the use of burrows by muskrats during winter in Delta Marsh. Efforts to monitor nine transmitter-equipped, bank-burrowing muskrats during the winter of 1974, failed, owing to the emigration of all implanted animals from their burrows in late October (see Part II).

##### Lodges

The location, water depth, and general construction of winter lodges resembled those described for summer. Winter lodges were differentiated into dwelling and feeding shelters primarily on the basis of external size (Fig. 2B and 2D, Table 2). The floor-to-water distance was also

much reduced in feeders (Table 2), in which the floor often sloped gradually into the water, and was sometimes totally submerged. The prevalence of rejected food items on the floor and in the plunge hole also typified feeders. The mean distance between a dwelling lodge and its associated feeder was 11.3 m (range = 2.1 to 23.2 m;  $n = 19$ ).

External and nest chamber dimensions, wall thickness, and floor-to-water distance were all significantly greater in winter than in summer dwelling lodges (Student's  $t$ -test,  $P < .01$ ). There also tended to be fewer chambers in winter lodges (Table 2), and when more than one was present, they were vertically rather than horizontally displaced (Fig. 2C). In winter, the occurrence of more than one chamber per lodge was only observed late in the season. In all 36 lodges dissected between November 26 and February 16, for example, only one chamber per lodge was recorded. In contrast, 2 lodges with 1 chamber, 4 with 2 chambers, and 2 with 3 chambers were documented between February 17 and March 22. Unlike the loose, porous wall often observed in summer, that of the winter lodge was a compacted matrix of vegetation which became solidly frozen through most of its depth as winter advanced.

#### Pushups and Air Spaces

Pushups varied from simple plugs of frozen submergent vegetation in ice cracks to relatively large domes of the

same material enclosing an open plunge hole and adjacent resting shelf (Fig. 2E through 2H, Table 3). The majority of pushups encountered in this study were of the type depicted in Fig. 2F. These structures tended to be located either within the zone of emergent vegetation, or 18 to 30 m from this zone, over open water. The mean distance between a dwelling lodge and its associated push-up was 38.7 m (range = 7.6 to 121.9 m;  $n = 19$ ). Both feeders and pushups were usually clustered within a 50 m radius of a central dwelling lodge, and often occurred in a "stepping-stone" pattern (Part IV). Pushup construction reached a peak in late November and early December; from the end of December until March the number of active pushups declined steadily in both years.

As winter progressed, air spaces commonly formed between adjacent layers of ice in the emergent zone (Fig. 2H). Telemetry and evidence of feeding activity revealed that muskrats made extensive use of these.

#### Ice Formation and Snow Accumulation

During the winters of 1973-74 and 1974-75, ice covered the marsh by mid-November, and thawed by the end of April. By late February of both years, shallow portions of the marsh had frozen to the bottom.

In both years, cumulative snowfall increased steadily between December and March. Owing to strong prevailing winds, snow distribution was extremely irregular in the

Table 3. Winter pushup measurements (cm) recorded between Nov. 26, 1974 and April 13, 1975

	External Dimensions			Wall Thickness	Chamber Dimensions			Water Depth
	Length	Width	Height		Length	Width	Height	
$\bar{X}$	37(2.3)	25(1.6)	15(0.9)	7(0.6)	23(2.1)	17(1.2)	11(0.6)	42
R	23-56	14-41	8-23	2-13	10-46	10-37	5-14	28-57
n	19	19	18	19	19	19	19	4

Note: winter pushup = types F and G (Fig. 2);  $\bar{X}$  = mean(standard error); R = range;  
n = sample size

marsh. Open bays and channels remained windswept throughout most of the winter, and pushups in such locations received little, if any, snow accumulation. On the other hand, stands of emergent vegetation (especially T. latifolia) retained a considerable amount of drifted snow, and by January and February many of the lodges examined were completely enveloped beneath a level mantle of snow 7 to 30 cm deep at the lodge peak.

#### Summer Microclimate

In the two summers of study, air  $T_a$  ranged from 9.0 to 34.0°C, while deep and shallow water  $T_a$  ranged from 10.0 to 24.0°C, and from 12.5 to 31.5°C, respectively (Table 4). As expected, deep water  $T_a$  lagged behind air  $T_a$  in early summer, but by the end of July, this trend was reversed. In 1974, air and water  $T_a$  reached a peak in the latter half of July, and then subsequently declined.

As indicated in Fig. 3, lodge  $T_a$  was elevated above air and water  $T_a$  during most hours of the day, with a mean daily amplitude of only 2 to 4°C. Summer lodge temperatures varied from 13.5 to 30.0°C (Table 4), and a comparison of mean daily values indicated that the latter averaged 2.2°C and 4.4°C higher than air and water  $T_a$ , respectively. Regression analysis indicated a strong correspondence between mean daily lodge  $T_a$  and mean daily air and water  $T_a$  during the period June 1 to August 16, 1974 (Fig. 4). At this time, the regression correlation between lodge

Table 4. Summary of hourly ambient temperatures (°C) recorded in Delta Marsh during summer (1974,1975)<sup>a</sup>

Thermistor site	Month(year) monitored	n (days)	Mean hourly T <sub>a</sub> (S.E.)	Range	Daily Amplitude		
					Mean(S.E.)	Range	
<u>Dwelling</u>							
<u>Lodge</u>	No.1	J,J,A,(74) <sup>b</sup>	47	22.4(0.12)	13.5-30.0	3.4(0.29)	0.5-9.0
	No.2	J,J,A,(74)	47	21.6(0.09)	15.0-29.5	3.5(0.22)	1.5-7.0
	No.3	July,(74)	24	23.2(0.10)	17.5-29.0	4.3(0.23)	2.5-6.5
	No.4	July,(74)	11	24.9(0.11)	19.0-29.0	4.1(0.66)	1.5-9.5
	No.5	J,J,(75)	15	23.9(0.14)	19.0-29.0	2.4(0.25)	1.0-5.0
<u>Shallow</u>							
<u>Burrow</u>	No.1	A,(74	12	18.6(0.04)	16.5-19.5	0.6(0.06)	0.5-1.0
	No.2	J,J,(75)	10	18.7(0.04)	17.0-20.5	1.1(0.19)	0.5-2.5
<u>Deep</u>							
<u>Burrow</u>	No.1	June,(75)	6	9.4(0.06)	8.5-11.0	0.5(0.17)	0.0-1.5
<u>Shallow</u>							
<u>Water</u>	No.1	J,J,A,(74)	46	18.7(0.10)	12.5-28.0	3.8(0.35)	1.0-8.5
	No.2	J,J,(75)	17	22.6(0.16)	12.5-31.5	8.0(0.90)	4.0-15.5
<u>Deep</u>							
<u>Water</u>	No.1	J,J,A,(74)	47	17.4(0.11)	10.0-24.0	1.2(0.13)	0.5-3.5
	No.2	J,J,(75)	34	17.7(0.09)	11.5-22.0	1.4(0.14)	0.4-4.0
<u>Air</u>							
	No.1	J,J,A,(74)	47	19.7(0.15)	10.0-34.0	11.9(0.48)	5.0-18.0
	No.2	J,J,(75)	34	19.0(0.16)	9.0-29.0	9.5(0.48)	3.5-15.5

<sup>a</sup> Major observation intervals: June 1-14, 18-25, July 6-30, Aug. 13-16, 1974; June 6-July 10, 1975

<sup>b</sup> Abbreviations: June, July-J; August-A



Figure 3. Mean hourly ambient temperatures recorded in Delta Marsh during July, 1974, 1975. Numbers in parentheses identify dwelling lodges. Shallow burrow temperature was monitored July 1-5, 1975 (n = 5 days); all other sites were monitored July 6-30, 1974 (n = 24 days), and July 1-10, 1975 (n = 10 days). Representative 24-hour records of ambient temperature in July are provided in Appendix 1.

- - Air
- - Deep water
- - Dwelling lodge
- ▲ - Shallow burrow

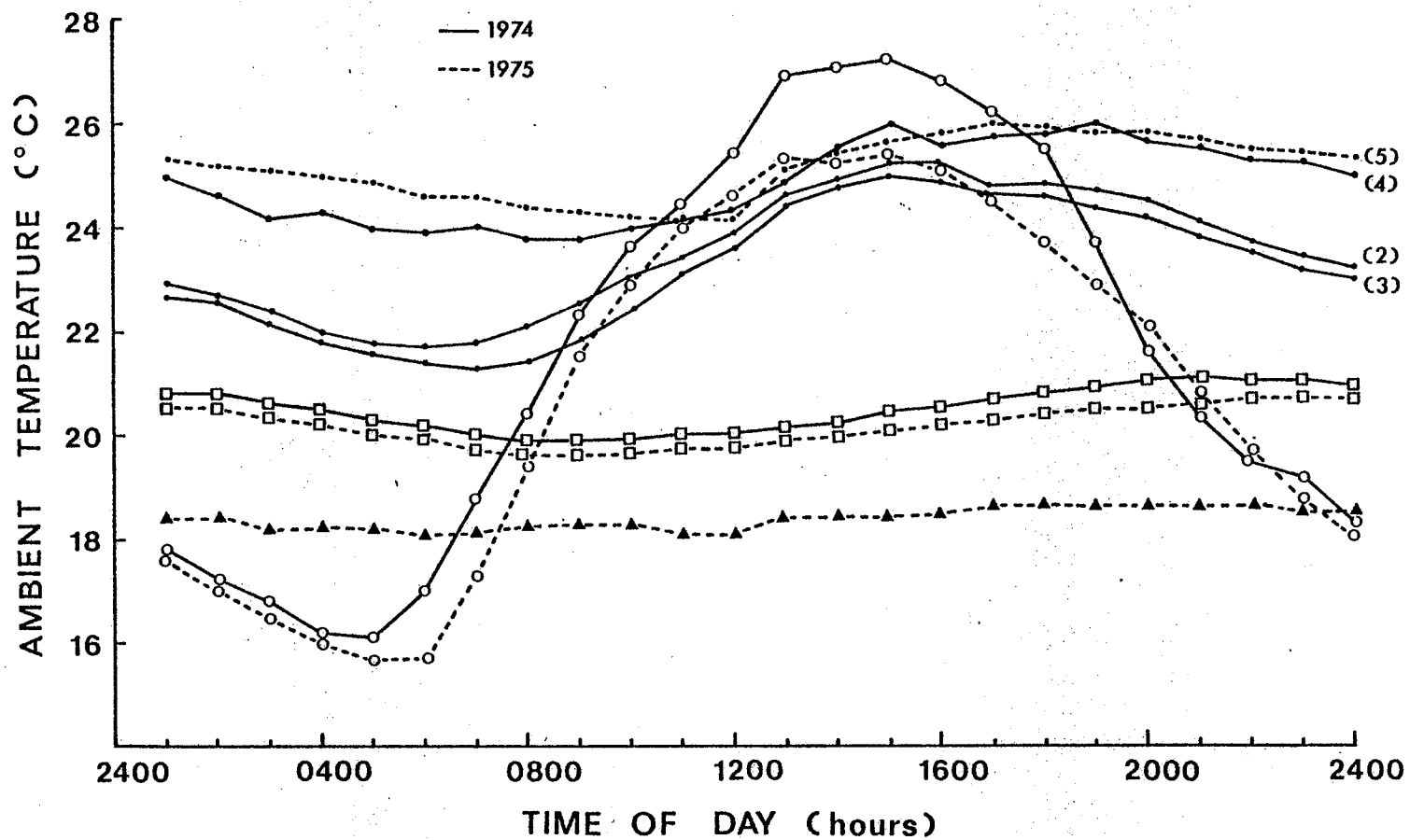
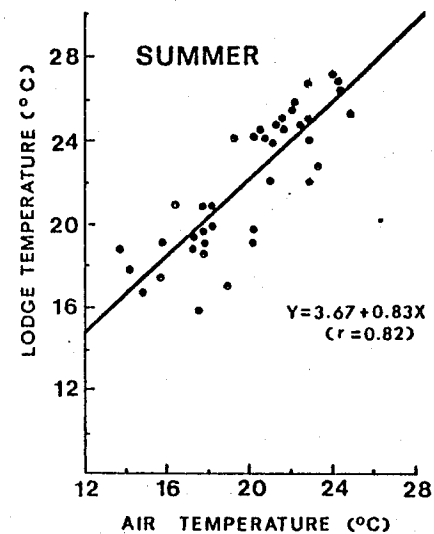
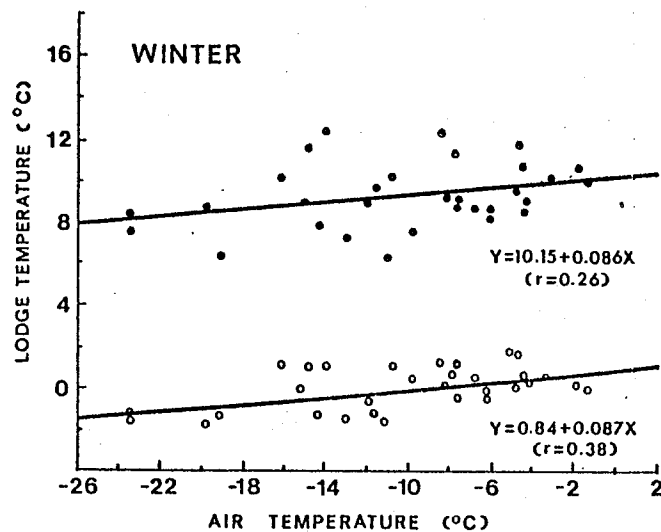
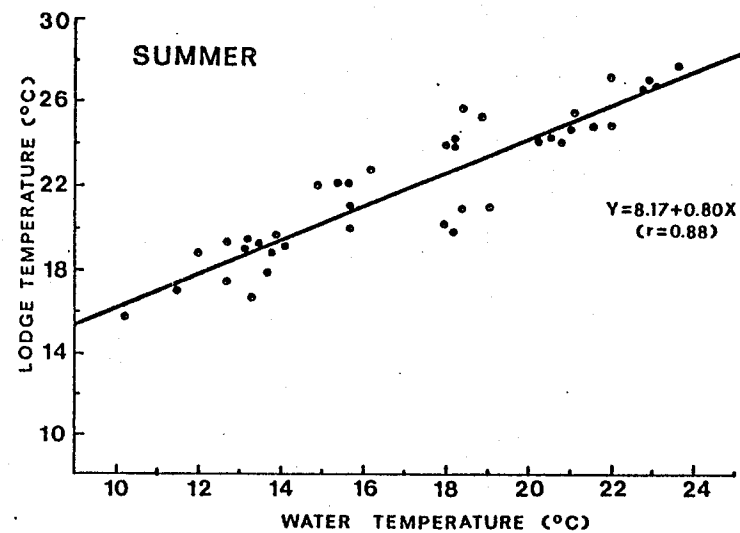
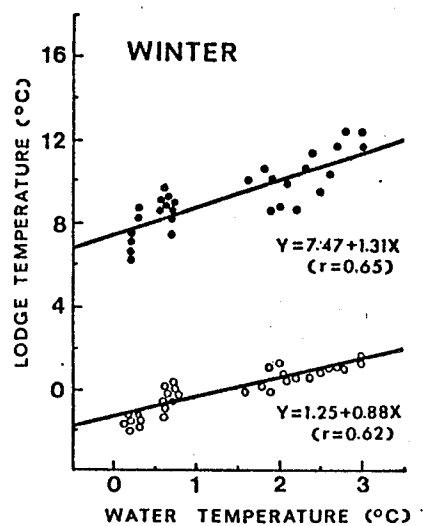


Figure 4. Regression analysis of mean daily dwelling lodge  $T_a$  in relation to air and water  $T_a$ , summer and winter. Values are based on hourly temperature recordings in Lodge Nos. 1 and 2 in summer (June 1-July 30;  $n = 44$  days), and Nos. 3 and 4 (occupied) and Nos. 7 and 9 (abandoned) in winter (Nov. 26-Jan. 5;  $n = 31$  days). Each point depicts the daily mean for two respective lodges ( $n = 48$  hours). Regression lines are fitted by the method of Least-Squares; all regressions were significant at  $P < .05$ .

- - Summer lodges and occupied winter lodges
- - Abandoned winter lodges



and air  $T_a$  was 0.82 ( $t = 13.4$ ,  $P < .001$ ), and between lodge and water  $T_a$  was 0.88 ( $t = 17.3$ ,  $P < .001$ ).

In summer, no consistent relationship was observed between lodge  $T_a$  and the presence or absence of transmitter-equipped animals in the nest chamber.

Ambient temperatures recorded from 2 separate shallow burrows in August, 1974, and June and July, 1975, respectively, were not significantly different ( $t = 1.06$ ,  $P > .05$ ), and ranged from 16.5 to 20.5°C (Table 4). Shallow burrow  $T_a$  averaged 6.4°C lower than lodge  $T_a$  in July, 1975, and 2.0°C lower in August, 1974. A single deep burrow monitored in June, 1975, averaged 12.8°C lower than lodge  $T_a$ , and 9.4°C lower than air  $T_a$  measured concurrently. Burrows represented the coolest, most stable microclimate encountered in summer, with a maximum recorded daily amplitude of only 2.5°C (Table 4, Fig. 3).

#### Winter Microclimate

In 1974-75, winter air  $T_a$  ranged from 7.0 to -30.0°C, whereas water  $T_a$  declined steadily from 3.5°C on November 26, to 0.0°C on February 14, when the marsh bottom was apparently frozen.

Winter dwelling lodges ranged from -4.5 to 20.0°C, and were distinguished as "occupied" or "abandoned" primarily on the basis of differences in the level and daily amplitude of  $T_a$  (Table 5, Fig. 5). Occupied lodges averaged 9.4°C (range = 3.5 to 14.0°C) higher than abandoned lodges, and 20.0°C (range = 11.0 to 35.0°C) higher than

Table 5. Summary of hourly ambient temperatures (°C) recorded in Delta Marsh during winter (1973-74, 1974-75)<sup>a</sup>

Thermistor site		Months(year) monitored	n (days)	Mean hourly T <sub>a</sub> (S.E.)	Range	Daily Amplitude	
						Mean(S.E.)	Range
<u>Dwelling</u>							
<u>Lodge</u>	No.1	D,J,F,(73/74) <sup>b</sup>	14	4.5(0.11)	1.0-10.5	4.4(0.56)	0.5-7.5
	No.2	D,J,F,(73/74)	14	3.1(0.13)	0.0-10.5	7.3(0.44)	3.0-10.0
	No.3	N,D,J,F,(74/75)	45	9.5(0.11)	2.0-20.0	5.9(0.40)	1.0-13.0
	No.4	N,D,J,(74/75)	37	10.2(0.07)	4.5-16.5	4.4(0.19)	3.0-7.0
	No.5	N,D,J,(74/75)	26	9.6(0.08)	5.0-20.0	4.2(0.42)	2.0-10.5
	No.6	N,D,J,(74/75)	42	11.0(0.25)	-0.5-20.0	6.3(0.65)	0.0-14.0
	No.7 <sup>c</sup>	N,D,J,F,(74/75)	46	-0.8(0.04)	-4.5-4.0	1.4(0.15)	0.0-4.0
	No.8 <sup>c</sup>	N,D,J,F,(74/75)	41	0.2(0.09)	-3.0-13.5	1.6(0.42)	0.0-11.0
	No.9 <sup>c</sup>	N,D,J,F,(74/75)	46	-0.4(0.05)	-3.5-8.0	1.2(0.20)	0.0-7.0
<u>Feeder</u>							
	No.1	N,D,J,F,(73/74)	14	1.3(0.05)	-1.0-3.0	0.7(0.11)	0.0-2.0
	No.2	N,D,J,F,(74/75)	40	0.4(0.06)	-4.0-4.0	1.7(0.14)	0.5-4.0
<u>Pushup</u>							
	No.1	D,(73)	3	-3.0(0.18)	-5.0 to -1.0	4.0(0.11)	4.0-4.5
	No.2	N,D,(74)	18	-3.5(0.09)	-9.0 to -0.5	2.3(0.39)	0.0-7.0
	No.3	N,D,(74)	18	-3.0(0.07)	-7.5 to -0.5	2.2(0.35)	1.0-6.5
	No.4	D,J,(74/75)	3	-4.0(0.16)	-7.0 to -1.5	3.7(0.54)	3.0-5.0
	No.5	D,J,(74/75)	5	-4.6(0.15)	-7.5 to -2.0	3.4(0.39)	2.0-4.0
	No.6	D,J,(74/75)	5	-3.0(0.09)	-5.5 to -1.0	2.6(0.38)	2.0-4.0
<u>Water</u>							
	No.1	N,D,J,(74/75)	42	1.1(0.03)	0.0-3.5	0.3(0.02)	0.0-0.5
<u>Air</u>							
	No.1	N,D,J,F,(74/75)	46	-11.7(0.22)	-30.0-7.0	11.7(0.83)	1.5-29.0

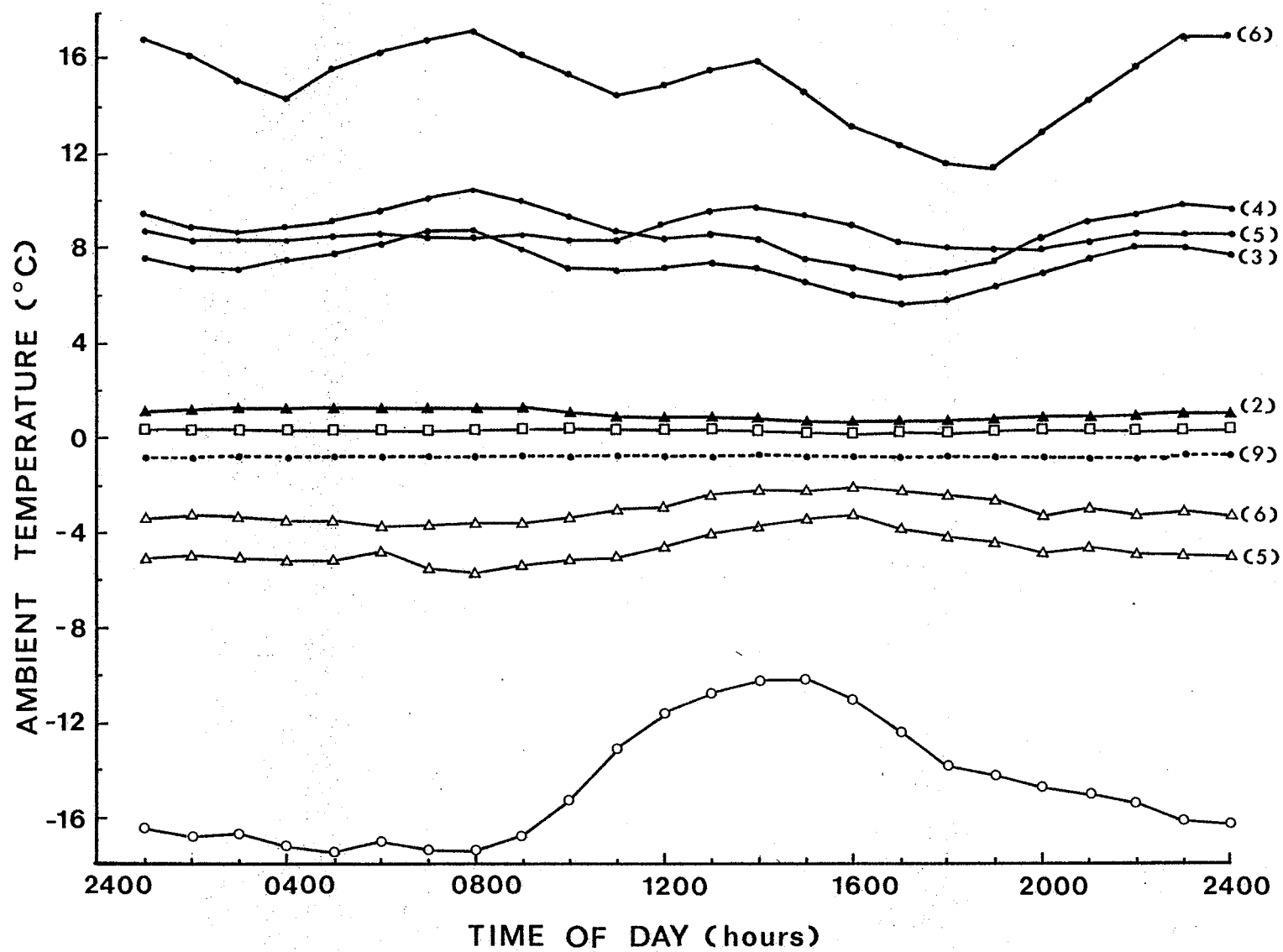
<sup>a</sup> Major observation intervals: Dec. 12-15, Jan. 13-21, Feb. 9-23, 1973-74; Nov. 15-Dec. 11, Dec. 27-Jan. 23, Feb. 14-18, 1974-75

<sup>b</sup> Abbreviations: November-N, December-D, January-J, February-F

<sup>c</sup> Believed to be abandoned during majority of observations

Figure 5. Mean hourly ambient temperatures recorded in Delta Marsh during January, 1975. Numbers in parentheses identify lodges and pushups. Lodge Nos. 5 and 6, and Pushup Nos. 5 and 6 were monitored Dec. 31-Jan. 5 (n = 5 days). All other sites were monitored Dec. 31-Jan. 5; Jan. 15-22 (n = 12 days). A representative 24-hour record of ambient temperature in January is provided in Appendix 2.

- - Air
- - Water
- - Dwelling lodge
- ▲ - Feeding lodge
- △ - Pushup
- - Abandoned dwelling lodge





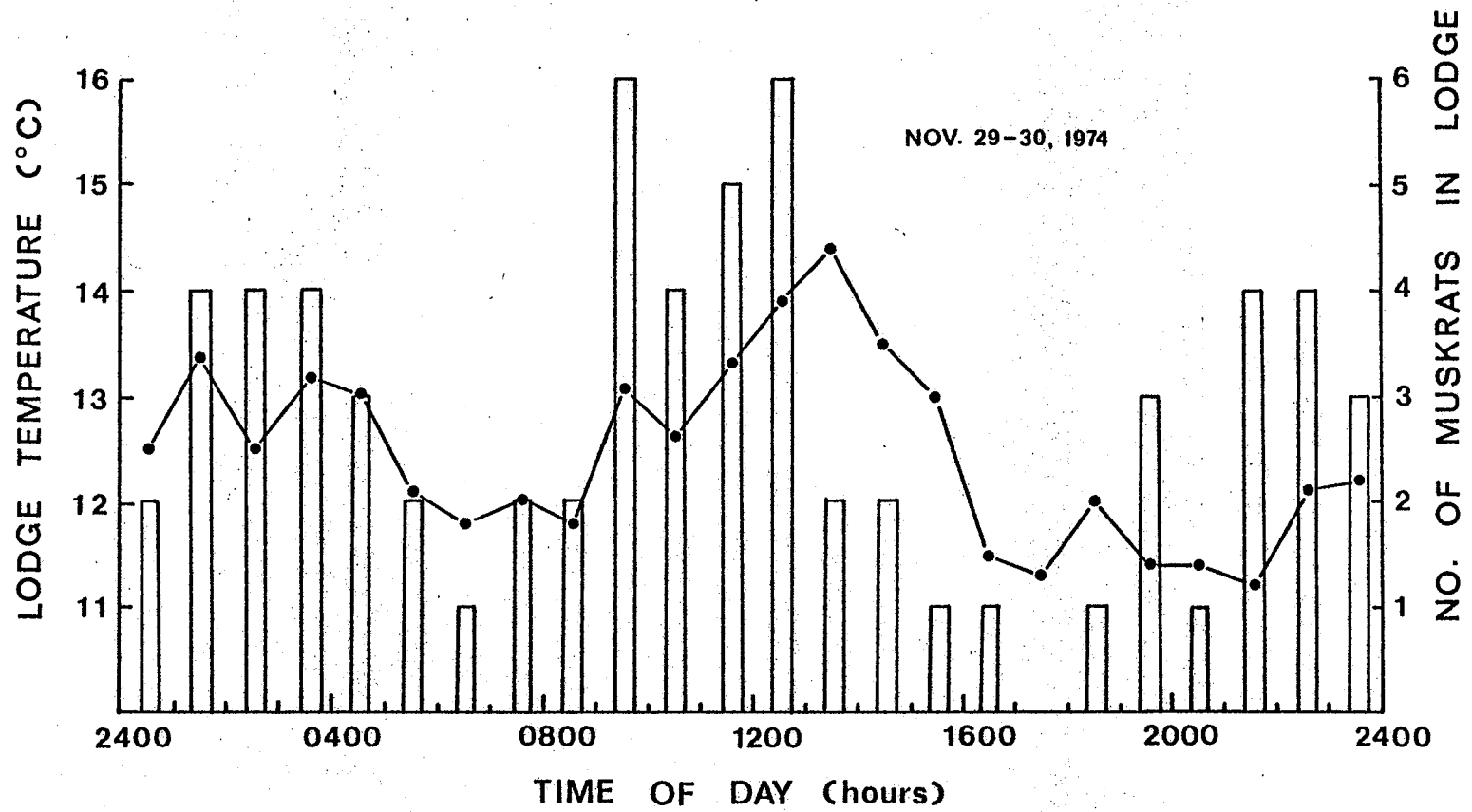
air  $T_a$  monitored simultaneously. As in summer, the mean daily temperatures within two occupied (Nos. 3 and 4) and two abandoned (Nos. 7 and 9) lodges were significantly correlated with water  $T_a$  ( $r = +0.65$ , and  $+0.62$ , respectively,  $P < .01$ ) in winter (Fig. 4). Seasonal regression comparisons for the latter variables (Covariance Analysis) revealed only moderate significance for the occupied lodges ( $F = 5.0$ ,  $P < .05$ ), and no differences in slope ( $F = 0.13$ ,  $P > .05$ ) when the two abandoned lodges were used in the comparison. The latter finding implies that the relationship between lodge and water  $T_a$  does not change appreciably between summer and winter.

In contrast to summer results, lodge  $T_a$  was only weakly correlated with air  $T_a$  in winter, with a correlation coefficient of  $+0.26$  ( $t = 2.06$ ,  $P < .05$ ) for occupied lodges, and  $+0.38$  ( $t = 3.18$ ,  $P < .05$ ) for abandoned lodges. In addition, the slope of the regression of lodge  $T_a$  on air  $T_a$  (Fig. 4) was significantly lower in winter than in summer (Covariance Analysis,  $F = 108.7$ ,  $P < .001$ ). These seasonal differences in correlation and slope imply an increased independence of lodge  $T_a$  from daily variation in external air  $T_a$  in winter.

Hourly variation in occupied lodge  $T_a$  contrasted sharply with the stable temperatures encountered in abandoned lodges (Fig. 5). As indicated in Fig. 6, a close correspondence was observed between hourly records of the number of muskrats occupying Lodge No. 5, and

Figure 6. A 24-hour record of nest chamber  $T_a$  fluctuations in winter Dwelling Lodge No. 5, measured in conjunction with hourly observations of the number of transmitter-equipped muskrats occupying the lodge.

- - Nest chamber  $T_a$  ( $^{\circ}\text{C}$ )
- - Total number of animals (maximum = 6) occupying the lodge



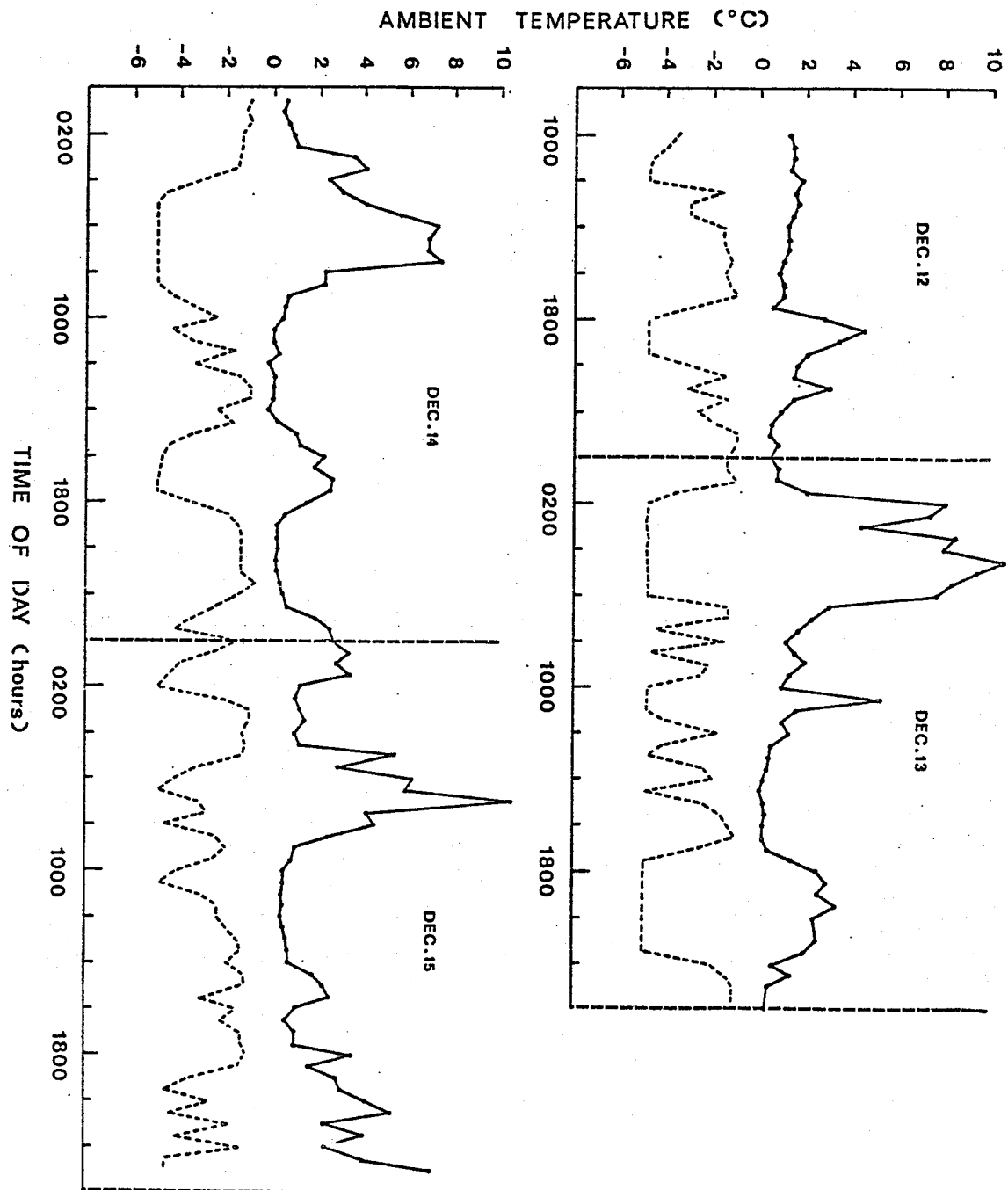
nest chamber  $T_a$ , on November 29-30, 1974. Further evidence of correspondence between lodge  $T_a$  and activity is presented in Fig. 7, where a significant negative correlation ( $r = -0.55$ ,  $P < .05$ ) was noted between the  $T_a$  of Lodge No. 1 and that of its associated pushup located 27.4 m away. Telemetry observations of two adult males inhabiting Lodge No. 1 corroborated the activity pattern implied by these inverse  $T_a$  rhythms. The relatively high temperatures recorded from Lodge No. 6 (Table 5, Fig. 5) are attributed to the close physical contact between thermistor and resident animals. This was verified by dissection of the lodge, revealing that the thermistor was located only 3 cm above the chamber floor.

In a few cases, the occupied/abandoned status of dwelling lodges appeared to change through the winter, such that presumed abandoned lodges became occupied, and vice versa (Appendix 3).

As with abandoned dwelling lodges, feeder  $T_a$  closely followed that of water (range = 1.0 to 4.0°C), and exhibited little diurnal variability (Fig. 5). The lowest temperatures encountered in winter shelters were recorded from pushups, which ranged from -1.0 to -9.0°C, and averaged only 5.4°C higher than surrounding air  $T_a$  (Table 5, Fig. 5).

Figure 7. Ambient temperatures recorded at 0.5 hour intervals from within Dwelling Lodge No. 1 (solid line) and its associated pushup (dashed line) in December, 1973.

Note: the lower scale limit of the Grant Miniature Temperature Recorder used to monitor  $T_a$  was  $-5^{\circ}\text{C}$ .



## DISCUSSION

### Summer Microenvironment

The configuration and internal dimensions of the one burrow system examined in this study were comparable to those described in the literature (Seton 1929; Warwick 1940; Beshears and Haugen 1953; Revin 1975). For instance, the mean chamber depth (29.2 cm) is very close to the mean value (25.4 cm;  $n = 56$  burrows) reported by Beshears and Haugen (1953). The prevalence of vegetation plugs in surface chambers, and their possible significance in ventilation, has also been referred to in the literature (Seton 1929; Warwick 1940). Chamber stratification not only enhances ventilation of deeper burrows, but also counteracts the deleterious effects of fluctuating water levels, and provides the resident animals with a broad spectrum of equable microclimates.

The basic floor plan of the summer dwelling lodge is similar to that described in the literature (Johnson 1925; Seton 1929; Warwick 1940), but insufficient published data are available for a quantitative comparison of dimensions. The loose, porous ceiling of the summer lodge resulted in a nest  $T_a$  that closely followed day-to-day variation in air  $T_a$ . The poor insulation provided by the summer lodge may account for the absence of well-defined changes in lodge  $T_a$  associated with the presence

or absence of transmitter-equipped animals. Despite these findings to the contrary, the presence of muskrats may have contributed in part to the observed elevation of lodge  $T_a$  above both air and water  $T_a$  in summer. However, the fermentation of water saturated, decomposing vegetation comprising the lodge base is probably a more significant source of heat in the summer lodge. Fermentative heat production may be especially important in old winter lodges used as summer residences, in which the vegetation is in an advanced state of decomposition.

Lodge  $T_a$  often exceeded the upper critical  $T_a$  of adults ( $25^{\circ}\text{C}$ ) established from laboratory metabolic studies (Hart 1962; McEwan et al. 1974). In fact, lodge  $T_a$  in July often approached  $30^{\circ}\text{C}$ ; a  $T_a$  which in the laboratory induces behavioral responses associated with heat stress (Part III). The unloading of excess metabolic heat at such temperatures in the field would be hindered further by the high relative humidity (assumed to be close to 100 percent) encountered in the nest chamber.

This potential thermal stress would therefore favor the use of open nests and shallow burrows in mid-summer, and some indication of this was obtained from telemetry studies (Part II). There is also limited evidence in the literature that lodges of non-breeding individuals deteriorate, and are sometimes abandoned in favor of these alternate shelters (Errington 1963; McLeod et al. 1951; Fuller 1951).



It was frequently observed that well-kept summer lodges contained litters of young, and this and other studies (Errington 1963; McLeod et al. 1951; Wragg 1953) indicate that the primary role of these structures is probably associated with reproduction. The thermoneutral zone of young mammals often exceeds the upper critical  $T_a$  established for adults (Hull 1973), and a positive correlation between growth rate and rearing  $T_a$  has been demonstrated in other rodents (Knudson 1962; Reading 1962). Therefore, the high, relatively stable  $T_a$  characteristic of the summer lodge may be conducive to the survival and growth of young muskrats.

#### Winter Microenvironment

As in summer, the configurations of the two types of winter lodges were comparable to those described in the literature (Johnson 1925; Dozier 1948; Bellrose 1950; Fuller 1951). Casual observations in this and previous studies (Johnson 1925; Sather 1958; Errington 1963) indicate that the major period of lodge construction is late summer and autumn, when photoperiod and air and water temperatures are rapidly declining. This is consistent with the observation that nest-building behavior by rodents in the laboratory is enhanced at low air temperatures (Kinder 1927; Sealander 1952). Such conclusions raise the possibility that northern populations of O. zibethicus construct larger, better insulated lodges than their

southern counterparts. In fact, there was some indication that lodges in Delta Marsh had thicker walls (28 to 78 cm) than winter lodges examined by Dozier (1948) in the southeastern United States (wall thickness = 10 to 31 cm), though similar to values (30 to 61 cm) obtained by Bellrose (1950) in Illinois. It is also evident that the insulative value of the dwelling lodge is maximal in winter, when it may be improved further by a heavy mantle of snow.

The tendency for fewer, and significantly larger chambers to be present in winter as opposed to summer lodges, may be interpreted as an adaptation for accommodating a greater number of animals in winter. This finding, combined with telemetry observations of variable numbers of muskrats (1 to 6) occupying a given winter lodge (Fig. 6), and aggregation studies in the laboratory (Part III), all suggest that huddling behavior plays a key role in the overwintering survival of this species. Certainly one would expect the elevation in nest  $T_a$  (mean increase =  $9.4^{\circ}\text{C}$ ) resulting from group occupation of a winter lodge to be of thermal significance to the animals. Moreover, as the data presented in Figs. 6 and 7 suggest, short-term changes in lodge  $T_a$  may actually provide reliable indices of group activity patterns in winter.

The appearance of one or more new chambers beneath the original one in late winter has also been observed by Errington (1963) in association with water recession

beneath the ice. This vertical stratification of chambers may reflect a need to maintain a close physical association with open water in order to benefit from the thermal-buffering influence of the latter. Alternatively, though less likely, the appearance of additional chambers may reflect a severe food shortage associated with freeze-out. Freezing of the marsh bottom may curtail access to rooted aquatic vegetation (Hamerstrom and Blake 1939; Errington 1963; Revin 1975), forcing animals to undermine and consume the lodge base, while leaving the upper portions (and hence insulation) intact. Freeze-out may also be responsible for the progressive abandonment of pushups through the winter, a phenomenon also observed on the Mackenzie Delta, North-West Territories, Canada (Stevens 1953). Owing to shallow water in Delta Marsh, freeze-out is probably a common occurrence in late winter, and has been considered a major source of mortality in this marsh in the past (McLeod et al. 1951; Errington 1963).

It appeared from this study that muskrats have a strong aversion to cold air, and will readily seal external breaks in ice layers overlying air spaces where the animals feed (Fig. 2H). There is some contention, however, as to whether or not muskrats maintain an open hole in the ice in early winter, or must rely on natural breaks for pushup construction (Fuller 1951; Stevens 1953). In the present study, it appeared that both methods were used. The sequence depicted in Fig. 2E

through 2G is thought to reflect the development of the pushup type with a dry resting shelf (Fig. 2G). Continual usage of a rudimentary pushup (Fig. 2E) probably results in chamber and plungehole enlargement (Fig. 2F). With the onset of cold weather, a skim of ice might readily form over the widened plungehole. The animals may then gain access to the chamber by gnawing a hole through one side of the old plungehole, leaving the remaining skim of ice intact to serve as a resting place.

Few published data exist concerning the orientation of lodges and pushups, although Fuller (1951) and Stevens (1953) noted that pushups often radiated away from the lodge or burrow in straight lines. Stevens (1953) also observed that the mean distance between associated pushups was 36.6 m, which is very close to the mean distance between lodges and pushups in the present study (38.7 m). These values may represent optimal, long-range distances over which the animals can safely swim beneath the ice. The spacing of feeders and pushups appears to be highly adaptive, in that the animals have access to all points in their home range via a series of relatively short excursions in cold water (see Part IV). The animals can replenish their oxygen stores at these points, and in some cases, climb out of the water to feed and rewarm in an equable microclimate.

### Seasonal Variation in Microclimate

The thermal-moderating influence of shelters used by O. zibethicus is clearly revealed in seasonal comparisons of macroclimatic and microclimatic temperatures. Between November, 1973, and July, 1975, the maximum range in air  $T_a$  in Delta Marsh was 73°C (-39 to 34°C). During this same period, the maximum range in microclimatic  $T_a$  recorded from within lodges, burrows, and pushups was only 39°C (-9 to 30°C). Moreover, the range of mean temperatures (3 to 25°C) recorded from within occupied dwelling lodges and burrows in summer and winter (Tables 4 and 5) was very close to thermal neutral zone (10 to 25°C) reported for this species (Hart 1962; McEwan et al. 1974).

In conclusion, O. zibethicus appears to minimize energy expenditure for temperature regulation through the construction and selective use of multiple shelters. The thermoregulatory significance of this behavior is greatest in winter when muskrats rest and feed in closely-spaced lodges and pushups. In contrast, shelter requirements are much reduced in summer, and lodge use by adults seems to be minimal during this season.

## PART II

Daily and Seasonal Patterns of Activity and Body Temperature  
in Free-Ranging Muskrats (Ondatra zibethicus)

## INTRODUCTION

Avoidance of climatic extremes through nest construction, huddling behavior, and activity reduction, are all believed to constitute major energy-conserving adaptations in northern small mammals (Sealander 1952; Hayward 1965; Muul 1968; Hart 1971). The thermoregulatory significance of multiple shelter construction and group occupation of winter lodges by Ondatra zibethicus was emphasized in Part I. Those behavioral adaptations undoubtedly account in large measure for the broad geographic distribution of this species (Storer 1937; Errington 1963).

Although data pertaining to the physical attributes of the microhabitat provide an index of the microclimatic range encountered by O. zibethicus, interpretation of their significance requires a knowledge of daily activity patterns, and the extent to which various types of shelters are utilized. Evaluation of activity in relation to external weather conditions may also provide evidence regarding the tempering effect of the microhabitat in shielding animals from macroclimatic extremes in winter.

Even more important, the need for the muskrat to forage periodically in near-freezing water in winter may pose potential problems of hypothermia. Previous laboratory studies (Hart 1962; Shcheglova 1965) indicating

that the muskrat has poor thermoregulatory capabilities in water seem inconsistent with field observations of under-ice foraging at subarctic latitudes (Fuller 1951; Stevens 1953). Such observations imply that the prevention of hypothermia during winter foraging may be largely behavioral.

It is the objective of the present study to: (1) characterize the nature of the daily activity pattern in free-living O. zibethicus in summer and winter, (2) examine the correspondence between daily activity and local meteorological conditions, and (3) study the relationship between activity and body temperature dynamics under field conditions. The latter investigation should clarify further the role of behavior in maintaining thermal homeostasis, and also shed light on the precision of body temperature regulation in nature.





## MATERIALS AND METHODS

### Study Area

Observations were made in the western sector of Delta Marsh, located on the southern end of Lake Manitoba, Canada ( $50^{\circ}11'N$ ;  $98^{\circ}23'W$ ). Vegetation and topography were described in Part I.

### Collection of Animals

A total of 27 muskrats of both sexes was used in this study. Sixteen (subadults and adults) were live-trapped during November, 1973, and October, 1974; the remaining 11 (3 juveniles and 8 adults) were obtained during June, 1974, 1975, and July, 1975. Trapping was done with National Live Traps (16.5 x 16.5 x 48.3 cm). In November, 1973, trapping was conducted principally at pushup sites. This involved placing an unbaited trap on the ice adjacent to the exposed plunge hole, and carefully darkening and insulating the entire set with burlap, styrofoam, and snow. In October, and during the summer months, traps baited with apple and carrot were placed directly on the side of the lodge wall, or at feeding stations along the shoreline.

The distinction between subadults and adults on the basis of size differences (Errington 1963) was not always clear, and for the sake of brevity, these age groups are collectively referred to as adults.

### Activity and Body Temperature Determination by Telemetry

The majority of activity, and all body temperature ( $T_b$ ) determinations were obtained via radio-telemetry. The transmitter used in this study was hand-constructed according to the circuit diagram published by Wang (1972). Each transmitter, complete with mercury battery, was encapsulated in the lower (4 cm) section of a disposable 10 cc syringe barrel, and all openings were sealed with epoxy resin. This unit was then dipped repeatedly into molten wax (50 percent beeswax; 50 percent paraffin) to provide a smooth, waterproof, and relatively inert exterior (Mackay 1970). The completed transmitter measured approximately 2 x 2 x 4 cm and weighed 14 to 20 g, which was less than 3.5 percent of body weight in all cases.

The continuous tone emitted by each transmitter was received at a specific carrier frequency (88 to 108 MHz) on the FM band of a transistor radio (Sony AM/FM Cassette-Recorder, Model CF-350 and CF-400). Transmission was highly directional, with a range through air of 15.5 to 30.5 m. The transmitter circuit incorporated a diode temperature sensor, and the frequency of the emitted signal was temperature dependent. Each transmitter was calibrated in a stirred waterbath at 1 to 2°C intervals prior to implantation in the animal. Frequency was determined with an audio generator (RCA, Model WA 44C) that permitted temperature differentiation to within  $\pm 0.2^\circ\text{C}$ . At least

two calibrations, 1 to 2 weeks apart, were performed on each transmitter, with the final calibration being completed within 1 week prior to implanting.

Each transmitter was surgically implanted into the abdominal cavity of the muskrat while the animal was under sodium pentobarbital anaesthesia (30 mg/kg body weight), supplemented with ether (anaesthesia grade). The transmitter was free-floating within the abdominal cavity, and the peritoneal and skin incisions were closed with katgut and silk sutures, respectively. Surgery was performed within 12 hours of capture, and each animal was released at the site of capture within 24 hours of completion of the operation.

Of 46 muskrats implanted with transmitters, only 27 provided useful data. The remaining 19 either disappeared from the study area shortly after implantation, or re-located at sites in the marsh that were impractical to monitor on a regular basis. All nine bank-burrowing muskrats equipped with transmitters in October, 1974, for example, emigrated from the burrow system within 1 to 2 weeks of release, and only one was subsequently located in a lodge 400 to 500 m away. Sporadic data obtained from such animals were not included in this study.

Although transmitters which showed signs of calibration drift in the laboratory were not used, there was some indication of long-term drift (less than 2.5°C over 1 to 3 months) in the field during the winter of 1974-75.

This conclusion is based on the gradual increase in  $T_b$  that was observed in some animals through the winter, and also on the unusually high temperatures recorded from these same individuals in mid-winter. Based on calibration drift in the laboratory, however, new calibration slopes were similar to original slopes. In no case did the average rate of drift in the laboratory exceed  $0.05^{\circ}\text{C}/\text{day}$ , which is well beyond the resolution accuracy of temperature determination. To avoid complication due to potential drift, much of the 1974-75  $T_b$  data has therefore been expressed as deviation ( $\pm$ ) from mean daily  $T_b$ . Observed body temperatures for individuals of both sexes and various body weights are summarized in Appendices 4 and 5.

Three basic methods of monitoring activity and  $T_b$  via telemetry were employed. First, to provide an overview of activity and  $T_b$  patterns, a census technique was used, in which as many animals as possible were located at periodic intervals (15 to 240 min) throughout the day. This involved location and continuous surveillance of each animal (often with visual contact in summer) for at least 5 min, and recording of the emitted tone on magnetic tape (Sony Cassette-Recorder) for future  $T_b$  analysis. Very slight movement by the animal resulted in detectable amplitude fluctuations on the receiver, and swimming or diving activity often produced a distinctive rhythmic tone, which aided in activity evaluation. Although triangulation techniques were not used to pinpoint

locations, the low range of the transmitter, coupled with careful lateral movements of the receiving antenna about the point of maximum signal strength, permitted detection of a stationary animal to within approximately  $\pm 4.0$  m in summer. The position of a muskrat was often verified by visual location of the same individual during the period of open water. In winter, the well-defined, discrete nature of the microhabitat (Part I) permitted detection of animals to within approximately  $\pm 2.0$  m. The location of a rapidly swimming animal was difficult to ascertain in both seasons.

A second method of data collection involved locating an individual animal, and maintaining continuous surveillance for 0.5 to 6.0 hours in order to detect subtle, short-term changes in activity and  $T_b$ .

Thirdly, in November, 1974, an automated monitoring system was implemented, which permitted the recording of activity and  $T_b$  at 5 ( $\pm 0.5$ ) min intervals throughout the day. To accomplish this, a radio receiver was installed in an electrically-heated weather box (Part I) situated 7.6 m from Dwelling Lodge No. 5. The radio was coupled with the lodge via antenna wire (T.V. twin-lead, 300 ohm), and was kept continuously "on," and tuned into one of five transmitter-equipped muskrats inhabiting the lodge. Output from the receiver was relayed via a coaxial microphone lead to a tape recorder (Sony Cassette-Recorder) situated within a heated building, 183 m away. The tape

recorder in turn, was activated at 5 ( $\pm$  0.5) min intervals (10 to 12 sec duration) by means of a timer constructed from a laboratory kymograph. Calibration checks on the timer were made at frequent intervals throughout the day. In most cases, data for a single animal were collected for at least 48 hours before switching to another animal. On occasion, two independent monitoring systems were in operation concurrently. In summer, 1975, the above system was used to monitor a single male occupying Lodge No. 5, and two bank-dwelling muskrats. In the latter case, the weather box housing the receiver was situated on the bank directly above the burrow.

Each signal received indicated presence or absence of the muskrat in the lodge or in its immediate vicinity, and if present, locomotor activity if any, and  $T_b$ . In evaluating excursions away from the lodge or burrow, only those trips of 10 min or more duration (i.e. two or more consecutive recordings indicating absence) were considered. The end of an excursion was identified by two or more consecutive signals indicating the presence of the animal in lodge or burrow. These criteria reduced the error of incorrectly identifying an excursion, or the completion of an excursion, on the basis of only a single, 10 to 12 sec recording.

Most telemetry observations have been expressed in terms of an hourly "activity index," which is defined as: (total observations per hour in which animal is active/

total observations per hour ) x 100. To evaluate the degree of nocturnalism, another index, the "N/D ratio," was utilized. This index is defined as the ratio of the mean hourly activity index for all hours between the hour of sunset and the hour of sunrise (N)/the mean hourly activity index for all other hours (D).

To assess the daily distribution and frequency of major activity periods, it was necessary to select a criterion for identification of those hours in which activity predominated. The overall, mean hourly activity index for muskrats in summer (39) did not differ significantly from that in winter (42), hence the same criterion was used in both seasons. Accordingly, each hour in which the activity index is greater than, or equal to 50 is defined as a "major activity bout." In a series of consecutive hourly activity indices (a,b,c,...), a "major activity peak" (b) is defined as an hourly activity index that meets the condition:  $a < b > c$ , where  $b \geq 50$ . When there are consecutive values of b ( $a, b_1, b_2, b_3, \dots, c$ ), the largest value is taken as the peak. The frequency of major activity peaks as thus defined, does not differ significantly from that observed when b is designated as any positive deviation from the mean daily activity index (based on each 24-hour period of recording).

### Determination of Winter Activity From Lodge Temperature Changes

Additional data concerning daily activity patterns in winter were obtained from temperature records of dwelling lodges. Details pertaining to lodge instrumentation for ambient temperature ( $T_a$ ) recording, as well as supporting evidence for the use of this method were provided in Part I.

### Microclimate and Weather Data

Hourly recordings of air and water  $T_a$  were obtained with thermistors connected to a Grant Miniature Temperature Recorder as described in Part I. In addition, maximum-minimum air  $T_a$ , precipitation, windspeed 10 m above ground level, and total hours of bright sunshine were available from the University of Manitoba Field Station, situated within 2.5 km of all observation sites.



## RESULTS

### Extent of Home Range

Activity in summer was often restricted to the immediate vicinity of a lodge or burrow (Fig. 1). In fact, 61 percent of all observations of activity ( $n = 577$ ) made in June and July, 1974 (5 adults; 3 juveniles), occurred within a 25 m radius of a lodge or burrow. Daily movements away from these shelters rarely exceeded 230 m in either adults or juveniles. Muskrats also proved highly sedentary in winter, with 50 percent or more of all activity occurring within a 15 m radius of the resident lodge, and few movements exceeding 150 m (Part IV).

### Daily Activity Pattern

Observations of 8 adult (7 males; 1 female) and 3 juvenile (all males) muskrats in summer (June and July, 1974, 1975) indicated periodic activity throughout the day, with peak levels of activity usually occurring between sunset and sunrise (Figs. 1 and 2). A bimodal trend in summer activity is suggested for adults in 1974 data (Figs. 1A and 1B); and is clearly discernible in the frequency distribution of major activity bouts of 1975 adults (Fig. 2B). There was no indication of bimodality in juvenile data (Fig. 1C).

Figure 1. Daily activity and body temperature patterns of O. zibethicus in summer, based on census data collected at 15 to 240 min intervals.

- A - Combined data for three lodge-dwelling, adult muskrats (Nos. 12, 15, 16) monitored June 18-25, 1974 (n = 223 observations)
- B - Combined data for two burrow-dwelling, adult muskrats (Nos. 13, 14) monitored July 8-30, 1974 (n = 332 observations)
- C - Combined data for three burrow-dwelling, juvenile muskrats (Nos. 17, 18, 19) monitored July 19-30, 1974 (n = 405 observations)
- - Mean hourly body temperature, based on all observations obtained within a given hour
- - Hourly index of total activity away from lodge or burrow:  $(\text{Total observations per hour in which animal is active away from lodge or burrow} / \text{Total of all observations per hour}) \times 100$
- ▣ - Hourly index of activity  $\geq 25$  m away from lodge or burrow:  $(\text{Total observations per hour in which animal is active } \geq 25 \text{ m away from lodge or burrow} / \text{Total of all observations per hour}) \times 100$
- - Period of darkness (sunset to sunrise)

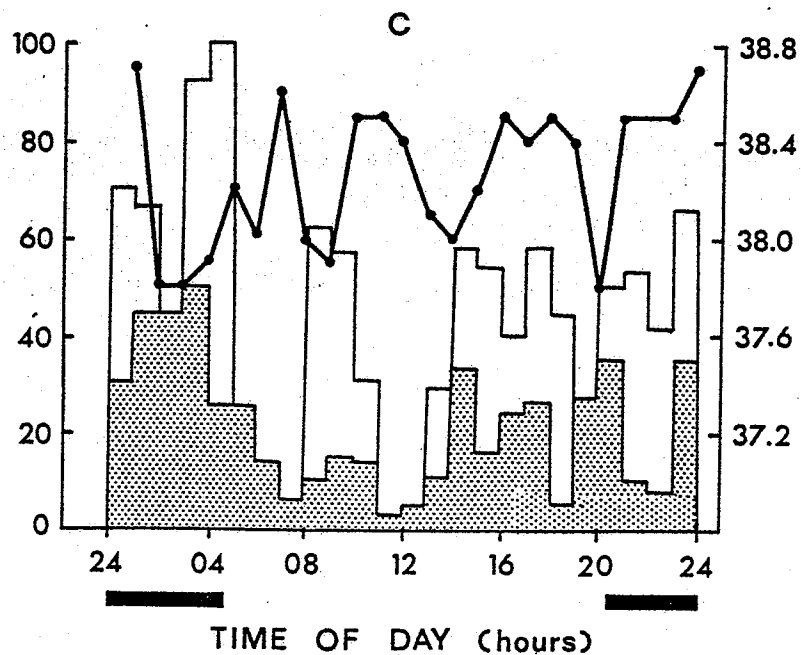
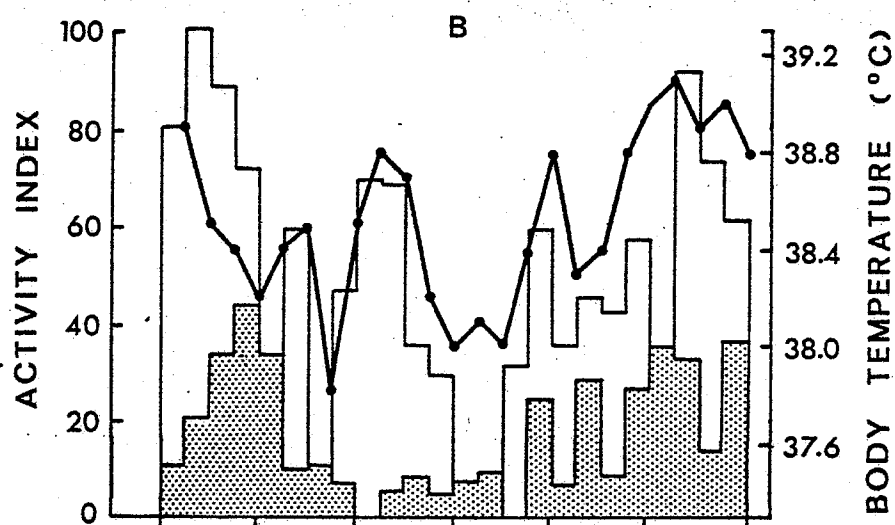
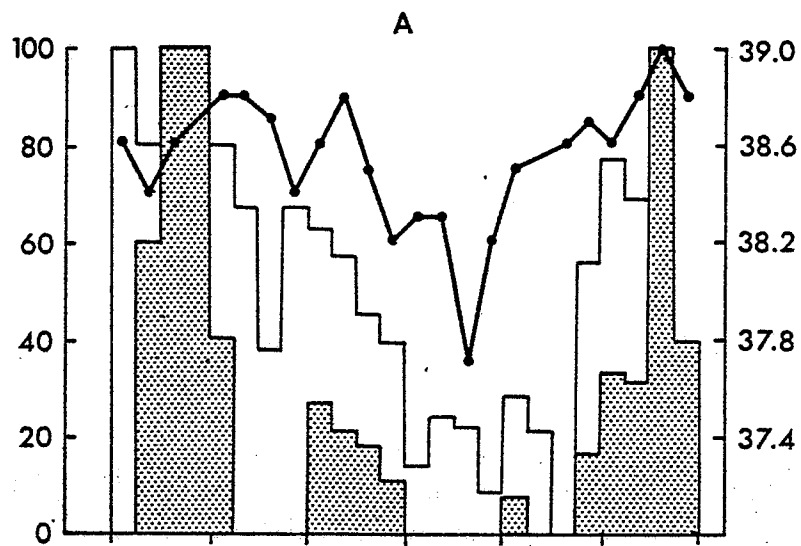
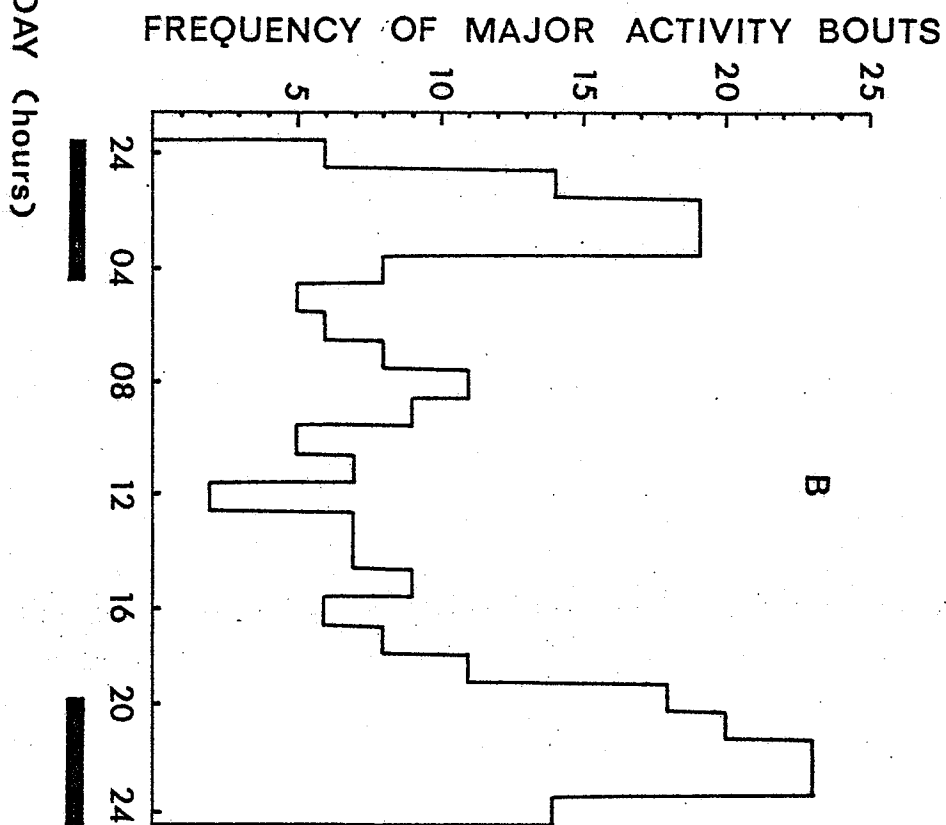
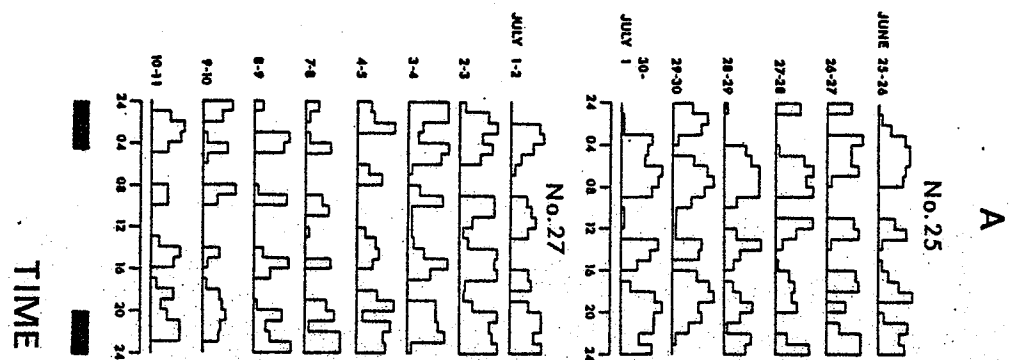


Figure 2A. Representative daily activity patterns of two burrow-dwelling, adult O. zibethicus (Nos. 25 and 27) remotely monitored at 5 ( $\pm$  0.5) min intervals in summer, 1975 (n = 14 days). For each 24-hour period, each bar depicts a mean hourly activity index based on all observations (11 to 13) made within a given hour. Additional 24-hour records are provided in Appendix 6A.

Figure 2B. Frequency distribution of major activity bouts (hourly activity indices  $\geq 50$ ) of all adult O. zibethicus (Nos. 25, 26, 27) remotely monitored at 5 ( $\pm$  0.5) min intervals in summer, 1975 (n = 32 days).



- Period of darkness (sunset to sunrise)



As in summer, muskrats in winter tended to be periodically active throughout the day (Figs. 3, 4, and 5). However, there was less evidence of bimodality in the frequency distribution of major activity bouts during the latter season (Fig. 4B). Maximal levels of activity generally occurred in late afternoon and early evening (1500 to 2000 hours) in winter. This trend is especially pronounced in lodge  $T_a$  data (Fig. 6), where the afternoon activity peak (maximum negative deviation from mean daily lodge  $T_a$ ) is accentuated as winter advances, while the early morning peak is gradually dampened.

Census data collected from 10 muskrats at hourly intervals during 2 days prior to, and during 2 days subsequent to the development of a persistent winter ice cover on Nov. 14-15, 1974, failed to demonstrate any major changes in activity pattern associated with freeze-up (Fig. 5). There was however, a significant reduction in the mean hourly activity index from 65 prior to freeze-up to 48 after freeze-up ( $t = 2.84$ ,  $P < .05$ ).

Nocturnalism was most pronounced in summer, when the N/D ratio was 1.96 for all census data ( $n = 8$  muskrats), and 1.94 for the automated series ( $n = 3$  muskrats). In winter, this ratio was 1.20 for 1974-75 ( $n = 10$  muskrats) census data, and 1.31 for the automated series in 1974-75 ( $n = 5$  muskrats). The summer and winter N/D ratios for the automated series (Tables 1 and 2) were significantly different ( $t = 3.8$ ,  $P < .01$ ).

Figure 3. Mean hourly activity and body temperature fluctuations in O. zibethicus (Nos. 20, 21, 22, 24) in relation to time of day in winter, 1974-75. Automated recordings were made at 5 ( $\pm 0.5$ ) min intervals, and data for all four muskrats are combined over the days indicated in each graph.

- - Mean hourly deviation ( $\pm$ ) from mean daily body temperature (based on deviations from daily means for each animal)
- - Mean hourly activity index
- - Period of darkness (sunset to sunrise)

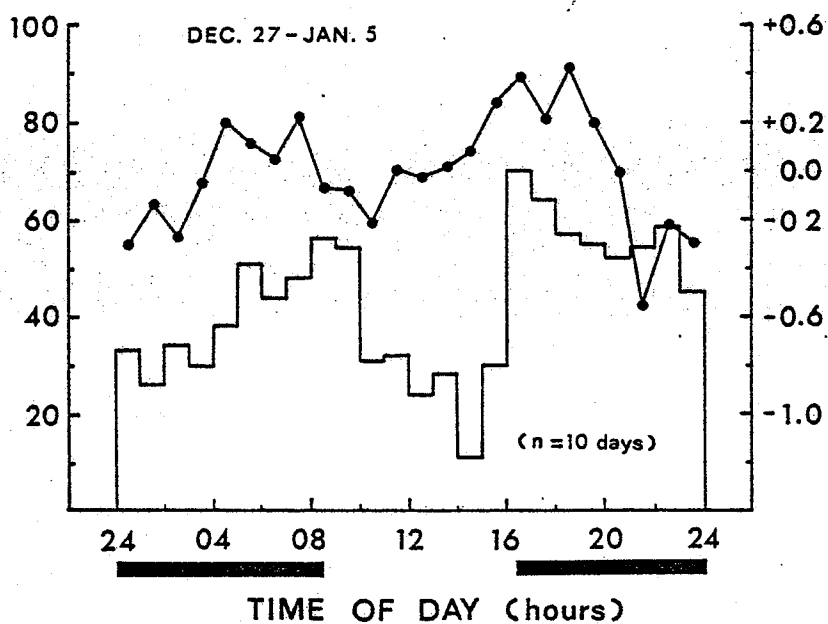
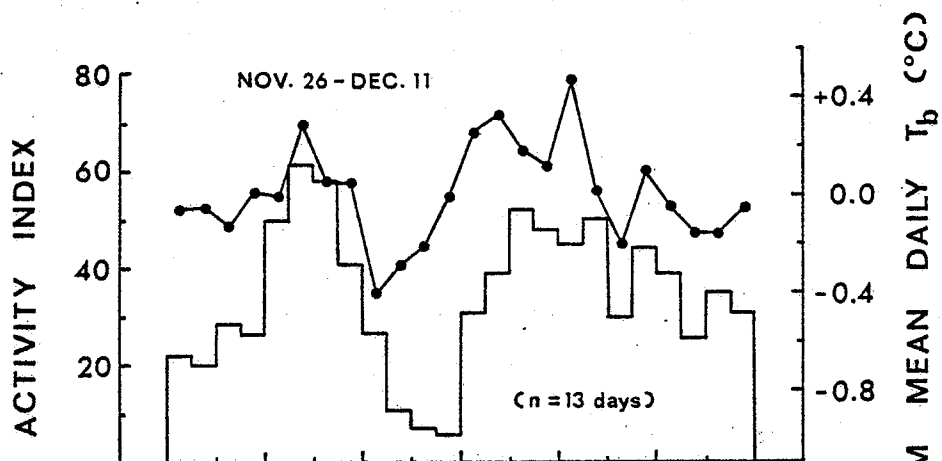
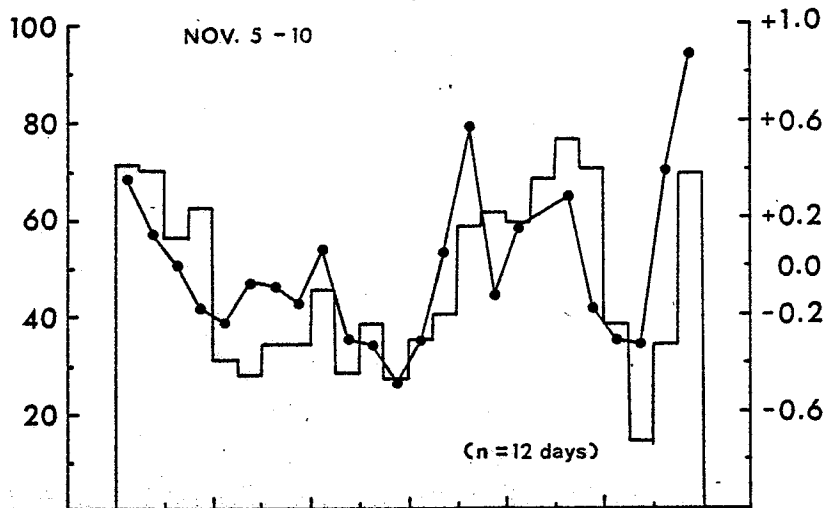
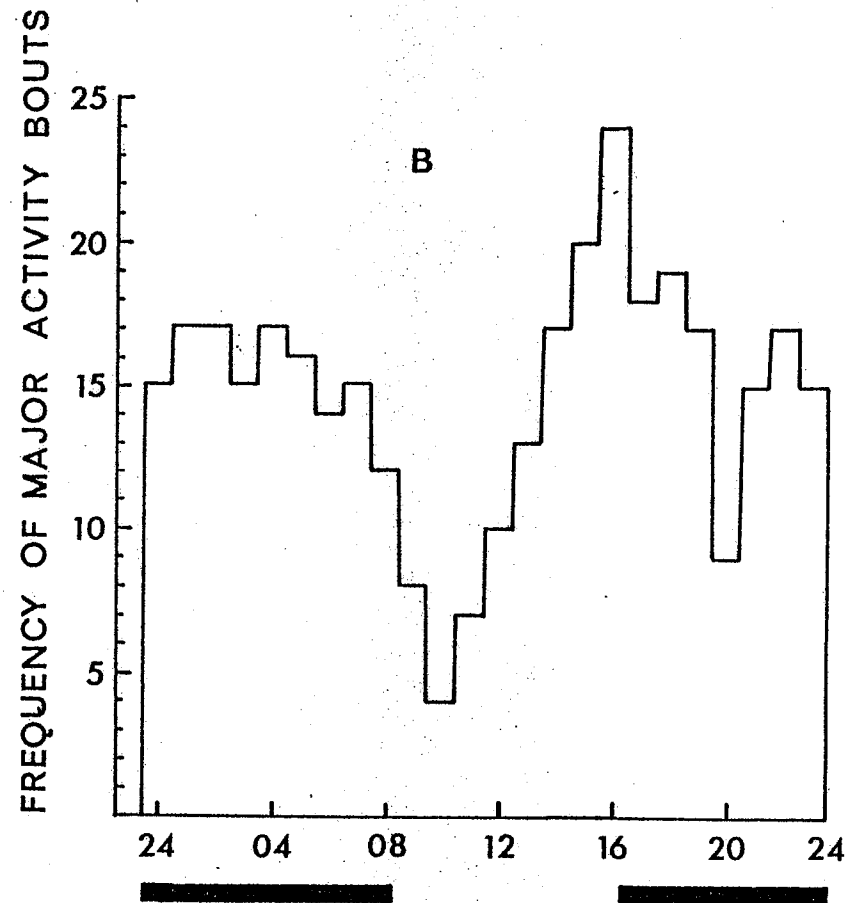
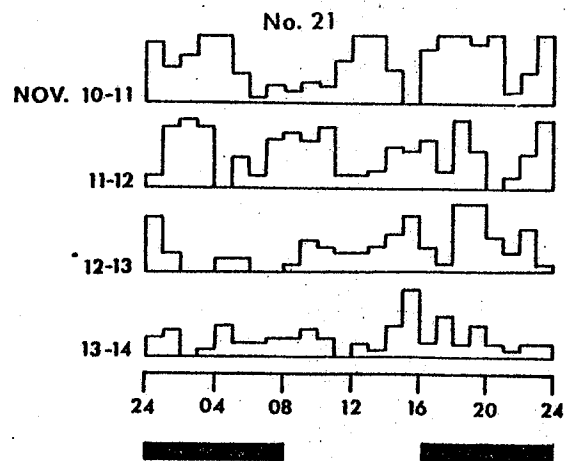
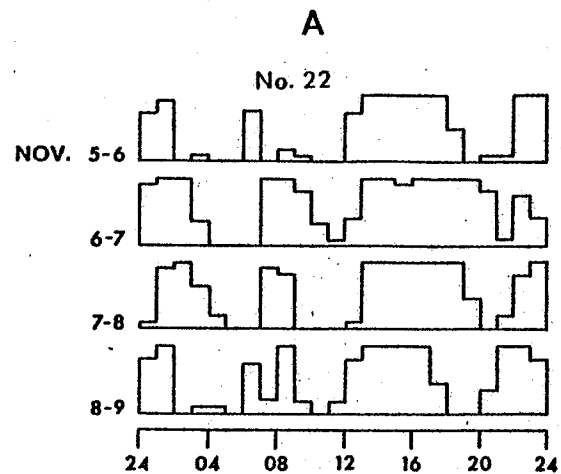




Figure 4A. Representative daily activity patterns of two O. zibethicus (Nos. 21 and 22) occupying Lodge No. 5, and remotely monitored at 5 ( $\pm 0.5$ ) min intervals in winter, 1974 (n = 8 days). For each 24-hour period, each bar depicts a mean hourly activity index based on all observations (11 to 13) made within a given hour. Additional 24-hour records are provided in Appendix 6B.

Figure 4B. Frequency distribution of major activity bouts (hourly activity indices  $\geq 50$ ) of five O. zibethicus (Nos. 20 to 24, inclusive) remotely monitored at 5 ( $\pm 0.5$ ) min intervals in winter, 1974-75 (n = 37 days).

■ - Period of darkness (sunset to sunrise)



TIME OF DAY (hours)

Figure 5. Daily activity patterns of O. zibethicus in early winter, just prior to (Nov. 6-7, 10-11) and shortly after (Nov. 17-18, 29-30) the development of a persistent ice cover on Nov. 14-15, 1974. Ten animals were censused at hourly intervals throughout each of the above 4 days, and data were pooled for each 2-day period.

- ☐ - Hourly activity index prior to freeze-up  
(mean hourly air  $T_a = 3.0^{\circ}\text{C}$ ;  $n = 48$ )
- ☒ - Hourly activity index after freeze-up  
(mean hourly air  $T_a = -10.0^{\circ}\text{C}$ ;  $n = 48$ )
- ☒ - Period of darkness (sunset to sunrise)

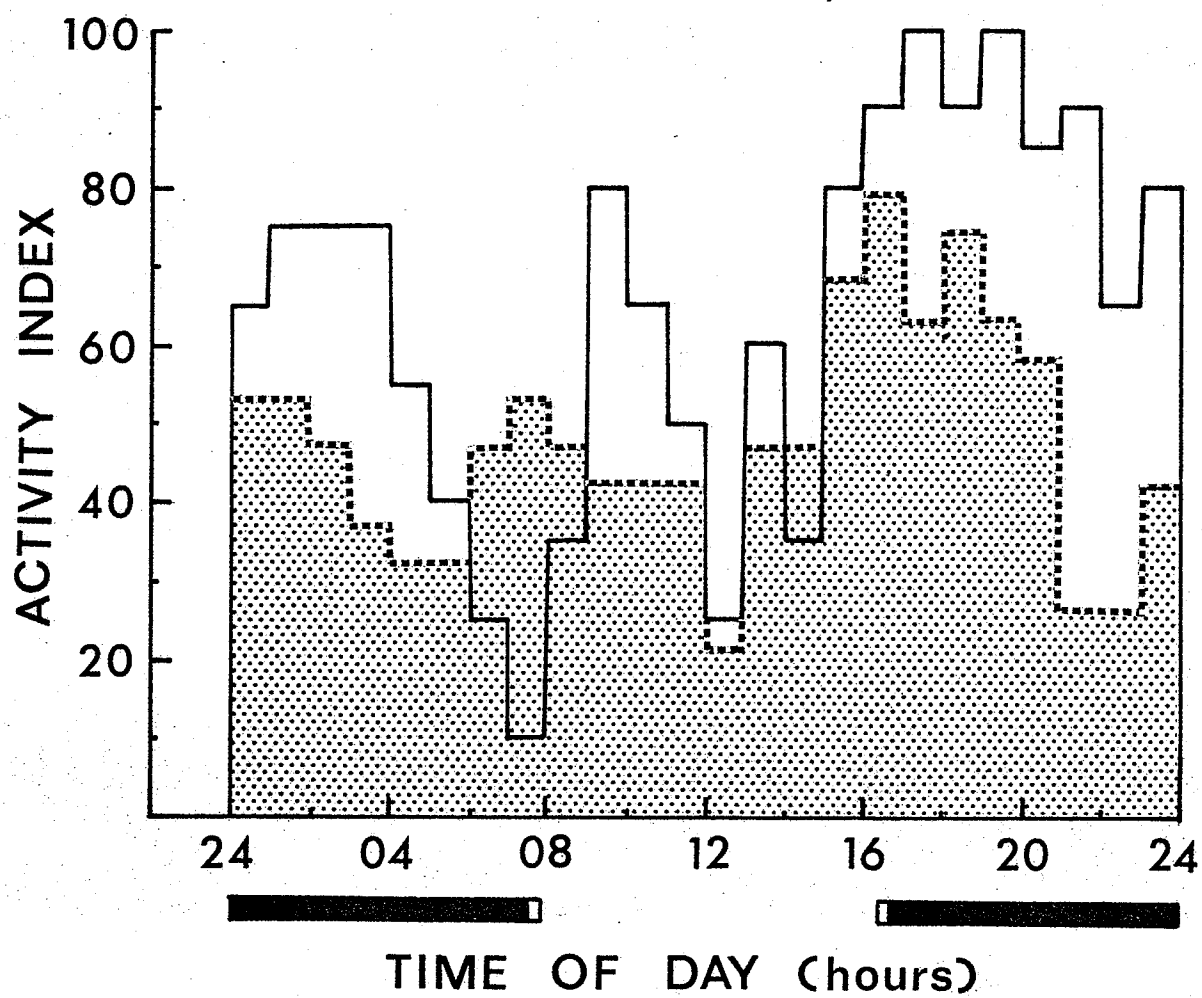
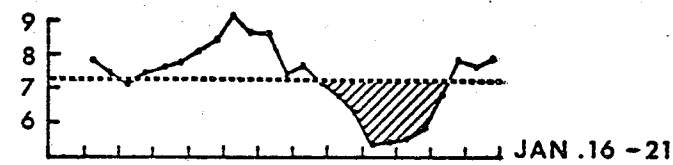
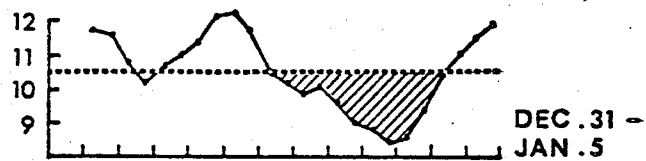
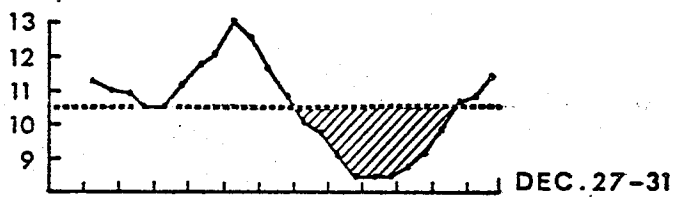
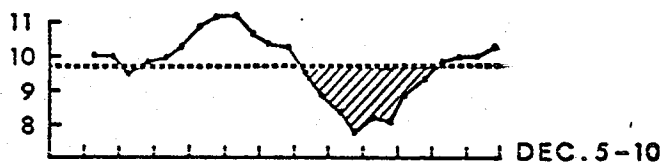
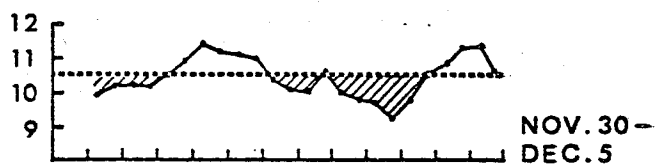
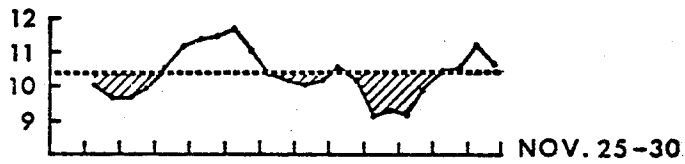
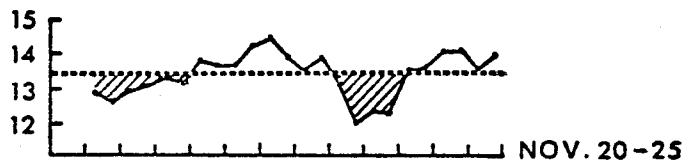


Figure 6. Changes in the daily activity pattern of a group of O. zibethicus occupying Lodge No. 4 between Nov. 20, 1974, and Jan. 21, 1975, as determined from hourly recordings of lodge  $T_a$ . For each 4- or 5-day observation interval, each point depicts the mean of 4 or 5 hourly recordings (averaged across days). Periods of presumed maximal activity away from the lodge are indicated as negative deviations (hatched areas) from the overall, 24-hour mean (dashed line). Additional examples are provided in Appendix 7.

■ - Period of darkness (sunset to sunrise)

# LODGE NO. 4

LODGE TEMPERATURE (°C)



24 04 08 12 16 20 24

TIME OF DAY (hours)

Table 1. Activity variables of O. zibethicus remotely monitored at 5 ( $\pm$  0.5) min intervals per 24-hour period in summer, 1975

Animal No.	Sampling Period (n days)	Time in lodge or burrow per day in hours	Excursions		Hourly Activity Index	N/D Ratio	STC <sup>a</sup> in hours
			Freq. per day	Dur. in min			
25	June 25-July 1 (6)	12.6(.64) <sup>b</sup> 10.3-14.3	12.0(.82) 9-15	57.0(7.37) 41.5-89	40.0(3.0) 34-50	0.92(.19) 0.44-1.50	6.0(.45) 2-11
26	June 7-15 <sup>c</sup> (8)	10.0(1.52) 2.6-16.3	11.5(.84) 6-14	79.6(22.0) 39-230	51.0(6.0) 27-86	1.55(.20) 0.83-2.44	5.7(.43) 2-9
27	June 11-July 11 (23)	14.4(0.39) 9.6-18.2	13.4(.91) 7-22	45.9(3.35) 21.5-83	34.0(1.0) 23-52	2.34(.11) 1.58-3.21	5.7(.26) 2-15
All Nos. Combined	(37)	13.1(.51) 2.6-18.2	12.8(.61) 6-22	55.0(5.56) 21.5-230	39.0(2.0) 23-86	1.94(.12) 0.44-3.21	5.8(.20) 2-15

<sup>a</sup>Short-term cycle of activity and rest

<sup>b</sup>Mean (standard error)  
Range

<sup>c</sup>Excluding period June 10-13 for calculation of STC

Table 2. Activity variables of *O. zibethicus* remotely monitored at 5 ( $\pm$  0.5) min intervals per 24-hour period in winter, 1974-75

Animal No.	Sampling Period (n days)	Time in lodge or burrow per day in hours	Excursions		Hourly Activity Index	N/D Ratio	STC <sup>a</sup> in hours
			Freq. per day	Dur. in min			
20	Nov. 16-Jan. 5 (11)	17.6(.63) <sup>b</sup> 13.9-20.2	8.3(.87) 4-13	65.5(12.5) 20-130.5	28.0(2.0) 20-43	1.41(.33) 0.37-3.28	7.1(.74) 2-16
21	Nov. 10-Jan. 4 (10)	13.4(1.3) 7.8-18.2	11.0(.93) 6-14	42.9(6.3) 22.5-74.5	43.0(6.0) 25-69	1.05(.13) 0.50-1.88	5.2(.42) 2-11
22	Nov. 5-Jan. 2 (9)	10.0(.47) 7.2-11.6	5.0(.62) 3-8	158.4(20.8) 100-250	55.0(2.0) 50-66	1.46(.18) 0.66-2.13	7.3(.60) 2-13
23	Nov. 14-16 (2)	13.1(1.17) 11.9-14.2	7.5(.5) 7-8	68.5(18.5) 50-87	41.0(6.0) 35-48	1.50(.22) 1.28-1.72	5.3(.73) 3-9
24	Nov. 16-Jan. 1 (6)	11.7(1.14) 8.8-15.8	9.2(1.9) 4-18	92.9(23.1) 44-190	50.0(5.0) 33-64	1.36(.26) 0.62-2.24	6.0(.50) 3-10
All Nos. (37) Combined		13.6(.65) 7.2-20.2	8.4(.59) 3-18	83.2(9.8) 20-250	42.0(2.0) 18-69	1.31(.10) 0.37-3.27	6.2(.28) 2-16

<sup>a</sup> Short-term cycle of activity and rest

<sup>b</sup> Mean (standard error)  
Range






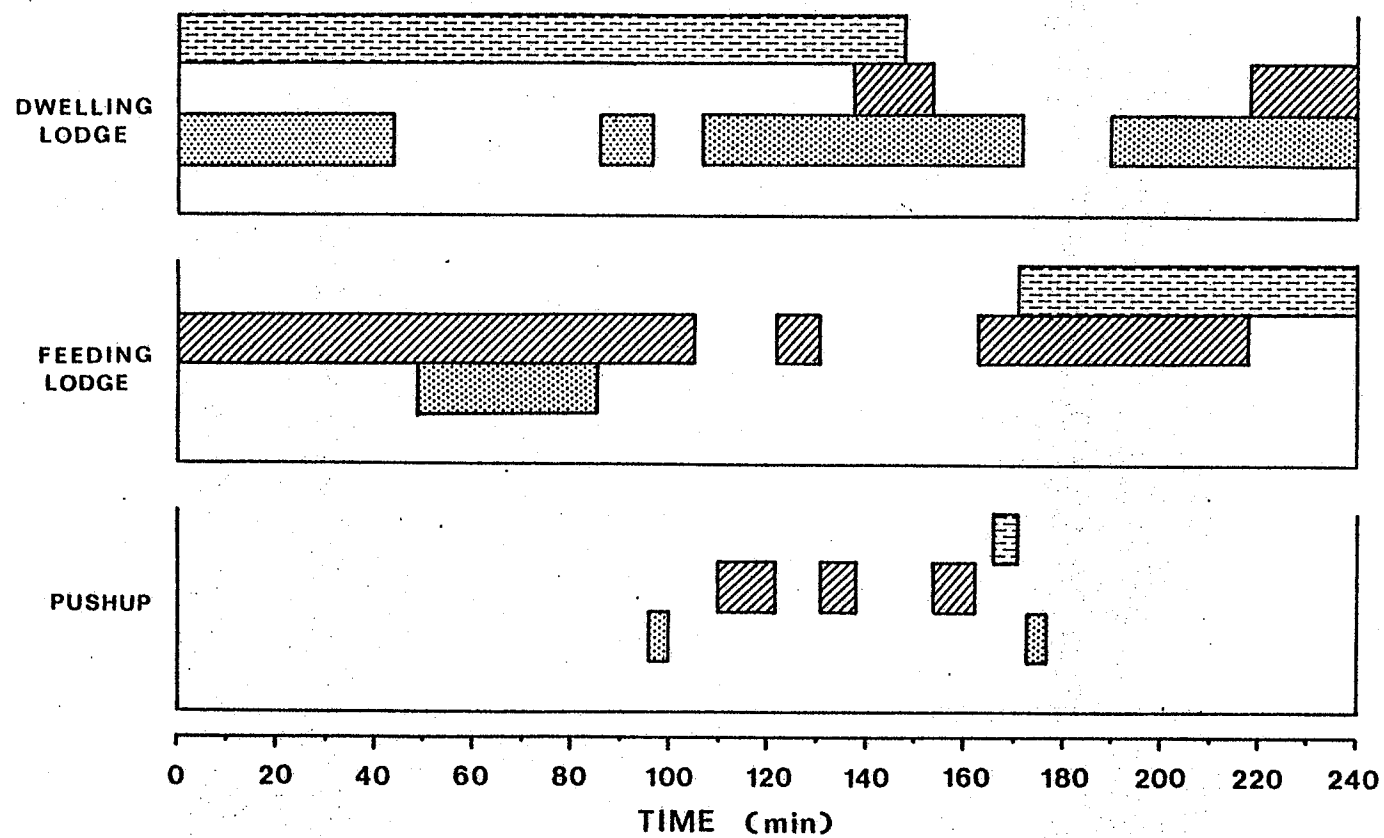
Day-to-day variation in the activity patterns of individual animals is apparent in both summer (Fig. 2A) and winter (Fig. 4A). Inter-individual variation is also suggested by these data, and is clearly evident in Fig. 7. This figure indicates that temporal variation in activity within an overwintering group of muskrats may result in partial staggering of lodge and pushup use.

Despite the above variability, a short-term cycle of activity and rest (STC) is strongly suggested in the 24-hour activity patterns of single animals (Figs. 2A and 4A). The mean period length of this cycle (based on the time span between successive, major activity peaks) was 5.8 hours (range = 2 to 15 hours) in summer, and 6.2 hours (range = 2 to 16 hours) in winter (Tables 1 and 2). In four cases involving Muskrat Nos. 14 and 19 in which continuous surveillance was maintained through a complete cycle of activity and rest in July, 1974, the STC varied between 5.0 and 5.5 hours.

The automated series also indicated that each STC consisted of one or more excursions away from the resident lodge or burrow. The mean daily frequency of excursions was 12.8 (range = 6 to 22) in summer and 8.4 (range = 3 to 18) in winter, with a mean duration of 55 min (range = 22 to 230 min) in summer and 83 min (range = 20 to 250 min) in winter (Tables 1 and 2). A hyperbolic relationship was observed between the daily frequency and mean daily duration of these excursions. When these data were

Figure 7. Short-term patterns of shelter use by three O. zibethicus (Nos. 7, 10, 14) overwintering together in a single dwelling lodge with its associated feeding lodge (distance = 18.3 m) and pushup (distance = 23.8 m). Horizontal bars denote approximate times in, or in the immediate vicinities of the above shelters. Observations were made at 5 to 15 min intervals on Dec. 4, 1974 (1404 to 1804 hours).

-  - Muskrat No. 7
-  - Muskrat No. 10
-  - Muskrat No. 14



transformed to logarithmic values (Fig. 8), the summer and winter regression slopes were not significantly different (Covariance Analysis,  $F = 1.30$ ,  $P > .05$ ). Similarly, the mean cumulative time spent in the lodge or burrow per day in summer (13.1 hours) was not significantly different ( $t = 1.07$ ,  $P > .05$ ) from that (13.6 hours) observed in winter (Tables 1 and 2).

#### Daily Activity in Relation to Environmental Factors

Simple regression analysis of daily activity (automated series) in relation to various meteorological variables was performed on pooled summer (3 muskrats; 29 days) and on pooled winter (5 muskrats; 37 days) data. To test for possible differences due to ice and snow cover in winter, these regressions were also calculated for the period of open water (Nov. 5-15), and during the interval when cumulative snowfall was less than 10 cm (Nov. 5-Dec. 11).

The above analyses failed to demonstrate strong correlations between either daily frequency or mean daily duration of summer and winter excursions, and daily variation in air and water  $T_a$ , windspeed, photoperiod (time in min between sunset and sunrise), hours of bright sunshine, and precipitation (Tables 3 and 4).

Total time spent in the lodge per day was, however, significantly correlated with photoperiod ( $r = -0.46$ ,  $P < .01$ ) and air  $T_a$  ( $r = -0.33$ ,  $P < .05$ ) between Nov. 5 and Jan. 5, 1974-75 (Table 4). Correlation with air  $T_a$

Figure 8. Logarithmic relationship between the daily frequency of excursions away from the lodge or burrow, and the mean daily duration of these excursions (based on automated recordings at  $5 \pm 0.5$  min intervals).

- - Muskrats monitored Nov. 5-Jan. 5, 1974-75  
(5 animals; 35 days)
- - Muskrats monitored June 7-July 11, 1975  
(3 animals; 37 days)

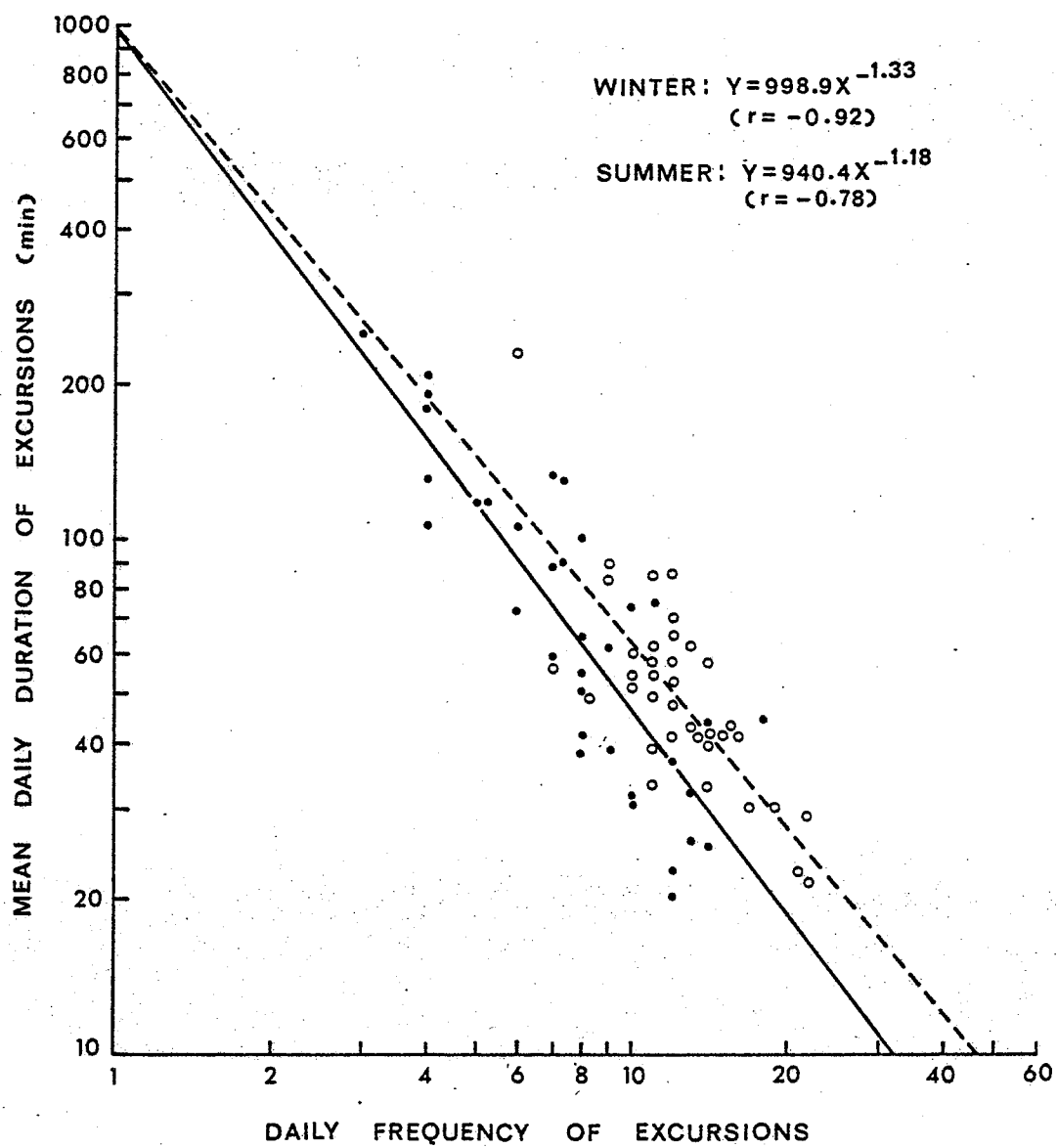


Table 3. Least-Squares regression analysis of activity in relation to environmental variables in summer (June 11-July 11, 1975)

Indep. Var. (X)	Dep. Var. (Y)	N; days <sup>a</sup>	r	t-value
Mean daily air T <sub>a</sub> (°C)	Time in burrow per day	2;29 1;23	-0.20 -0.23	1.06 1.06
	Freq. of excursions per day	2;29 1;23	+0.18 +0.18	0.94 0.94
	$\bar{X}$ daily dur. of excursions	2;29 1;23	-0.01 +0.03	0.04 0.14
Photoperiod (min)	Time in burrow per day	2;29 1;23	-0.53 -0.55	3.28** 3.01**
	Freq. of excursions per day	2;29 1;23	+0.36 +0.42	1.99* 2.13*
	$\bar{X}$ daily dur. of excursions	2;29 1;23	-0.02 -0.08	0.08 0.36
Hours of bright sunshine per day	Time in burrow per day	2;29 1;23	-0.13 -0.04	0.58 0.20
	Freq. of excursions per day	2;29 1;23	-0.03 0.00	0.14 0.03
	$\bar{X}$ daily dur. of excursions	2;29 1;23	0.00 +0.04	0.03 0.16
Mean daily windspeed (mph)	Time in burrow per day	2;29 1;23	+0.37 +0.41	2.06* 2.08*

<sup>a</sup>

Number of animals (Nos. 25, 27); number of days monitored

\*P < .05

\*\*P < .01

Table 4. Least-Squares regression analysis of activity in relation to environmental variables in winter (Nov. 5-Jan. 5, 1974-75)

Indep. Var. (X)	Dep. Var. (Y)	Period <sup>a</sup> (N; days)	r	t-value
Mean daily air T <sub>a</sub> (°C)	Time in lodge per day	Nov.5-Jan.5(5;37)	-0.33	2.09*
		Nov.5-Nov.15(3;9)	-0.81	3.65**
		Nov.5-Dec.11(5;27)	-0.53	3.16**
	Freq. of excursions per day	Nov.5-Jan.5(5;37)	+0.12	0.72
		Nov.5-Nov.15(3;9)	-0.47	1.42
		Nov.5-Dec.11(5;27)	0.00	0.01
	$\bar{X}$ daily dur. of excursions	Nov.5-Jan.5(5;37)	+0.09	0.56*
		Nov.5-Nov.15(3;9)	+0.76	3.14*
		Nov.5-Dec.11(5;27)	+0.10	0.43
Photoperiod (min)	Time in lodge per day	Nov.5-Jan.5(5;37)	-0.46	3.11**
		Nov.5-Nov.15(3;9)	-0.36	0.97**
		Nov.5-Dec.11(5;27)	-0.66	4.45**
	Freq. of excursions per day	Nov.5-Jan.5(5;37)	-0.19	1.14
		Nov.5-Nov.15(3;9)	-0.61	2.02
		Nov.5-Dec.11(5;27)	+0.10	0.48
	$\bar{X}$ daily dur. of excursions	Nov.5-Jan.5(5;37)	-0.17	1.00*
		Nov.5-Nov.15(3;9)	+0.74	2.94*
		Nov.5-Dec.11(5;27)	+0.07	0.36
Hours bright sunshine per day	Time in lodge per day	Nov.5-Jan.5(5;37)	+0.07	0.42
		Nov.5-Nov.15(3;9)	+0.16	0.42
		Nov.5-Dec.11(5;27)	+0.23	0.78
	Freq. of excursions per day	Nov.5-Jan.5(5;37)	-0.04	0.21
		Nov.5-Nov.15(3;9)	-0.66	2.29
		Nov.5-Dec.11(5;27)	+0.01	0.04
	$\bar{X}$ daily dur. of excursions	Nov.5-Jan.5(5;37)	-0.06	0.38
		Nov.5-Nov.15(3;9)	-0.45	1.34
		Nov.5-Dec.11(5;27)	-0.13	0.64
Mean daily wind- speed (mph)	Time in lodge per day	Nov.5-Jan.5(5;37)	0.00	0.00
		Nov.5-Nov.15(3;9)	+0.56	1.82
		Nov.5-Dec.11(5;27)	-0.01	0.07
Cumulative snowfall (cm)	Time in lodge per day	Nov.5-Jan.5(5;37)	+0.20	1.20

<sup>a</sup> Number of animals (Nos. 20 to 24, inclusive); number of days monitored

\* P < .05

\*\* P < .01



was improved ( $r = -0.53$ ,  $P < .05$ ) for the period spanning Nov. 5-Dec. 11 when snow accumulation was negligible (Fig. 9), and was greatest ( $r = -0.81$ ,  $P < .01$ ) just prior to freeze-up in early November (Table 4).

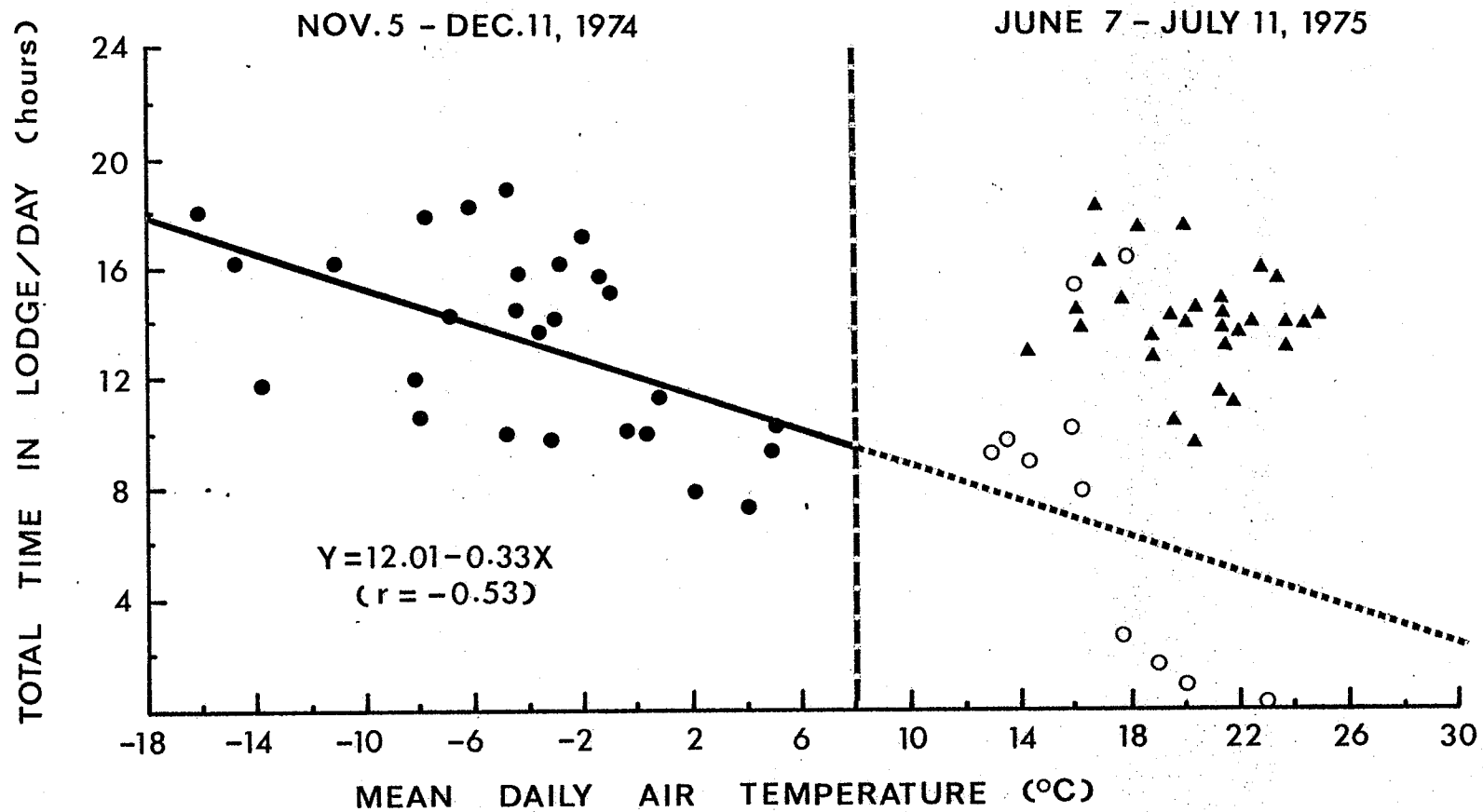
Although sample size was limited, the period of open water (Nov. 5-15) was also characterized by an increase in time spent in the lodge with increasing wind speed ( $r = +0.56$ ,  $P > .05$ ). During this same period, there was an increase in the frequency ( $r = -0.47$ ,  $P > .05$ ) and concurrent decrease in the duration ( $r = +0.76$ ,  $P < .05$ ) of excursions, with declining air  $T_a$  (Table 4).

In summer, only photoperiod ( $r = -0.53$ ,  $P < .01$ ) and mean daily windspeed ( $r = +0.37$ ,  $P < .05$ ) were significantly correlated with total time spent in the burrow per day (Table 3). As indicated in Fig. 9, this latter variable was relatively stable with respect to air  $T_a$  in June and July.

Based on the above regression analysis, photoperiod and air  $T_a$  in winter, and photoperiod and windspeed in summer, were deemed the most important environmental variables correlating with activity. However, multiple regression of these factors (X variables) on total time in the lodge or burrow per day (Y variable) indicated that the maximum variability of Y that could be attributed to these environmental variables ( $R^2$ ) was less than 50 percent, both summer and winter.

Figure 9. Total time spent by O. zibethicus in lodge or burrow per day in relation to mean daily air  $T_a$ , summer and winter. Each point is based on data for a single animal recorded at 5 ( $\pm 0.5$ ) min intervals per 24-hour period. Regression line is fitted to winter data by the method of Least-Squares.

- - Muskrats (Nos. 20 to 24, inclusive) occupying Lodge No. 5 between Nov. 5 and Dec. 11, 1974 (n = 27 days)
- - Single muskrat (No. 26) occupying Lodge No. 5 between June 7 and June 18, 1975 (n = 10 days)
- ▲ - Burrow-dwelling muskrats (Nos. 25 and 27) monitored June 11-July 11, 1975 (n = 29 days)



### Seasonal Changes in Shelter Use




The use of Lodge No. 5 peaked in early December, and thereafter declined (Fig. 10). In summer, the sole occupant of this lodge was a single adult male (No. 26). The total time per day spent by this animal in Lodge No. 5 diminished from 16.3 hours on June 7 to 1.8 hours on June 18, 1975, parallel with concurrent increases in air and water  $T_a$  (Figs. 9 and 10). By June 20, this lodge was totally abandoned, and the muskrat was subsequently located using an open nest constructed within 100 m of Lodge No. 5. This same lodge remained abandoned throughout the remainder of summer, and was reconstructed in the following fall for winter occupancy.

There was also evidence of a reduction in lodge use by a single male (No. 16) and a single female (No. 15) muskrat in mid-summer, in favor of inland burrows. Each of these animals appeared to be the sole occupant of a separate dwelling lodge in June, 1974, when there was no indication of inland burrow use. However, during the period July 5-20, 49 percent of all observations made between 0900 and 1700 hours ( $n = 39$  observations  $\geq 0.5$  hours apart) indicated each of these two muskrats to be using a shallow burrow located inshore from its respective lodge.

### Body Temperature and Activity

It is evident from Figs. 1 and 3 and Tables 5 and 6,

Figure 10. Seasonal utilization of Lodge No. 5 by O. zibethicus (expressed as mean cumulative time in lodge per animal per 24-hour period) in relation to snowfall, and air and water  $T_a$  measured concurrently. Winter observations are based on five muskrats (Nos. 20 to 24, inclusive); summer observations were made on a single animal (No. 26) that was the sole occupant of the lodge during this season.

-  - Mean cumulative time in lodge per animal per day
-  - Mean daily air  $T_a$
-  - Mean daily water  $T_a$

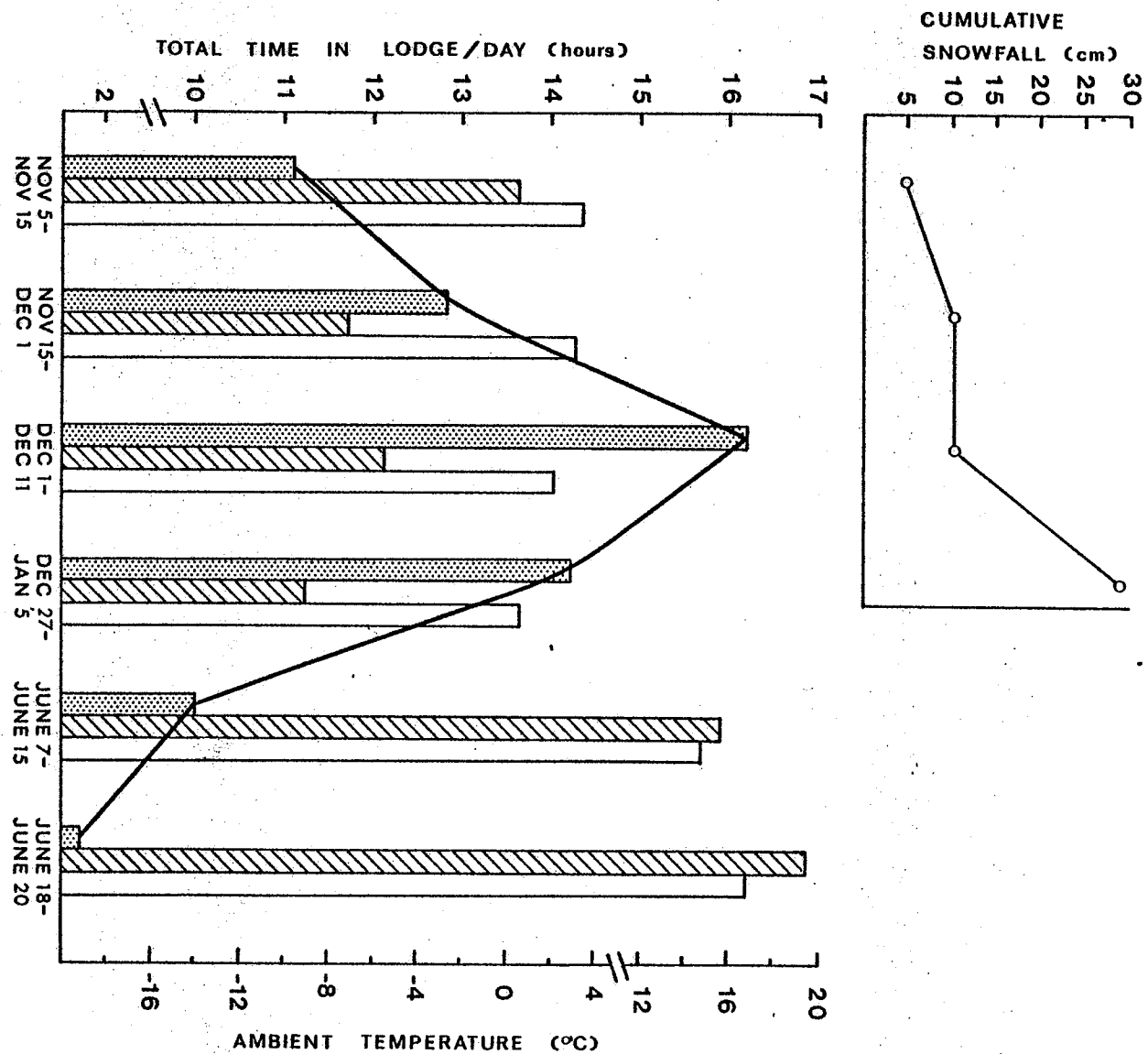


Table 5. Least-Squares regression analysis of the relationship between mean hourly body temperature (Y) and hourly activity index (X) for O. zibethicus censused at 15 to 240 min intervals, June-July, 1974

Animal No.	AM (2400-1200 hours)			PM (1200-2400 hours)			AM + PM (2400-2400 hours)			
	r	t	D.F.	r	t	D.F.	r	t	D.F.	Reg.Eq. (Y=a+bX)
12	+0.65	2.56*	10	+0.52	1.74	9	+0.57	3.04**	20	Y=37.8 + 0.70X
13	+0.55	2.10	11	+0.54	2.04	11	+0.56	3.15**	23	Y=37.9 + 0.74X
14	+0.26	0.85	11	+0.83	4.73**	11	+0.51	2.78*	23	Y=38.3 + 0.58X
15	-	-	-	-	-	-	+0.04	0.12	12	Y=39.1 + 0.03X
16	+0.74	2.96*	8	+0.92	7.2**	10	+0.89	8.49**	19	Y=38.0 + 1.02X
All <sup>a</sup> adults	+0.55	4.26**	43	+0.61	5.03**	44	+0.58	6.70**	88	Y=38.0 + 0.75X
17	-0.23	0.74	11	-0.53	1.98	11	-0.36	1.80	23	Y=38.8 - 0.42X
18	-0.14	0.45	11	-0.06	0.18	11	-0.16	0.78	23	Y=37.8 - 0.19X
19	-0.63	2.57*	11	-0.53	2.00	11	-0.60	3.56**	23	Y=38.8 - 0.94X
All juveniles	-0.36	2.24*	35	-0.32	1.98	35	-0.36	3.23**	71	Y=38.5 - 0.63X

<sup>a</sup>All adults except No. 15

\* P < .05

\*\* P < .01

Table 6. Least-Squares regression analysis of the relationship between mean hourly body temperature (Y)<sup>a</sup> and hourly activity index (X) for adult *O. zibethicus* remotely monitored at 5 ( $\pm$  0.5) min intervals in summer (Nos. 25, 26, 27) and winter (Nos. 20, 21, 22, 24), 1974-75

Animal No.	AM (2400-1200 hours)			PM (1200-2400 hours)			AM + PM (2400-2400 hours)			
	r	t	D.F.	r	t	D.F.	r	t	D.F.	Reg.Eq. (Y=a+bX)
20	-	-	-	-	-	-	+0.39	6.70 <sup>**</sup>	368	Y=-0.18 + 0.75X
21	-	-	-	-	-	-	+0.40	6.02 <sup>**</sup>	279	Y=-0.27 + 0.83X
22	-	-	-	-	-	-	+0.38	3.82 <sup>**</sup>	203	Y=-0.19 + 0.76X
24	-	-	-	-	-	-	+0.30	3.46 <sup>**</sup>	312	Y=-0.21 + 0.52X
25	+0.71	8.49 <sup>**</sup>	71	+0.56	5.64 <sup>**</sup>	71	+0.64	10.0 <sup>**</sup>	143	Y=-0.45 + 1.10X
26	+0.46	3.02 <sup>**</sup>	35	+0.36	2.25 <sup>*</sup>	35	+0.41	3.72 <sup>**</sup>	71	Y=-0.17 + 0.46X
27	-0.27	2.32 <sup>*</sup>	71	+0.23	1.95	71	+0.01	0.13	144	Y=-0.01 + 0.02X

<sup>a</sup> Body temperature expressed as deviation ( $\pm$ ) from daily mean

\* P < .05

\*\* P < .01



that hourly fluctuations in  $T_b$  and activity level were usually positively correlated in adults, and negatively correlated in juveniles. These variables were significantly correlated ( $P < .05$ ) in all but three animals. The exceptions were two juveniles (Nos. 17 and 18) and an adult female (No. 15) monitored in summer, 1974. In addition, one adult male (No. 27) extensively monitored in June and July, 1975, exhibited a negative correlation ( $r = -0.27$ ,  $P < .05$ ) between 2400 and 1200 hours, and a positive, but non-significant correlation ( $r = +0.23$ ,  $P > .05$ ) between 1200 and 2400 hours. In other muskrats, no consistent differences were observed between morning and afternoon correlations (Tables 5 and 6). The strongest positive correlation between hourly fluctuations in  $T_b$  and activity level occurred in Muskrat No. 25 ( $r = +0.64$ ,  $P < .001$ ) inhabiting a dry ditch (Table 6).

Temporal  $T_b$  changes recorded prior to exit from, and subsequent to re-entry into a dwelling lodge or burrow indicated pronounced seasonal differences. In the winter of 1973-74, limited census data ( $n = 3$  muskrats) revealed an elevation of  $T_b$  during the 25 min period preceding exit from the lodge (Fig. 11). More conclusive results were obtained from automated recordings in 1974-75 (Figs. 12 and 13). These data indicate that the magnitude of  $T_b$  elevation was related to the length of the excursion, and was maximal for excursions in excess of 40 min duration (Fig. 12).

Figure 11A. Mean body temperature changes of three O. zibethicus (Nos. 1, 2, 3) in winter (Dec. 15-Feb. 14, 1973-74), during the 25 min period immediately preceding exit from the lodge, and during the succeeding 25 min interval when the animals were foraging at a pushup or feeding lodge. Vertical lines denote the 95 percent confidence limits of the means; numbers in parentheses indicate the number of observations made at 15 to 240 min intervals.

Figure 11B. Mean body temperature changes of three O. zibethicus (Nos. 1, 2, 3) in winter (Dec. 15-Feb. 14, 1973-74), during the 25 min period immediately preceding, and during the 25 min period immediately following return to the lodge from a foraging excursion. Vertical lines denote the 95 percent confidence limits of the means; numbers in parentheses indicate the number of observations made at 15 to 240 min intervals.

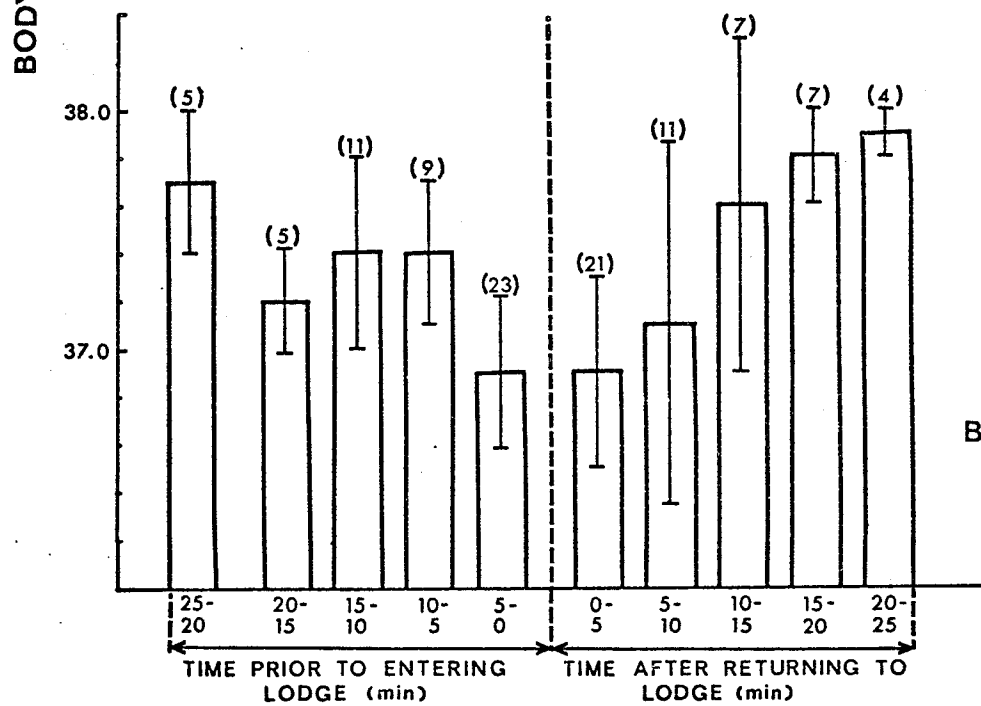
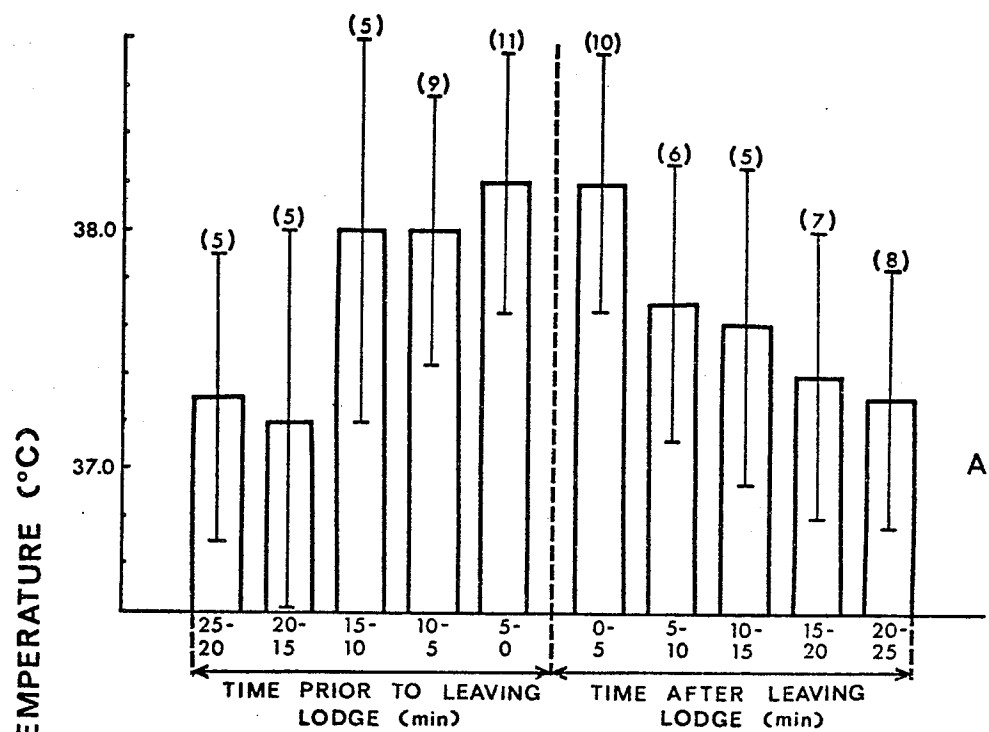


Figure 12. Mean body temperature changes in O. zibethicus (Nos. 20, 21, 22, 24) associated with the duration of foraging excursions away from Lodge No. 5, Nov. 26-Dec. 11, 1974. Vertical lines denote the 95 percent confidence limits of the means; values in parentheses indicate the number of observations recorded automatically at 5 ( $\pm 0.5$ ) min intervals.

- A - Body temperature (expressed as deviation [ $\pm$ ] from daily mean) at the time of departure from the lodge in relation to excursion duration
- B - Body temperature change during foraging (i.e. last temperature recorded prior to exit - first temperature recorded after return) in relation to excursion duration

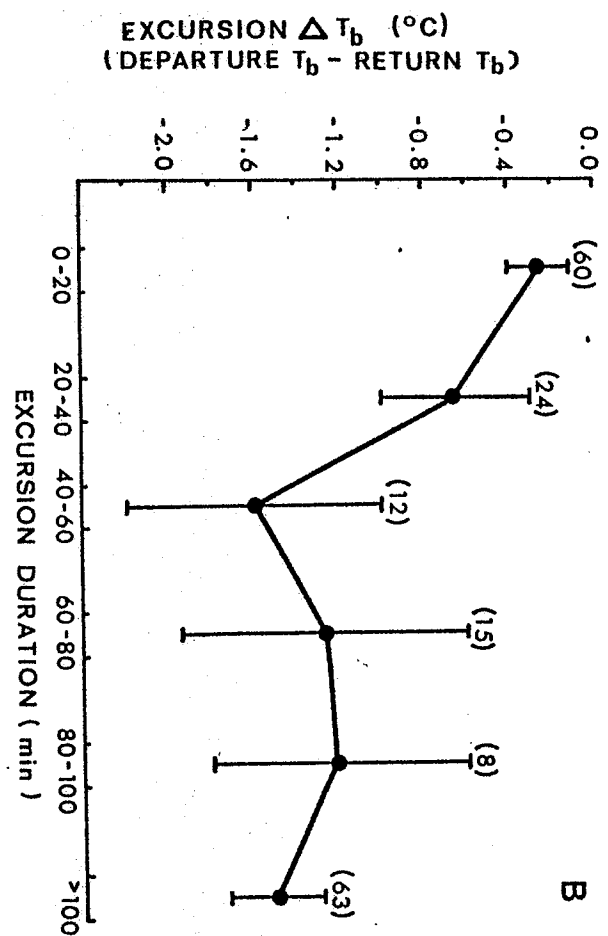
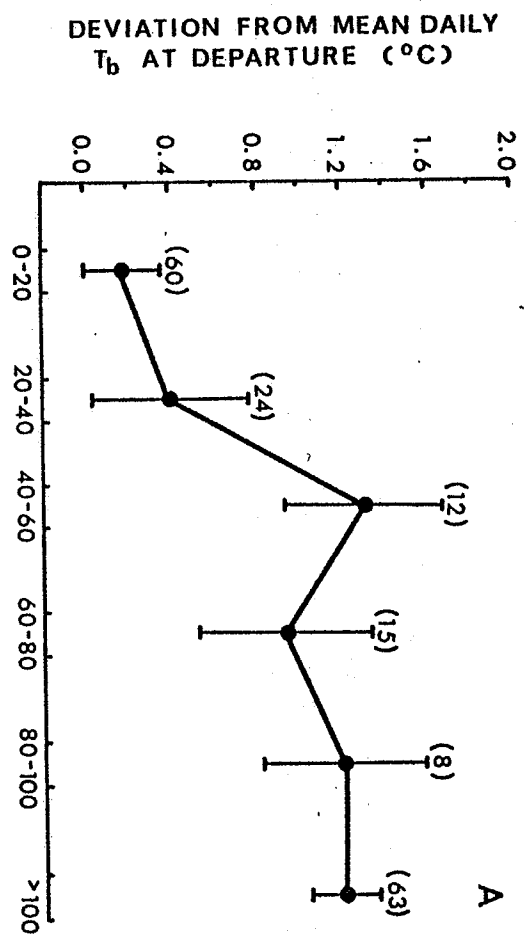
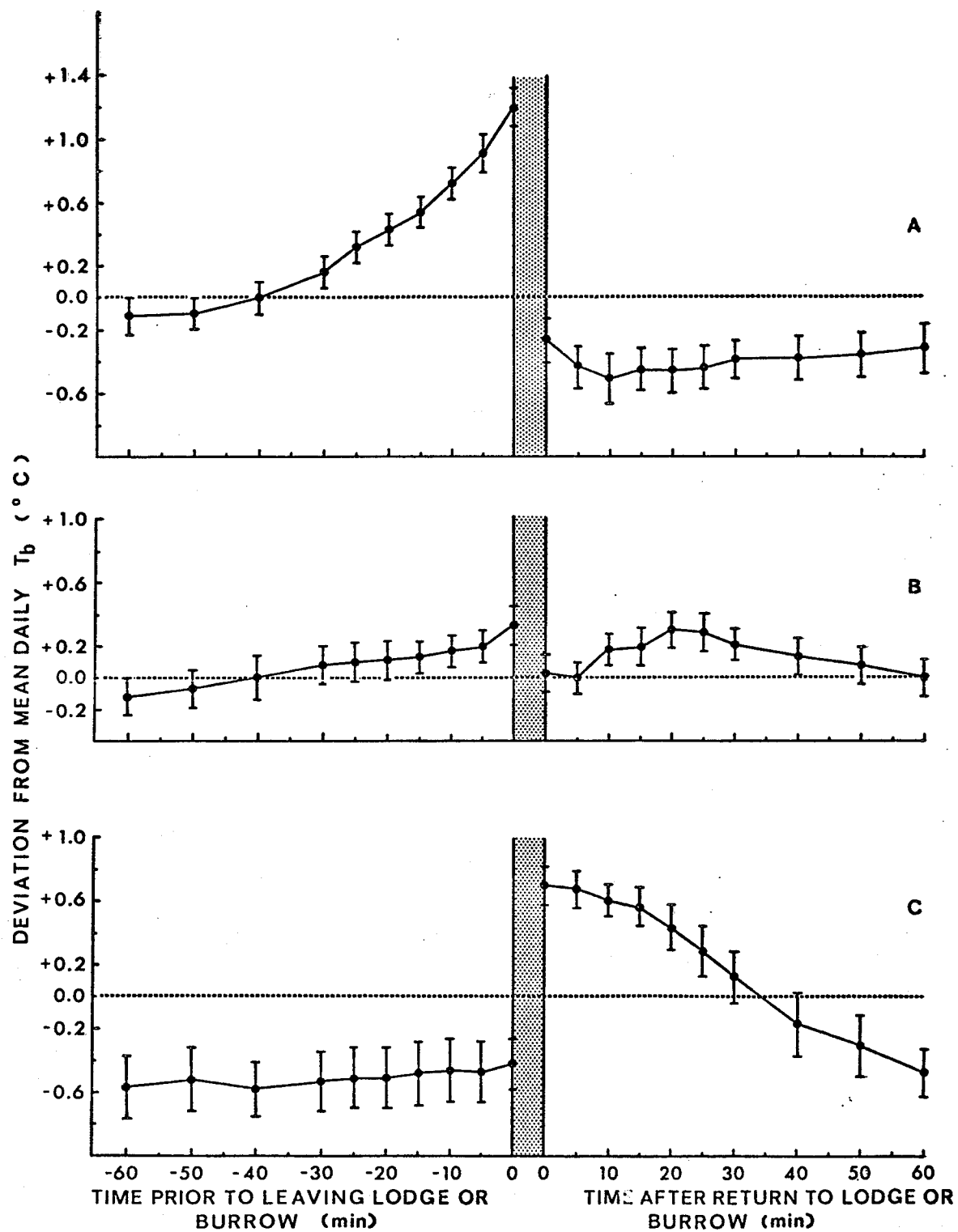


Figure 13. Mean body temperature changes in O. zibethicus during one hour immediately preceding, and during one hour immediately following major excursions ( $\geq 40$  min duration) away from the lodge or burrow. Body temperature data are presented as deviations ( $\pm$ ) from daily means. Vertical lines denote the 95 percent confidence limits of the means.

- A - Lodge-dwelling muskrats (Nos. 20, 21, 22, 24) monitored Nov. 26-Dec. 11, 1974  
(n = 97 excursions)
- B - Lodge- (No. 26) and burrow- (No. 27) dwelling muskrats monitored June 7-July 11, 1975  
(n = 67 excursions)
- C - A single burrow-dwelling muskrat (No. 25) occupying a dry ditch, June 25-July 1, 1975 (n = 24 excursions)



Considering only those excursions  $\geq 40$  min duration, a curvilinear increase in  $T_b$  was observed during the last 60 min prior to exit from the winter lodge (Fig. 13A). This increase attained a mean maximum value of  $1.2^\circ\text{C}$  immediately prior to exit from the lodge. In summer, only a slight rise in  $T_b$  ( $< 0.5^\circ\text{C}$ ) occurred during the last 60 min prior to exit from a lodge or burrow in the case of Nos. 26 and 27 (Fig. 13B), and virtually no increase was observed in No. 25 (Fig. 13C). Covariance Analysis of winter (Fig. 13A) and summer (Fig. 13B) warming slopes (after logarithmic transformation) confirmed the above differences ( $F = 20.0$ ,  $P < .001$ ).

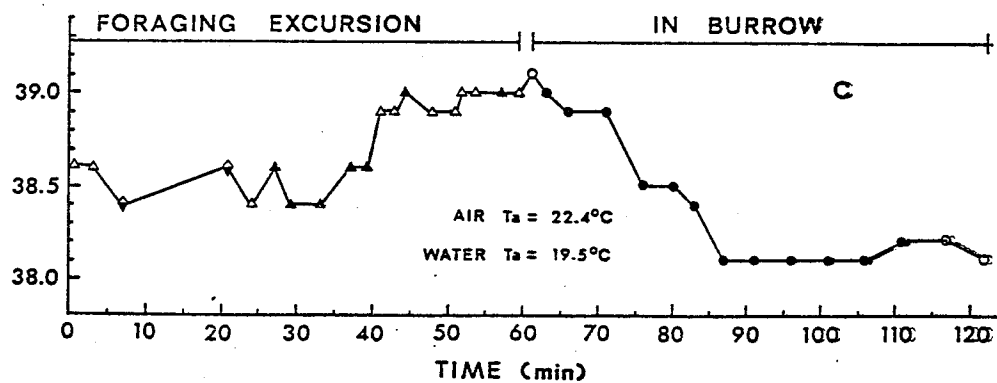
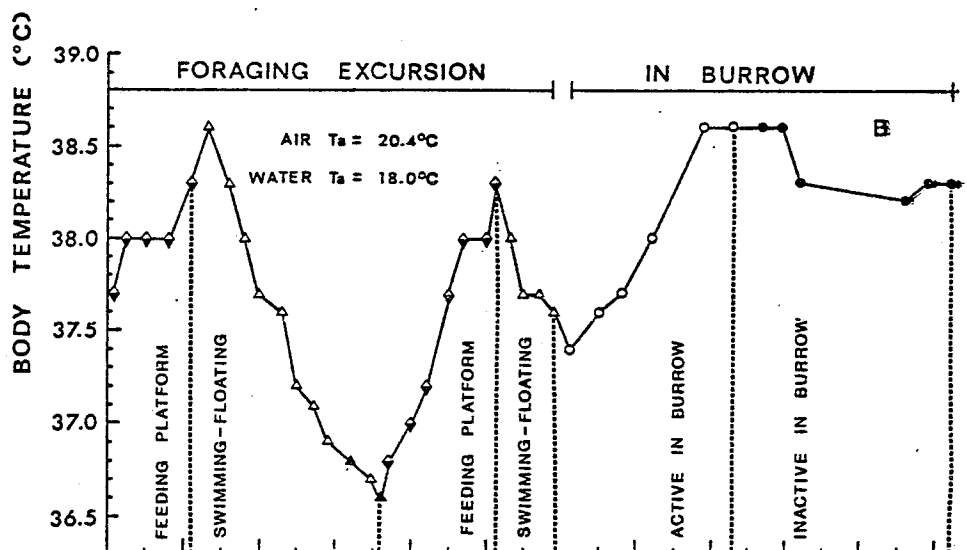
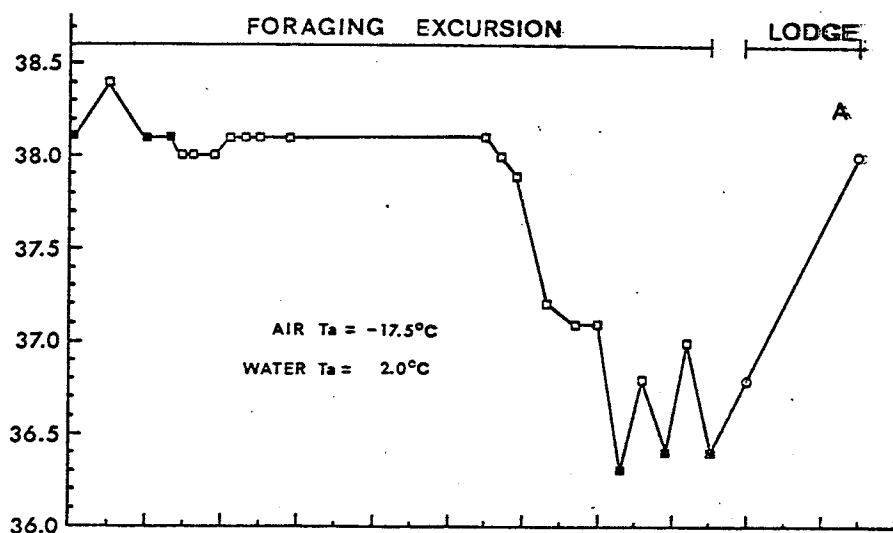
When muskrats foraged beneath the ice,  $T_b$  always underwent a net decline, and often continued to drop during the first 10 min after return to the lodge, followed by a gradual rewarming phase (Figs. 11, 13, and 14A). Cooling during immersion in water, followed by rewarming upon withdrawal to a feeding platform or burrow was also documented in juveniles in summer (Fig. 14B). In adults, the pattern was usually reversed in summer, with  $T_b$  rising during the course of an excursion, and then declining after return to the lodge or burrow (Fig. 14C). This latter trend was especially pronounced in Muskrat No. 25 (Fig. 13C).

Body temperature fluctuations during winter or summer excursions seldom followed uniform declines or elevations, and often varied with the type of activity (Figs. 14 and



Figure 14. Body temperature dynamics of O. zibethicus associated with short-term changes in activity during winter and summer.

- A - Adult male (No. 1) monitored Dec. 5, 1973  
(1404 to 1604 hours)
  - B - Juvenile male (No. 19) monitored July 25,  
1974 (0807 to 0959 hours)
  - C - Adult male (No. 14) monitored July 9,  
1974 (0923 to 1145 hours)
- 
- - Inactive in lodge or burrow
  - - Active in lodge or burrow
  - - Inactive in pushup
  - - Active in, or in immediate vicinity of  
pushup
  - ▲ - Active in emergent vegetation (not  
visible)
  - △ - Swimming/floating in water (visible)
  - ◆ - Resting/feeding on platform or bank  
(visible)





15). When muskrats were actively swimming during summer,  $T_b$  usually increased in adults, and decreased in juveniles ( $t$ -difference = 6.84,  $P < .01$ ). When these animals were floating stationary, as often occurred during feeding, a comparable decline in  $T_b$  ( $t$ -difference = 1.23,  $P > .05$ ) was observed in both groups (Fig. 15). The body temperatures of these muskrats in water also varied with time of day, and tended to increase in both groups between 0500 and 2100 hours--roughly parallel with concurrent increases in shallow water  $T_a$  (Fig. 16). The greatest rate of  $T_b$  decline occurred in adults engaged in swimming or diving behavior during winter (Fig. 15).

An elevation of  $T_b$  was often observed when muskrats were recorded feeding, grooming, or simply resting on a bank or feeding platform in summer, or in a pushup or feeding lodge in winter (Figs. 14 and 15). In juveniles during summer, and in adults during winter, such behavior appeared to retard the net decline in  $T_b$  associated with foraging. A dramatic example of alternate cooling in water and rewarming on a feeding platform is presented for a juvenile (No. 19) in Fig. 14B.

Potential error associated with long-term drift in some transmitters (see "Materials and Methods") precluded statistical comparisons of  $T_b$  levels in summer and winter. However, there was no indication of pronounced seasonal differences in  $T_b$  level, and the mean daily amplitude of  $T_b$  in winter ( $2.2^\circ\text{C}$ ) was only slightly greater than

Figure 15. Rates of body temperature change ( $^{\circ}\text{C}/\text{min}$ ) associated with different activities of O. zibethicus during excursions away from the lodge or burrow, in summer and winter. Rates are calculated from consecutive observations made at 1 to 5 min intervals during periods of continuous surveillance. Data are based on observations of five muskrats in winter (Nos. 1, 2, 3, 6, 7), and two adult (Nos. 13, 14) and three juvenile (Nos. 17, 18, 19) muskrats in summer. Horizontal and vertical bars denote means and ranges, respectively; rectangular boxes define the 95 percent confidence limits of the means. Values in parentheses indicate number of observations.

 - Adults

 - Juveniles

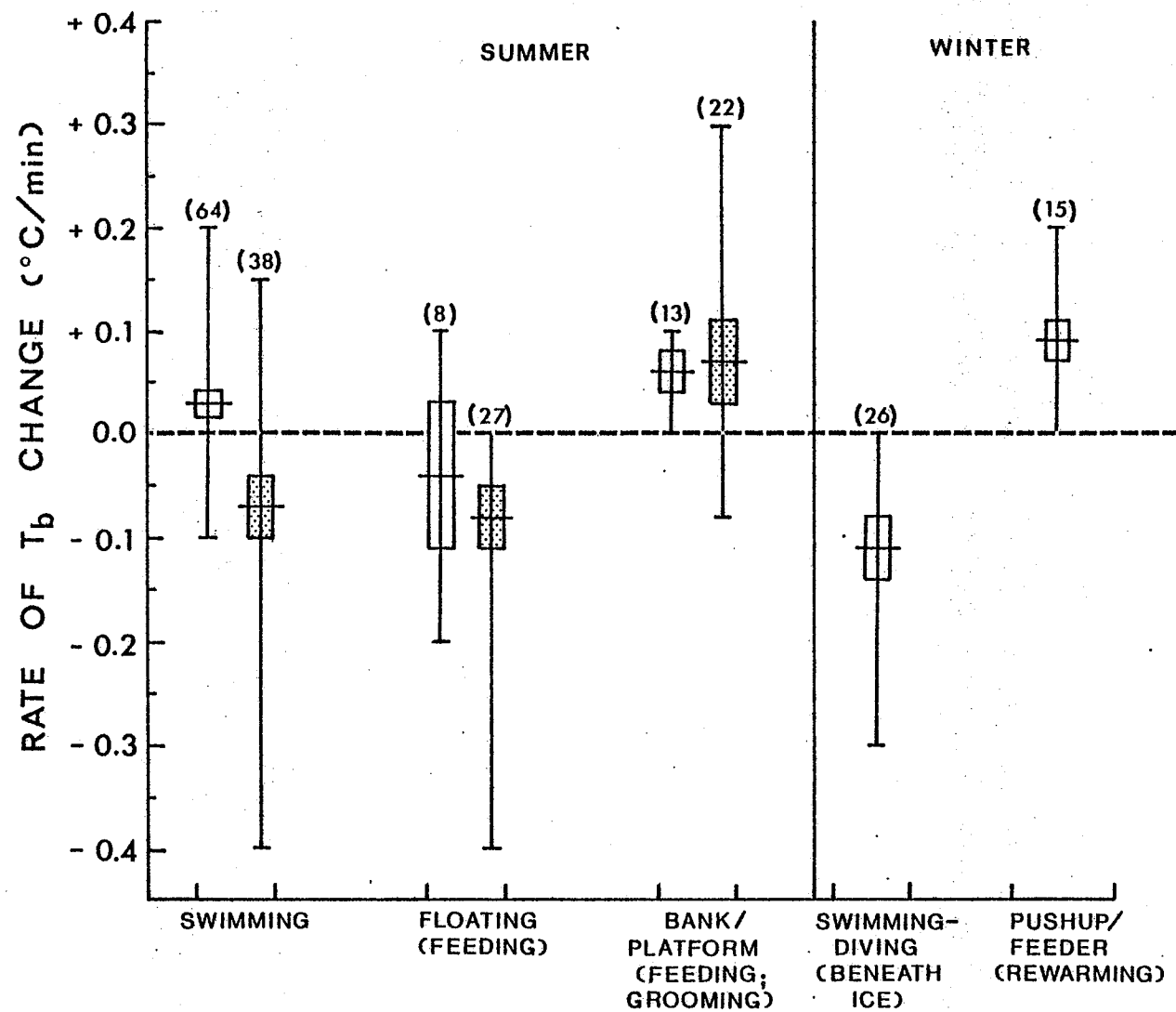



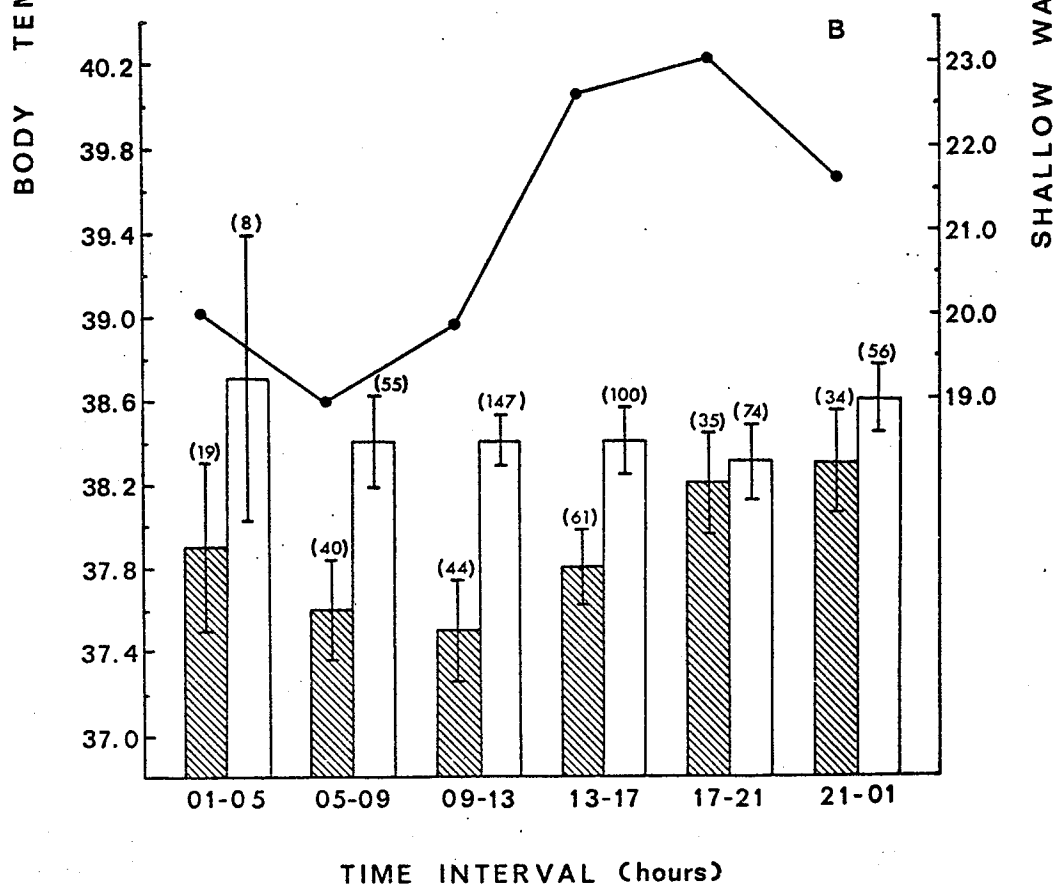
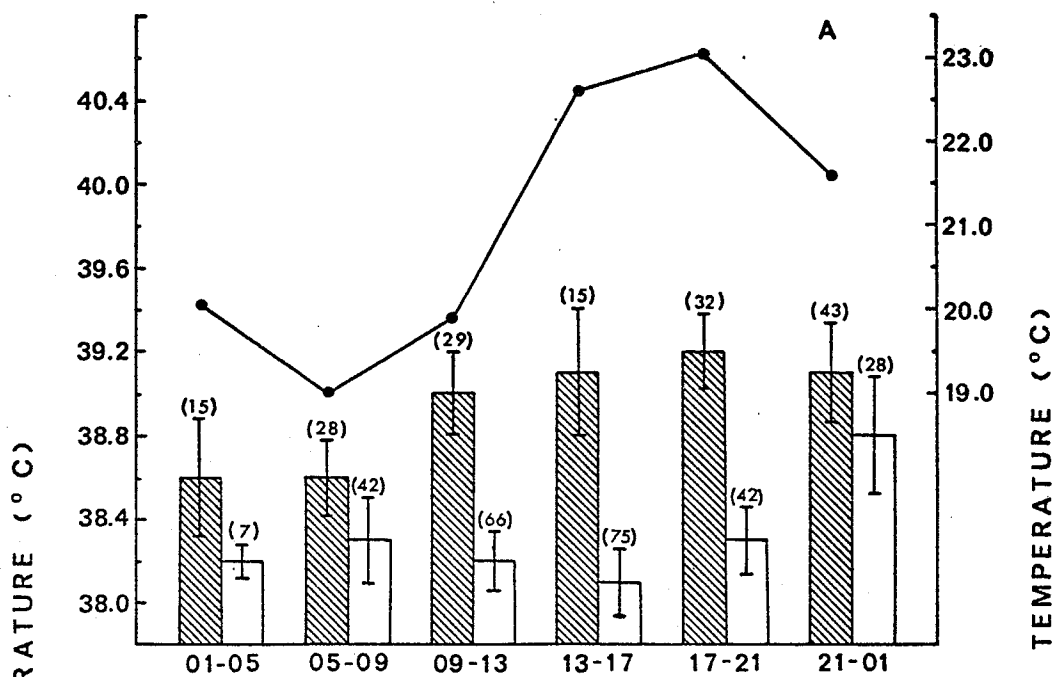


Figure 16A. Mean body temperatures of adult O. zibethicus (Nos. 13, 14) during periods of swimming, and during periods of inactivity within the burrow, in relation to time of day and shallow (3 to 20 cm) water  $T_a$ , July 8-29, 1974. Vertical lines denote the 95 percent confidence limits of the means; numbers in parentheses indicate the number of observations ( $\geq 5$  min apart).

Figure 16B. Mean body temperatures of juvenile O. zibethicus (Nos. 17, 18, 19) during periods of swimming, and during periods of inactivity within the burrow, in relation to time of day and shallow (3 to 20 cm) water  $T_a$ , July 19-30, 1974. Vertical lines denote the 95 percent confidence limits of the means; numbers in parentheses indicate the number of observations ( $\geq 5$  min apart).

-  - Swimming
-  - Inactive in burrow
-  - Shallow water  $T_a$



that (1.7°C) in summer. Individual values are given in Appendices 4 and 5.



## DISCUSSION

### Daily Activity Pattern

The occurrence of activity in O. zibethicus throughout the diel cycle, with nocturnal peaks near dusk and dawn, agrees with casual observations reported in the literature (Johnson 1925; Errington 1963; Lowery 1974). Similar patterns have been documented in other microtine rodents as well (Davis 1933; Calhoun 1945; Brown 1956; Wiegert 1961; Getz 1968; Gorecki 1968). The predominance of the late afternoon-early evening activity peak, and increased diurnalism in winter, have also been observed in this species by Van Horn (1975). Seasonal studies of shrews, Sorex spp. and Neomys spp. (Buchalczyk 1972), the short-tailed vole, Microtus agrestis (Erkinaro 1961), and the deer mouse, Peromyscus maniculatus (Behney 1936), have also indicated a tendency towards increased diurnalism in winter.

As in various other mammals (Brown 1956; Kavanau 1962; Aschoff 1966), dawn and dusk appear to be key points in the diel activity cycle of O. zibethicus, and a reduction in winter light intensity may well be the immediate cause of increased diurnalism in this species. Enhanced activity resulting from decreased light intensity has been reported for other, predominantly nocturnal mammals (Blair 1943; Calhoun 1945; Getz 1968; Jahoda 1973).

From an energetic standpoint, nocturnal behavior in summer coincides with relatively cool air temperatures, thus alleviating potential heat stress in very warm weather. Conversely, the increased prevalence of diurnal behavior in winter permits activity when macroenvironmental conditions are most favorable (Part I). Errington (1963) points out that Iowa muskrats forage above ground when subjected to winter drought conditions, and at such times limit feeding to midday when air temperatures are highest. Examination of 24-hour records of feeder and pushup temperatures in Delta Marsh, however (Part I), indicate little diel variation, and hence it is unlikely that diurnal behavior significantly reduces thermoregulatory costs in winter. Increased daytime activity may instead reflect a decrease in predation pressure resulting from protection afforded by ice and snow, or as suggested for the Weddell seal, Leptonychotes weddelli (Kooyman 1975), visual cues may facilitate under-ice navigation.

Of perhaps greater ecological significance is the pronounced inter- and intra-individual variability in the detailed records of activity. Temporal staggering of activity bouts ensures continuous, or nearly continuous occupation of winter lodges by a variable number of muskrats, and hence facilitates the maintenance of a favorable microclimate characterized by low-amplitude chamber  $T_a$  fluctuations. Such behavior would also impede the formation of ice in the open plunge hole, which

could be especially significant in exposed pushups situated 30 m or more from the resident lodge. In this context, it is interesting to note that there is also evidence of inter-group sharing of pushups (Part IV), which again, may inhibit ice formation within these structures.

Periodic, and often asynchronous activity in winter may also serve an important role in averting social stress due to overcrowding at feeding sites. As indicated in Part IV, the foraging range of O. zibethicus is closely linked to the distribution of feeders and pushups. The limited number of these shelters, coupled with the diminutive size of the winter pushup (Part I), would thus favor staggered patterns of foraging activity among overwintering animals. By enhancing inter-group compatibility, such behavior may indirectly contribute to social, or group thermoregulation within the winter dwelling lodge.

The mechanism responsible for the labile activity pattern of O. zibethicus is unknown. In winter, one possible hypothesis involves the expression of individual free-running activity periods in the absence of environmental cues ("zeitgebers"), as described for the beaver, Castor canadensis (Potvin and Bovet 1975). The presence of ice and snow may effectively shield O. zibethicus from a potential zeitgeber such as the daily light cycle, with the result that individual activity patterns gradually drift out of phase with sidereal time. According to this hypothesis, inter-individual differences may reflect intra-

specific variation in the free-running period length.

In the present study, lack of continuous, day-to-day telemetry observations of individual muskrats precluded statistical testing for free-running periodicity in winter. However, there was no evidence of regular, daily phase shifts in winter activity based on lodge  $T_a$  data. This, together with the occurrence of inter- and intra-individual differences in activity in summer, indicate that the above mechanism alone cannot explain the observed variability of activity in O. zibethicus.

#### Daily Activity in Relation to Environmental Factors

The weak association observed between daily fluctuations in activity and weather further strengthens previous conclusions (Part I) regarding the buffering role of the winter microclimate. In a year-round field study of burrow-dwelling muskrats in Wisconsin, Van Horn (1975) also observed only weak correlations between these variables. As in the winter phase of the present study, he found the most significant environmental factors correlating with activity to be photoperiod and air  $T_a$ . An elevation of activity in response to precipitation was not observed in the present study, in contrast to the results of Stewart and Bider (1974).

Poor correlation of activity with short-term changes in weather are often observed in small-mammal field studies (Gentry et al. 1966; Doucet and Bider 1974; O'Farrell

1974), although a number of workers (Linduska 1947; Pruitt and Lucier 1958; Getz 1961; Muul 1968; Kenagy 1973; Pauls, pers. comm.) have reported a general suppression of activity with declining air  $T_a$ . The latter trend is particularly pronounced in the arboreal squirrels: Tamiasciurus hudsonicus (Pauls, pers. comm.), and Glaucomys volans (Muul 1968), which are active in the macroenvironment both summer and winter.

In the case of O. zibethicus, exposure to potentially stressful macroclimatic conditions occurs principally in late fall and early spring when low air and water temperatures prevail in the absence of ice and snow cover. It is therefore not surprising that the strongest inverse relationship between total time in the lodge per day and mean daily air  $T_a$  occurred just prior to freeze-up, and that a weaker, though still significant negative correlation persisted through early winter in the absence of a significant snow cover. In this context, the reduction in activity observed shortly after freeze-up in November (Fig. 5) may reflect a decline in air  $T_a$ , as well as a restriction of movement imposed by the ice cover. Too few data are available at the present time, however, for definitive conclusions concerning these latter relationships.

Failure to demonstrate a strong correlation between activity and weather in summer suggests that factors other than thermal stress, such as reproductive and

territorial behavior, may be more important in determining day-to-day variation in the level and pattern of activity. The limited evidence indicating abandonment of summer lodges by adult O. zibethicus implies a decreased need for shelter protection from low air temperatures during this season. The use of inland burrows by two lodge-dwelling adults in mid-summer may instead reflect a need to avoid high temperatures encountered in summer lodges (Part I).

In contrast, the weak positive correlation between time spent in lodge or burrow per day and mean daily windspeed in summer and early winter, suggests that wind may inhibit activity during the period of open water. Foraging behavior in O. zibethicus often involves frequent transitions between water and air, and during such activity, wind may enhance both convective and evaporative cooling. The combined effects of wind and wave action may also increase the energy cost of swimming, reducing foraging efficiency still further. A reduction in activity associated with wind has also been observed in the varying hare, Lepus americanus (Bider 1961), and in the deer mouse, Peromyscus maniculatus (Hammer 1969).

Of all environmental variables tested, only photoperiod changed in a uniform, predictable manner, and this variable proved most strongly correlated with total time spent in lodge or burrow. This element of time-dependency is consistent with winter movement data (Part IV) indicating

increased activity and utilization of peripheral home range in early winter. An hypothesis dealing with the energetic significance of peripheral resource utilization in early winter is presented in Part IV.

#### Concept of Constancy in Daily and Seasonal Activity

Despite the variability in the daily level and distribution of activity in O. zibethicus, close examination of the automated series of recordings also reveals an underlying element of constancy. Thus, the mean total time per day spent in the lodge in winter does not differ significantly from that spent in the lodge or burrow in summer. Similarly, the logarithmic regression of daily excursion frequency on mean daily excursion duration is similar in summer and winter, and the hyperbolic relationship between these variables suggests that their product is a constant value. Moreover, the mean periodicity of short-term activity bouts is similar in summer (5.8 hours) and winter (6.2 hours), implying the existence of an underlying metabolic rhythmicity. Short-term rhythms of 2 to 4.8 hours have been described for other microtine rodents (Davis 1933; Pearson 1947; Brown 1956; Wiegert 1961; Ambrose 1973), the laboratory rat, Rattus norvegicus (Richter 1927), and various species of shrews (Crowcroft 1953).

### Body Temperature in Relation to Activity

The positive correlation between activity level and  $T_b$  usually observed in adult O. zibethicus is in general agreement with other mammalian studies conducted under natural or semi-natural (Folk and Folk 1964; MacArthur and Wang 1973; Aleksuk 1977), and laboratory (Bartholomew and Cade 1957; Morrison et al. 1959; Yousef et al. 1973) conditions. However, the data reported herein clearly indicate that the association between these two variables is complicated by the interaction of a number of biotic and abiotic factors. For example, the  $T_b$  response varies with type of activity (Fig. 15), and hence inter- and intra-individual variability in the proportion or intensity of the different activity types (i.e. swimming, diving, floating, feeding on bank or platform) may alter both the direction and degree of correlation between these variables.

The elevation of  $T_b$  frequently noted during swimming activity in adult O. zibethicus in summer may be partially attributed to a temporary rise in metabolic heat production, which is not immediately compensated for by a concurrent increase in thermal conductance. This hypothesis (McNab and Morrison 1963) is consistent with the excellent insulation of this species (Part III), and the observation that surface swimming is the energetically most demanding mode of aquatic locomotion in vertebrates (Schmidt-Nielsen 1972). In contrast, the  $T_b$  decline often observed in



swimming juveniles may be attributed to the relatively large surface area-to-volume ratio and probable inferior pelage insulation of these animals, and hence their greater capacity for cooling in water.

The cooling capacity of water is strongly evident in the comparison of three adult muskrats (Nos. 25, 26, 27) in summer, one of which (No. 25) lacked access to open water (Fig. 13). As expected, No. 25 demonstrated the most dramatic increase in  $T_b$  associated with activity in this study. It might be inferred from these data that immersion in water facilitates heat loss and prevents hyperthermia during activity bouts in hot summer weather.

Time of day also has a bearing on the relationship between activity and  $T_b$ . In both adults and juveniles (Fig. 16) there is evidence that  $T_b$  during foraging excursions is highest in late afternoon and early evening. This corresponds to the period when shallow water  $T_a$  is highest, and hence the thermal gradient between skin and water is minimal. These results are somewhat comparable to studies of terrestrial mammals indicating that the  $T_b$  elevation associated with exercise is greatest at high air temperatures (Hart and Heroux 1955; Wunder 1970; Yousef et al 1973).

In winter, the unexpected finding that activity and  $T_b$  were positively correlated while  $T_b$  invariably declined during foraging excursions, is explained by the marked rise in  $T_b$  prior to exit from the lodge. Thus, despite the net drop in  $T_b$  while foraging, most of the temperatures recorded during activity are still elevated above resting values

in winter.

Elevation of abdominal  $T_b$  prior to the onset of activity has also been observed in the red squirrel, Tamiasciurus hudsonicus kept in outdoor enclosures during winter (Pauls, pers. comm.), and there is some evidence suggesting that this phenomenon may occur in free-ranging beaver (Aleksiuk 1977). Laboratory studies of the Belding ground squirrel, Spermophilus beldingi (Morhardt and Molt 1975), the laboratory rat (Gollnick and Ianuzzo 1968), and the domestic chicken, Gallus gallus (Aschoff 1968) have also indicated a rise in rectal or abdominal  $T_b$  preceding the onset of activity. These results imply an "anticipatory" elevation of the hypothalamic set-point, and in fact, increases in hypothalamic temperature associated with feeding or locomotor activity have been clearly demonstrated in the laboratory rat (Abrams and Hammel 1964), and in the domestic cat, Felis catus (Adams 1963). Abrams and Hammel (1964) also noted that abdominal  $T_b$  closely paralleled changes in hypothalamic temperature, although sometimes lagging behind the latter.

Furthermore, Aschoff (1968) has summarized published data indicating a phase-lag between  $T_b$  and activity in both entrained and in free-running circadian rhythms, and he advances the hypothesis that the two rhythms are separate oscillators. Aschoff postulates further that while these oscillators may be mutually coupled, it should not

be assumed a priori that their relationship is always one of cause and effect.

Applying this reasoning to O. zibethicus, endogenous oscillators governing activity and  $T_b$  rhythms may be closely synchronized in summer, whereas a significant phase-lag may exist in winter, such that  $T_b$  elevation precedes onset of activity in the latter season. Thus, the increase of  $T_b$  observed in adults foraging during summer may reflect an elevation of hypothalamic set-point temperature coinciding with the onset of exercise. The effects of such factors as intensity and type of activity and water  $T_a$  may then be superimposed on this endogenous  $T_b$  increase.

Approached from an ecological perspective, the elevation of  $T_b$  prior to entry into water in the winter is of distinct advantage in retarding the development of hypothermia. By initiating activity at an elevated  $T_b$  baseline, the muskrat can withstand a greater degree of cooling, and hence can remain active in near-freezing water for longer periods. The importance of an elevated  $T_b$  in enhancing the capacity for muscular work has been previously emphasized (Asmussen and Boje 1945; Nielson 1968), and in O. zibethicus, such an elevation could be expected to improve the locomotor efficiency associated with foraging in cold water.

Aside from the tremendous capacity for heat loss to water via conductive and convective routes, the fact that

O. zibethicus must sustain dives beneath the ice also implies a depression in metabolism and drop in  $T_b$  associated with diving (Andersen 1966; Costello and Whittow 1975). Although metabolic data are lacking, Drummond and Jones (1972) demonstrated pronounced bradycardia in O. zibethicus within 200 msec of entering a dive, and it is highly probable that a depression of metabolic rate also occurs. Pre-warming, then, may offset a drop in  $T_b$  resulting not only from enhanced heat loss to water, but also from a marked reduction in metabolic rate incurred while diving beneath the ice.

The pre-exit elevation of  $T_b$  is maximal for excursions >40 min duration (Fig. 12A) when it may be assumed that the animals are foraging at a distant pushup or feeder, where the problem of  $T_b$  cooling is most critical. It was commonly observed that when initiating a major activity bout, a muskrat often swam directly from the lodge to a distant pushup, and the underwater traversal of this distance constituted the longest sustained dive during the excursion. Thus, it would seem highly adaptive for the muskrat to elevate its  $T_b$  immediately prior to embarking on these relatively long-distance underwater excursions. The enhanced potential for cooling during diving may also account for the rapid (usually < 2 min) transit of animals between lodge and pushup. The duration of these under-ice movements never approached the diving endurance limit of 12 min reported for this species

(Irving 1939).

The observation that the increase in  $T_b$  prior to activity is far more pronounced in winter than in summer may reflect a reduction in the proportion of diving behavior, and/or the prevalence of warm ambient temperatures during the latter season.

Examination of activity and  $T_b$  dynamics during foraging excursions also reveals the significance of feeding and resting shelters (*i.e.* pushups, feeders, and feeding platforms) in permitting periodic re-warming, and retarding the development of hypothermia. This behavioral thermoregulation attains maximal significance during winter, but it is also clearly adaptive in offsetting body cooling in juveniles foraging in water during summer. The results illustrated in Fig. 14 are in marked contrast to the uniform cooling curves obtained from free-swimming muskrats in the laboratory, where there was no facility for voluntary withdrawal from water (Part III).

The finding that net decline in  $T_b$  during winter increased with time away from the lodge for excursions  $< 40$  min duration, but became relatively independent of excursion duration for longer periods of absence (Fig. 12B), provides further support for behavioral thermoregulation. Besides implying an increased dependence on shelter use with increasing absence from the resident lodge, these data suggest that  $T_b$  may drop to a critical level before behavioral avoidance of further cooling is activated.

Although speculative, this view is compatible with the results of Weiss and Laties (1961) indicating that operant-conditioned laboratory rats will bar-press for heat reinforcement only after undergoing an initial decline in deep  $T_b$ .

The need to re-warm periodically during a foraging excursion may, as hypothesized by Smyth (1973) for the platypus, Ornithorhynchus anatinus, prolong the total time required to satisfy energy demands, and hence reduce overall foraging efficiency. This need to periodically re-warm may account for the greater mean excursion duration in winter (83 min), as opposed to summer (55 min).

In conclusion, this investigation reveals that O. zibethicus is capable of fairly precise thermoregulation in nature, with little seasonal variation in either level or daily amplitude of  $T_b$  oscillations. This precision appears to be achieved in part, through behavioral mechanisms for maintaining an optimal microclimate, as well as behavioral adaptations for limiting exposure to cold during foraging. There is also evidence that muskrats may "prepare physiologically" for foraging activity in winter by elevating  $T_b$  prior to departing from the dwelling lodge and entering water at near-freezing temperatures.

### PART III

#### A Laboratory Study of Temperature Regulation in Seasonally- Acclimatized Muskrats (Ondatra zibethicus)

## INTRODUCTION

Previous field studies of O. zibethicus (Parts I and II) have emphasized the role of behavior in avoiding climatic stress and regulating body temperature in a temperate zone marsh. Despite behavioral adaptations for minimizing exposure to cold, muskrats must dive periodically in near-freezing water to gain access to the submerged and rooted vegetation upon which they feed during winter (Bellrose 1950). Surprisingly, the few physiological data available in the literature suggest that this species has a poor tolerance to hypothermia in water (Hart 1962; Shcheglova 1965). Furthermore, neither Hart (1962) nor McEwan et al. (1974) were able to demonstrate seasonal changes in the metabolic response to air temperature in this species. However, the period of acclimation was not clearly defined in either of these latter studies.

It is the aim of the present investigation to provide new information concerning temperature regulation in the muskrat maintained under laboratory conditions. In view of the pronounced annual range of water temperatures (0 to 30°C) encountered in Delta Marsh (Part I), it is also relevant to examine potential seasonal differences in the thermoregulatory capabilities of this species in air and water. Seasonal adaptations under consideration



include huddling behavior, resistance to deep body cooling, and the role of brown adipose tissue during swimming in cold water.

## MATERIALS AND METHODS

### Collection of Animals

Muskrats used in this study were live-trapped in Delta Marsh (50°11'N; 98°23'W), approximately 120 km northwest of Winnipeg, Manitoba. Trapping was done with National Live Traps (16.5 x 16.5 x 48.3 cm) as described in Part II, and animals were transported to the University of Manitoba within 48 hours of capture. Most data were obtained from 24 subadult and adult muskrats (550 to 1170 g) of both sexes. Fourteen of these animals (9 males, 5 females) were trapped during December, January, and February, 1975, and the remaining 10 (8 males, 2 females) during July and August, 1975. Additional data were collected from 6 males and 2 females (550 to 630 g) trapped in September, 1973, and from a single female (1100 g) obtained in June, 1974.

### Care of Muskrats in the Laboratory

Once in the laboratory, animals were immediately placed in a walk-in environmental chamber that was kept at 10 ( $\pm$  1.0)°C with a photoperiod of 9L:15D during winter, and at 20 ( $\pm$  1.0)°C with a photoperiod of 16L:8D during summer. Each animal was housed in a separate wire cage (National Live Trap described above) throughout the experimental period. All cages were mounted on a slight

incline in a fibreglass tank (10.2 x 76.2 x 121.9 cm) supplied with running water (10 to 11°C in winter; 20 to 21°C in summer). The lower half of each cage was immersed in the water to a depth of 3 to 5 cm. All animals were fed commercial rat chow supplemented with fresh apple and carrot. Adjustment to captivity was excellent, and most animals gained weight on the diet provided. Although other methods of housing muskrats were attempted (Appendix 8), the above system proved most practical. Upon completion of laboratory studies, animals were returned to Delta Marsh and released.

#### Oxygen Consumption

The oxygen consumption of individual muskrats in air was measured over an ambient temperature ( $T_a$ ) range of -17 to 30°C during summer and winter. To obtain an estimate of standard metabolic rate (SMR), animals were fasted 12 to 14 hours prior to oxygen consumption determinations at thermoneutral temperatures of 15 to 25°C (Hart 1962; McEwan *et al.* 1974). All other tests were performed on animals fed prior to, but not during metabolism runs. In order to evaluate the metabolic efficiency of huddling, the oxygen consumption of an aggregate of three non-fasted animals was measured over an air  $T_a$  range of -17 to 20°C during winter.

Oxygen consumption was measured in an open-circuit system using a Beckman F-3 Paramagnetic Oxygen Analyzer

connected to a strip chart recorder (Fisher Recordall 5000). The metabolism chamber used for runs on single animals consisted of a rectangular metal box (20.3 x 21.6 x 53.8 cm) fitted with a removable plexiglass top. This unit just accommodated a single holding cage (National Live Trap). The chamber used in huddling experiments consisted of a glass aquarium (26.7 x 31.8 x 50.8 cm) fitted with a wire mesh floor and a removable plexiglass top. Each chamber was equipped with inlet and outlet air ports, and a port for insertion of a YSI (No. 402) Tele-Thermometer probe for air  $T_a$  measurements. The metabolism chamber was housed in a walk-in environmental chamber that could be regulated to within  $\pm 1.0^\circ\text{C}$  of the desired  $T_a$ . Air was supplied to the metabolism chamber from a compressed air outlet after decompression to 3 psi by a Matheson low pressure regulator and passage through a copper coil in the environmental chamber to achieve  $T_a$  equilibrium. Flow rate to the chamber was measured with a calibrated Matheson flow meter, and was kept constant at 1570 cc/min during runs on single animals, and 3500 or 4000 cc/min during runs on huddled animals. Water was removed from the downstream airflow by passage through two plexiglass tubes containing Drierite ( $\text{CaSO}_4$ ). Water was not removed from the upstream airflow, except when frost build-up in the inlet tubing necessitated dessication at air temperatures of  $-10^\circ\text{C}$  and lower.

All measurements were made in total darkness, with the exception of the huddling experiments in which dim, incandescent illumination (approximately 4 foot-candles) was used to observe the animals. Rectal body temperatures were not recorded during oxygen consumption runs to avoid stressing animals. All experiments were performed between 0900 and 2100 hours, and the duration of each run was 3 to 4 hours at a specified  $T_a$ . For each run, the minimum oxygen consumption for a period of at least 12 min duration was calculated, and corrected to Standard Temperature and Pressure (STP).

To minimize acclimation effects, metabolic experiments were initiated within 24 hours of bringing the animals into the laboratory, and all major tests were finished within 15 days. Measurements at air temperatures of 15 to 25°C were completed during the first week of tests; all other runs (10 to -17°C) were conducted after 7 to 15 days in captivity. As a check for possible acclimation at temperatures of 8 to 20°C, the metabolic responses of 8 animals (6 in winter; 2 in summer) measured over this temperature range during the first 5 days, were repeated after 12 to 18 days in captivity.

#### Body Temperature

Resistance to body cooling in air and water, and the role of brown adipose tissue during swimming were assessed from abdominal and subcutaneous body temperature ( $T_b$ )

measurements. Except for a limited number of rectal determinations made with a YSI (No. 402) Tele-Thermometer probe, all laboratory observations of  $T_b$  were obtained via radio telemetry. Abdominal  $T_b$  measurements were made with continuous tone FM transmitters (Wang 1972) surgically implanted into the abdominal cavity. Surgery was performed within 24 hours of bringing the animals into the laboratory, and telemetry observations were initiated 2 to 3 days subsequent to the operation. Details concerning the construction, calibration and decoding techniques, and surgical procedure have been presented in Part II. Transmitters were selected which showed no signs of drift during initial calibrations. Upon completion of experiments all transmitters were removed from the animals and recalibrated. In the few cases in which detectable drift had occurred ( $< .5^\circ\text{C}$ ), linearity of drift was assumed (calibration slope remaining constant), and the  $T_b$  values were corrected on a daily basis.

Subcutaneous  $T_b$  measurements were obtained by means of commercial AM transmitters (Mini-Mitters Inc.) that measured 8 x 8 x 15 mm and weighed approximately 2 g. These transmitters were waterproofed and calibrated in a waterbath as described for the FM units (Part II), with the exception that the temperature-dependent frequency of the pulsed signal was determined with the aid of a stopwatch. The AM transmitters were employed to measure subcutaneous  $T_b$  overlying interscapular brown adipose

tissue (IBAT), and the mid-dorsal lumbar region (MDL) approximately 10 cm posterior to the IBAT. Each transmitter was inserted through a 1 cm incision in the skin, and was positioned over the desired site approximately 1 to 2 cm lateral to the incision. Transmitters were implanted in animals that had been in captivity for 19 to 20 days, and observations were begun 2 to 3 days subsequent to surgery. Problems with frequency overlap precluded the use of AM transmitters in both sites in the same individual. Only those muskrats equipped with the IBAT transmitter also carried the FM abdominal unit simultaneously.

#### Body Temperature and Activity in Relation to Air Temperature

Abdominal temperatures of 5 muskrats kept in holding cages within a walk-in environmental chamber were monitored by telemetry over a  $T_a$  range of  $-20$  to  $30^{\circ}\text{C}$  during summer, after 3 to 15 days in captivity. At each  $T_a$  setting,  $T_b$  was recorded at 10 to 20 min intervals over a 3 hour period, during which time activity was visually monitored at 2 to 3 min intervals. For two of these animals,  $T_b$  was also recorded during oxygen consumption runs between  $0^{\circ}\text{C}$  and  $-20^{\circ}\text{C}$ .

#### Body Temperature in Relation to Water Temperature

The  $T_b$  responses during and following immersion in water ranging in temperature from  $0$  to  $30^{\circ}\text{C}$  were evaluated

in 5 animals during summer, and in 5 animals during winter, after 3 to 20 days in captivity. During each run the water  $T_a$  was held within  $1^\circ\text{C}$  of the desired level, and most tests were conducted in a laboratory room where air  $T_a$  varied from 20 to  $23^\circ\text{C}$ . Each run consisted of releasing a single animal into a circular fibreglass tank (diam = 1.22 m; ht = 0.93 m) filled with water to a depth of 31 to 36 cm. The animal was permitted to swim and dive undisturbed in the tank for 25 min, while  $T_b$  was recorded at 2 min intervals, beginning with the time of entry into water. Upon completion of the run, the animal was returned to its holding cage (usually voluntarily). Following removal of an animal from water at  $6^\circ\text{C}$ ,  $T_b$  was recorded at 5 to 10 min intervals during rewarming at an air  $T_a$  of  $0^\circ\text{C}$ ,  $10^\circ\text{C}$ , or 20 to  $23^\circ\text{C}$ .

For tests involving concurrent measurements of abdominal and subcutaneous  $T_b$ , the above tank was placed in an environmental chamber kept at  $5^\circ\text{C}$ , and with a water  $T_a$  held constant at 0 to  $2^\circ\text{C}$ . Here, runs of 25 and 50 min duration were conducted.



## RESULTS

### Oxygen Consumption of Single Animals

The metabolic responses of muskrats to air temperatures ranging from  $-15$  to  $30^{\circ}\text{C}$  did not differ significantly between summer and winter (Fig. 1A). In both seasons oxygen consumption was minimal at  $25^{\circ}\text{C}$ , and increased above and below this value, with no indication of a well-defined thermoneutral zone. The mean SMR at  $25^{\circ}\text{C}$  was  $0.75 \text{ cc O}_2/\text{g.h}$  (range =  $0.66$  to  $0.83 \text{ cc O}_2/\text{g.h}$ ) in both summer (4 animals) and winter (4 animals). The irregularity in the metabolic curve between  $5^{\circ}\text{C}$  and  $25^{\circ}\text{C}$  precluded accurate definition of the lower critical  $T_a$ , but the increase in oxygen consumption appeared to be linear at air temperatures below  $5^{\circ}\text{C}$ . The slope of thermal conductance (i.e. coefficient of heat transfer,  $C$ ) was derived by Least-Squares regression for values between  $0^{\circ}\text{C}$  and  $-15^{\circ}\text{C}$ , and did not differ significantly between summer ( $-0.028 \text{ cc O}_2/\text{g.h.}^{\circ}\text{C}$ ) and winter ( $-0.027 \text{ cc O}_2/\text{g.h.}^{\circ}\text{C}$ ).

Considerable variability existed in the body weights ( $W_b$ ) of animals used for metabolic studies (range =  $550$  to  $1170 \text{ g}$ ), and a significant logarithmic regression ( $r = +0.68$ ,  $P < .01$ ) was obtained between minimal oxygen consumption and body weight, over a  $T_a$  range of  $15$  to  $30^{\circ}\text{C}$  (Fig. 2A). The exponential regression equation

Figure 1A. Mean minimal oxygen consumption (MR) of seasonally-acclimatized O. zibethicus at different ambient temperatures. Vertical lines denote 95 percent confidence limits of means; numbers above and below lines indicate sample size. Regression lines for summer ( $Y = 1.17 - 0.028X$ ) and winter ( $Y = 1.16 - 0.027X$ ) data were fitted by the method of Least-Squares over a  $T_a$  range of 0 to  $-15^{\circ}\text{C}$ , and extrapolated to  $\text{MR} = 0$  (dashed line).

Figure 1B. Minimal oxygen consumption (MR) of single, and of aggregates of three O. zibethicus at different ambient temperatures in winter. Mean values are presented for single animals and the results of individual runs for grouped animals. Regression lines for single ( $Y = 1.20 - 0.024X$ ) and for aggregates ( $Y = 1.04 - 0.016X$ ) of animals were fitted by the method of Least-Squares over a  $T_a$  range of 10 to  $-17^{\circ}\text{C}$ , and extrapolated to  $\text{MR} = 0$  (dashed line).

- - Muskrats 1 to 15 days in captivity in summer (8 animals; 84 measurements)
- - Muskrats 1 to 15 days in captivity in winter (12 animals; 94 measurements)
- △ - Muskrats fasted 12 to 14 hours prior to start of run in winter (11 animals; 11 measurements)
- ▲ - Muskrats fasted 12 to 14 hours prior to start of run in summer (8 animals; 8 measurements)
- - Aggregate of 3 muskrats 1 to 15 days in captivity in winter

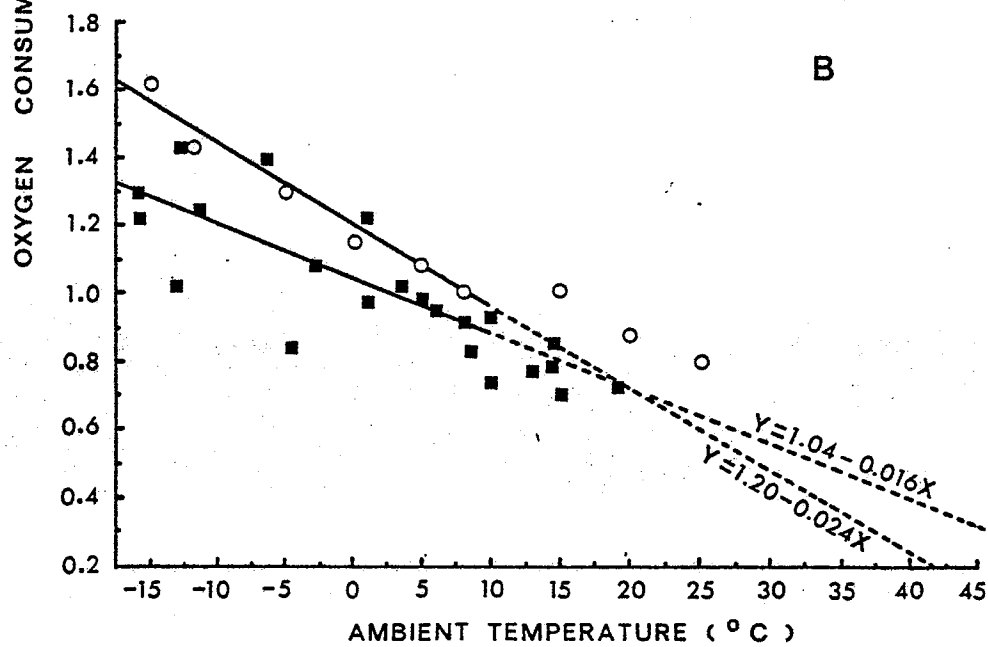
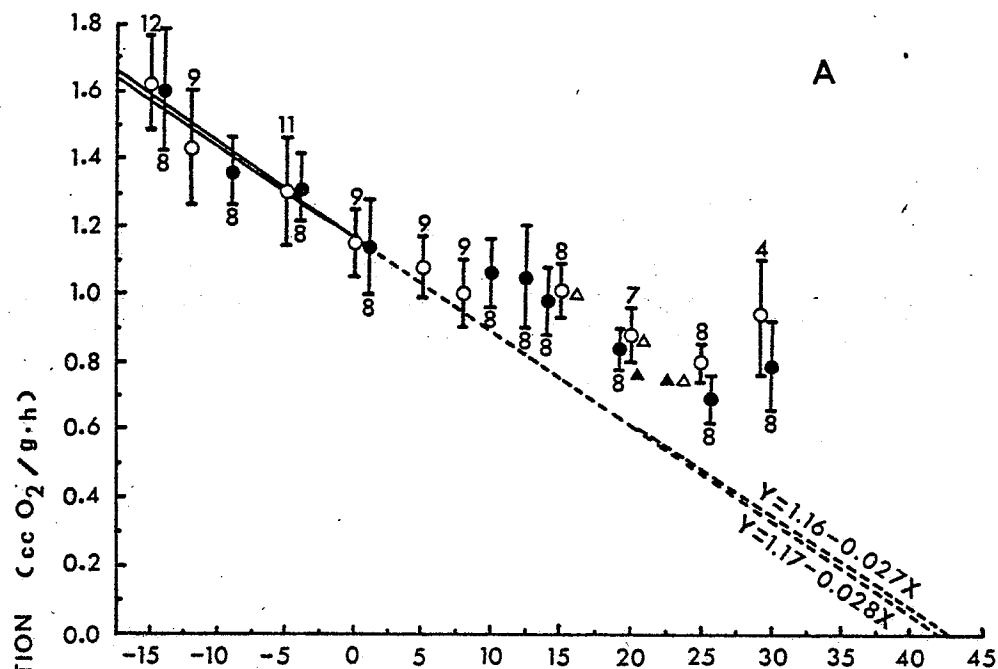
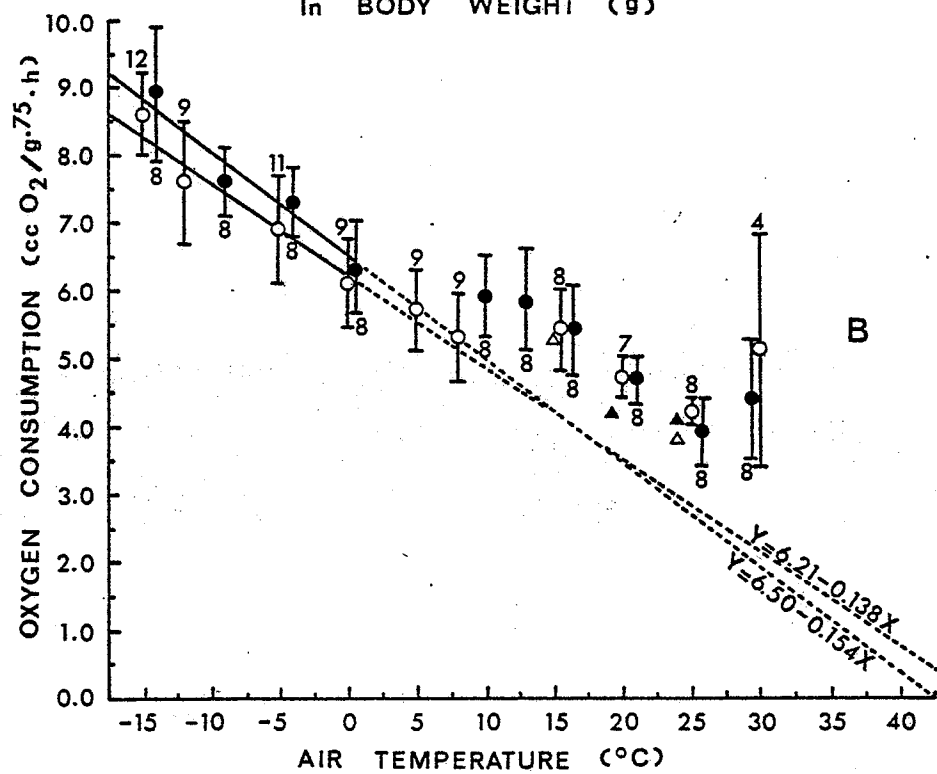
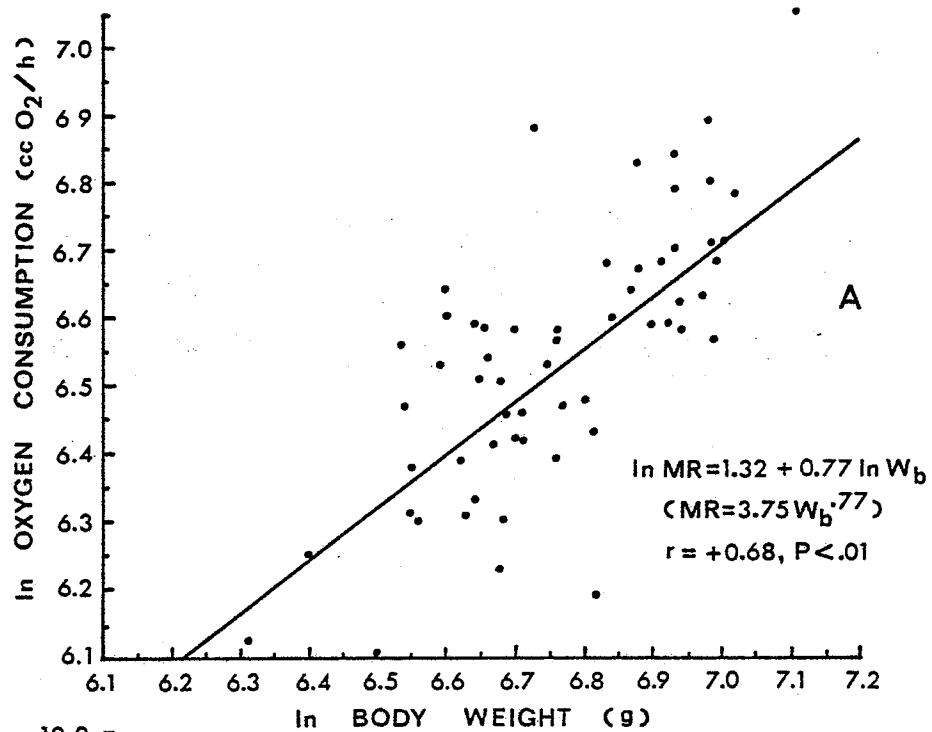


Figure 2A. The relationship between  $\ln$  body weight and  $\ln$  minimal oxygen consumption (MR) of seasonally-acclimatized O. zibethicus over an air  $T_a$  range of 15 to 30°C (summer and winter data pooled). Regression line was fitted by the method of Least-Squares.

Figure 2B. Mean minimal oxygen consumption (MR) of seasonally-acclimatized O. zibethicus at different ambient temperatures, after correction for metabolic size. Vertical lines denote 95 percent confidence limits of means; numbers above and below lines indicate sample sizes. Regression lines for summer ( $Y = 6.50 - 0.154X$ ) and winter ( $Y = 6.21 - 0.138X$ ) data were fitted by the method of Least-Squares over a  $T_a$  range of 0 to -15°C, and extrapolated to  $MR = 0$  (dashed line).

- - Muskrats 1 to 15 days in captivity in summer (8 animals; 84 measurements)
- - Muskrats 1 to 15 days in captivity in winter (12 animals; 94 measurements)
- △ - Muskrats fasted 12 to 14 hours prior to start of run in winter (11 animals; 11 measurements)
- ▲ - Muskrats fasted 12 to 14 hours prior to start of run in summer (8 animals; 8 measurements)



( $Y = 3.75 X^{0.77}$ ) did not differ significantly from the Brody-Proctor Equation,  $Y = 3.80 X^{0.73}$  (Brody 1945). Correction for metabolic size (dividing hourly oxygen consumption values by  $W_b^{0.75}$ ) as advocated by Hart (1971) and Kleiber (1975), did not significantly alter either the variability or pattern of oxygen consumption values, although it did increase the discrepancy between summer and winter conductance slopes (Fig. 2B).

No significant differences in oxygen consumption resulted from fasting animals 12 to 14 hours, as opposed to providing food ad libitum immediately prior to tests at 15 to 25°C (Fig. 1A).

Replication of metabolic experiments 12 to 18 days after initial tests resulted in a mean increase of 0.14 cc  $O_2$ /g.h (range = -0.17 to +0.45 cc  $O_2$ /g.h). However, this increase was not significant ( $t = 1.63$ ,  $P > .05$ ), and in 50 percent of the cases, the increase was less than 0.05 cc  $O_2$ /g.h. Details for individual animals are given in Appendix 9.

Although too few activity data were obtained in the laboratory for meaningful correlation with oxygen consumption, it was observed that maximal activity (active 58 percent of all observations made at 2 to 3 min intervals per 3 hour period) occurred at a  $T_a$  of 10°C. At 0 to 5°C, and at 25°C, activity was reduced to 31 and 28 percent, respectively. At sub-freezing temperatures, animals assumed spherical postures, punctuated by intermittent

bursts of activity. At a  $T_a$  of  $30^{\circ}\text{C}$ , muskrats often laid prostrate on the cage floor, with tails extended, and with the ventral surfaces of the hind feet exposed to air.

#### Oxygen Consumption of Grouped Animals

The weight-specific metabolic rate of an aggregate of three muskrats was generally lower than that of a single animal measured at a corresponding air  $T_a$  between  $20^{\circ}\text{C}$  and  $-17^{\circ}\text{C}$  during winter (Fig. 1B). Over a  $T_a$  range of  $10$  to  $-17^{\circ}\text{C}$ , the elevation, but not the slope of the regression of oxygen consumption on air  $T_a$  was significantly lower (Covariance Analysis,  $F = 11.1$ ,  $P < .01$ ) in grouped, than in single individuals. As in single animals, there was no clear demarcation of thermoneutrality in the grouped animals, although here, the mean oxygen consumption between  $10^{\circ}\text{C}$  and  $20^{\circ}\text{C}$  ( $0.79 \text{ cc O}_2/\text{g.h}$ ) did not differ significantly from that of single, non-fasted animals at  $25^{\circ}\text{C}$  ( $0.80 \text{ cc O}_2/\text{g.h}$ ).

The  $T_a$  between adjacent individuals (measured with a YSI No. 402 Tele-Thermometer probe) in a "close huddle" ranged from  $24$  to  $28^{\circ}\text{C}$ , when the air  $T_a$   $15 \text{ cm}$  above the group was varied between  $0^{\circ}\text{C}$  and  $10^{\circ}\text{C}$ .

#### Aggregation Behavior of Muskrats in Winter

In all runs involving aggregations of muskrats, the animals proved highly gregarious, with no outward manifestations of aggression. Group conformation was highly

variable, ranging from animals piled one on top of the other to individuals sitting side by side. The two extremes of this behavioral gradient are illustrated in Appendix 10. No consistency was observed between conformation pattern and air  $T_a$ , although there was a greater tendency for horizontal rather than vertical displacement at warmer temperatures. Periodic re-shuffling of individuals within the group occurred at all air temperatures, with a mean periodicity of 12 min (range = 2 to 35 min,  $n = 256$  observations) over a  $T_a$  range of 0 to 10°C. Re-shuffling was frequently accompanied by vocalizations, and the movement of one animal over the bodies of other individuals often involved pronounced extension of the hind feet of the former animal.

#### Body Temperature

The abdominal temperatures of five muskrats in summer ( $n = 74$ ), and of five muskrats in winter ( $n = 79$ ) recorded via telemetry at an air  $T_a$  of 20 to 23°C, varied from 35.8 to 39.3°C. For these same individuals, the mean ( $\pm$  S.E.)  $T_b$  in summer ( $37.5 \pm .07^\circ\text{C}$ ) was not significantly different from that in winter ( $37.6 \pm .07^\circ\text{C}$ ). With the exception of a single female (No. 7), no  $T_b$  differences were observed between sexes. In the case of No. 7, the mean  $T_b$  rose from 37.5 (June 6-9,  $n = 105$ ) prior to giving birth to a litter on June 12, to 38.2°C (June 13-16,  $n = 123$ ) after giving birth, and while the female was nursing young.



This increase was highly significant ( $t = 19.2$ ,  $P < .001$ ).

The rectal  $T_b$  of eight animals examined during September at an air  $T_a$  of 20 to 23°C varied from 36.4 to 39.1°C, with a mean ( $\pm$  S.E.) of  $38.0 \pm .28^\circ\text{C}$ . Owing to potential stress incurred while restraining the animals, these rectal values should be viewed with caution.

Abdominal temperatures determined by rapid insertion of a YSI thermistor probe through a small abdominal incision in five lightly-anaesthetized animals indicated a mean  $T_b$  gradient of  $1.1^\circ\text{C}$  between the lower and upper abdomen. Highest temperatures were recorded in the vicinity of the liver and diaphragm (Appendix 11).

#### Abdominal Temperature in Relation to Air and Water Temperature

It is evident from Fig. 3 that abdominal  $T_b$  is relatively constant over an air  $T_a$  range of -20 to 30°C.

Linear, or slightly curvilinear rates of abdominal cooling were observed at all water temperatures tested in summer, and at all water temperatures below, but not including 30°C in winter (Fig. 4). Least-Squares regression of  $T_b$  or  $\ln T_b$  on time in water resulted in summer and winter cooling slopes which were significantly different at all water temperatures tested (Covariance Analysis,  $P < .01$ ). Also, as indicated in Table 1, Least-Squares regression of the thermal gradient,  $\ln (T_b - \text{Water } T_a)$  on time in water resulted in summer

Figure 3. Body temperatures of O. zibethicus at different air temperatures in the laboratory during July and August, 1974 (5 animals; 449 observations). Horizontal and vertical lines denote means and ranges, respectively; rectangular boxes define the 95 percent confidence limits of the means. Values in parentheses indicate the number of observations made at 10 to 20 min intervals per 3 hour surveillance period.

- ☐ - Measurements made in holding cages (5 animals)
- ☒ - Measurements made in metabolism chamber during oxygen consumption runs (2 animals)

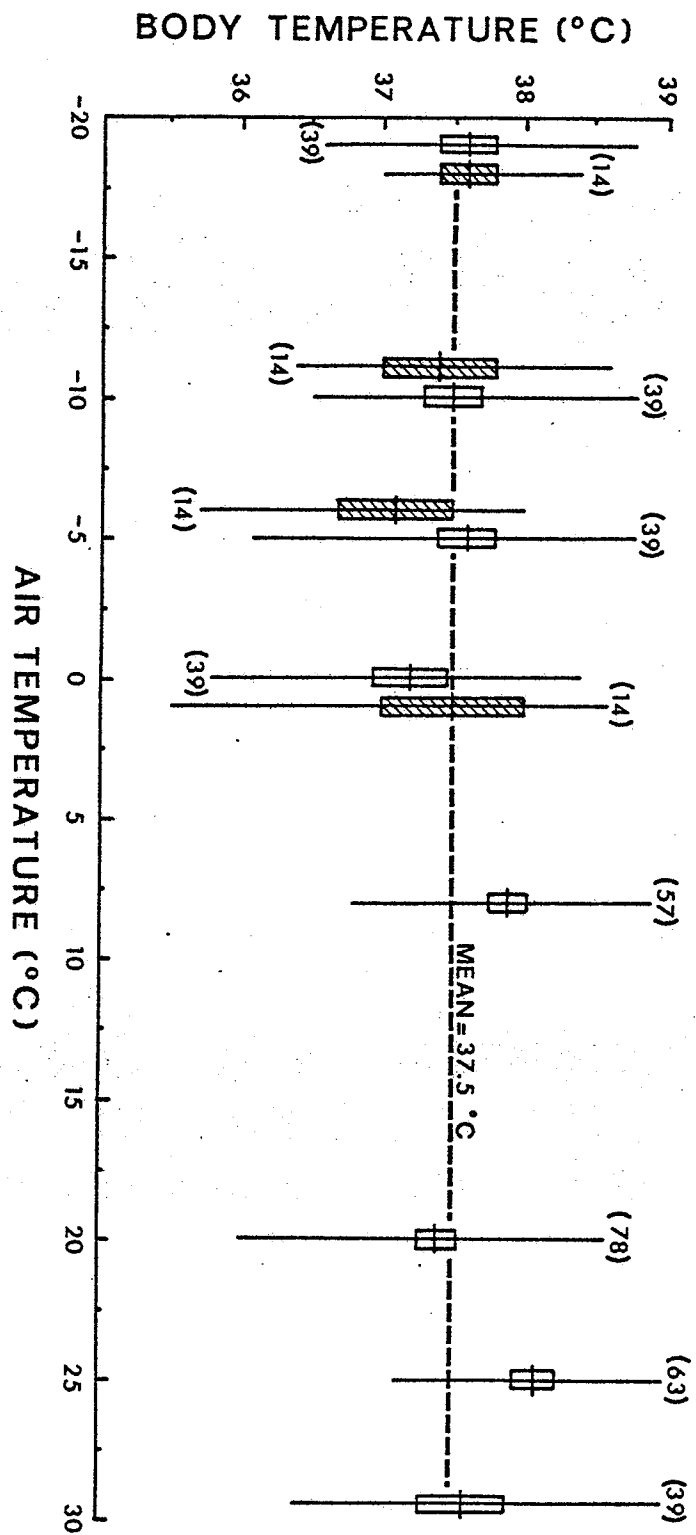


Figure 4. Abdominal temperature changes of O. zibethicus during immersion in water ranging from 6 to 30°C in summer (5 animals; 1036 observations) and in winter (5 animals; 1106 observations). Symbols denote mean values (9 to 29 observations per 2 min interval); numbers in parentheses indicate rates of cooling (°C/min) based on Least-Squares regression of  $T_b$  on time in water.

		No. of Runs	
Water $T_a$ (°C)		Winter	Summer
○ -	6	29	23
● -	10	10	9
△ -	15	10	10
▲ -	20	10	10
□ -	25	10	12
■ -	30	10	10

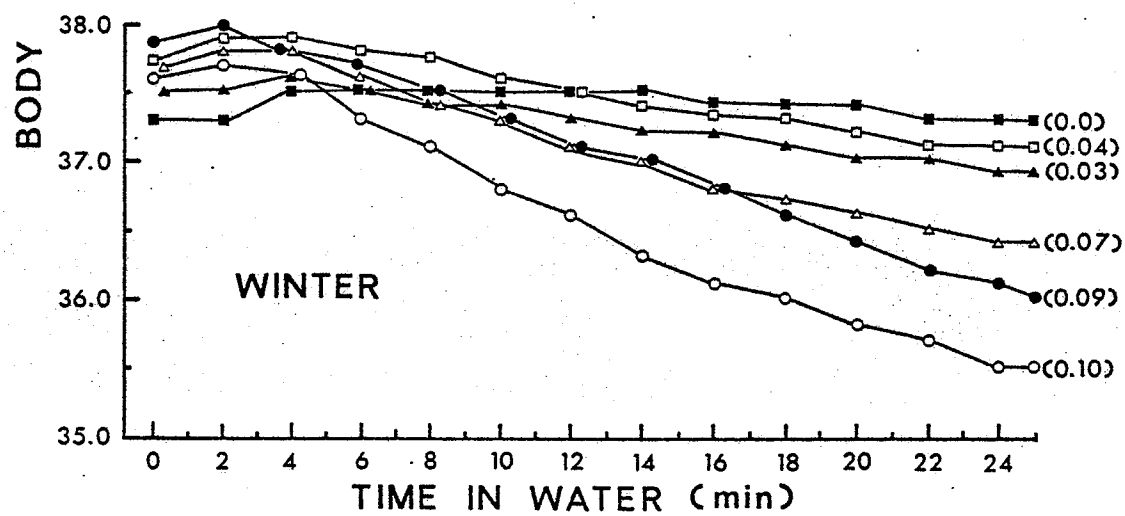
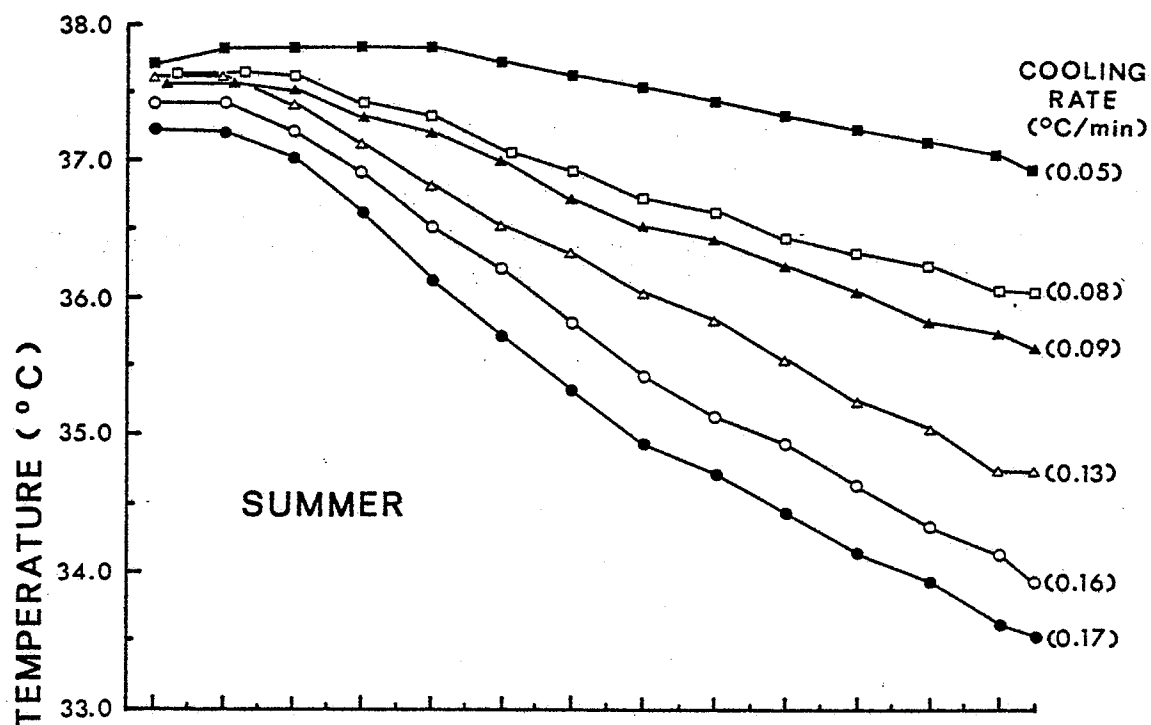


Table 1. Least-Squares regression analysis of the relationship between  $\ln (T_b - \text{Water } T_a)$  and time in water (X variable) for O. zibethicus in summer and winter

Period	Water $T_a$ (°C)	n <sup>a</sup>	Reg. coeff.	r	t-value	Reg. Eq. (Y=a+bX)
Summer	6	253	-0.0054	-0.75	18.00	Y=3.46 - 0.0054X
	10	99	-0.0068	-0.64	8.50	Y=3.32 - 0.0068X
	15	110	-0.0064	-0.75	11.88	Y=3.13 - 0.0064X
	20	110	-0.0057	-0.70	10.29	Y=2.89 - 0.0057X
	25	132	-0.0069	-0.49	6.47	Y=2.56 - 0.0069X
	30	110	-0.0062	-0.53	6.56	Y=2.10 - 0.0062X
Winter	6	319	-0.0034	-0.61	13.60	Y=3.46 - 0.0034X
	10	110	-0.0033	-0.79	12.22	Y=3.34 - 0.0033X
	15	110	-0.0030	-0.58	7.39	Y=3.13 - 0.0030X
	20	110	-0.0020	-0.32	3.48	Y=2.87 - 0.0020X
	25	110	-0.0033	-0.41	4.70	Y=2.57 - 0.0033X
	30	110	+0.0012	-0.10	1.04*	Y=2.02 - 0.0012X

<sup>a</sup> No. of observations recorded at 2 min intervals (5 muskrats in summer; 5 muskrats in winter)

\* Not significant ( $P > .05$ ); all other t-values significant at  $P < .01$ .

regression coefficients (-0.0054 to -0.0069) which were usually at least double those in winter (-0.0020 to -0.0034). Whereas the latter seasonal differences were highly significant (Covariance Analysis,  $P < .01$ ), the regression coefficients within either season were independent of water  $T_a$  (Covariance Analysis,  $P > .05$ ). The net decline in  $T_b$  per 25 min excursion appeared to increase in direct proportion to decreasing water  $T_a$ , at temperatures ranging from 10 to 30°C in summer, and from 6 to 30°C in winter (Fig. 5). An unexpected reversal of this trend was observed at 6°C during summer, and at 2°C during winter.

#### Abdominal Rewarming Following Immersion in Water

No significant correspondence was observed between the rate of abdominal rewarming following immersion in water at 6°C, and the air  $T_a$  at which rewarming occurred, either summer or winter (Fig. 6). Seasonal comparisons of rewarming slopes were not attempted, owing to significant differences in the  $T_b$  levels of muskrats in summer and winter at the time of removal from water ( $t$ -difference = 4.72,  $P < .01$ ).

#### Abdominal and Subcutaneous Temperature Responses to Immersion in Water at 2°C

The temperature response of a telemeter in contact with IBAT was reversed from that of telemeters situated

Figure 5. Mean net abdominal temperature changes ( $\Delta T_b$ ) of O. zibethicus during immersion in water ranging from 6 to 30°C in summer (5 animals; 97 runs), and from 2 to 30°C in winter (5 animals; 74 runs). Vertical lines denote the 95 percent confidence limits of the means; values above and below these lines indicate the number of runs.

○ - Summer

● - Winter



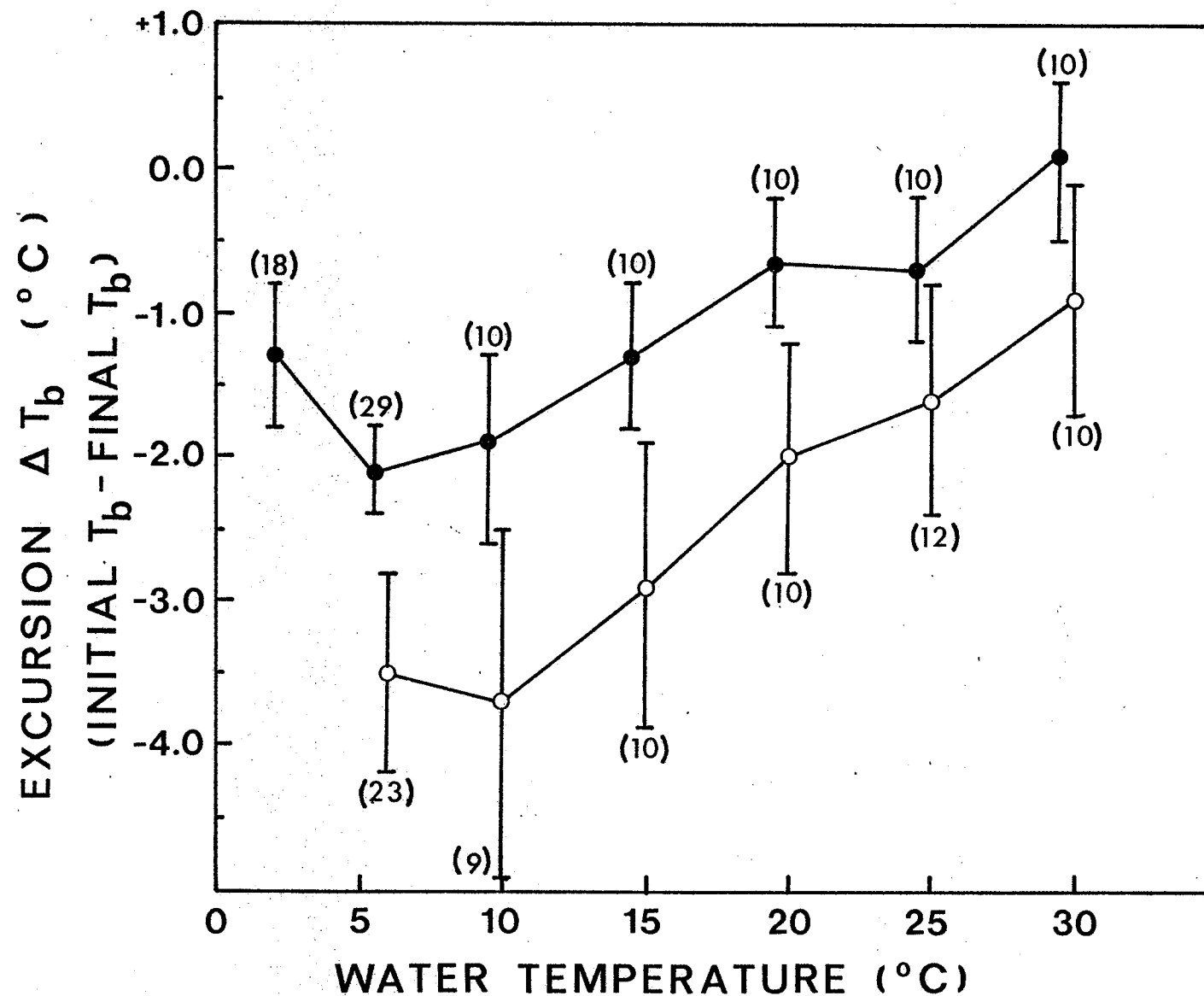
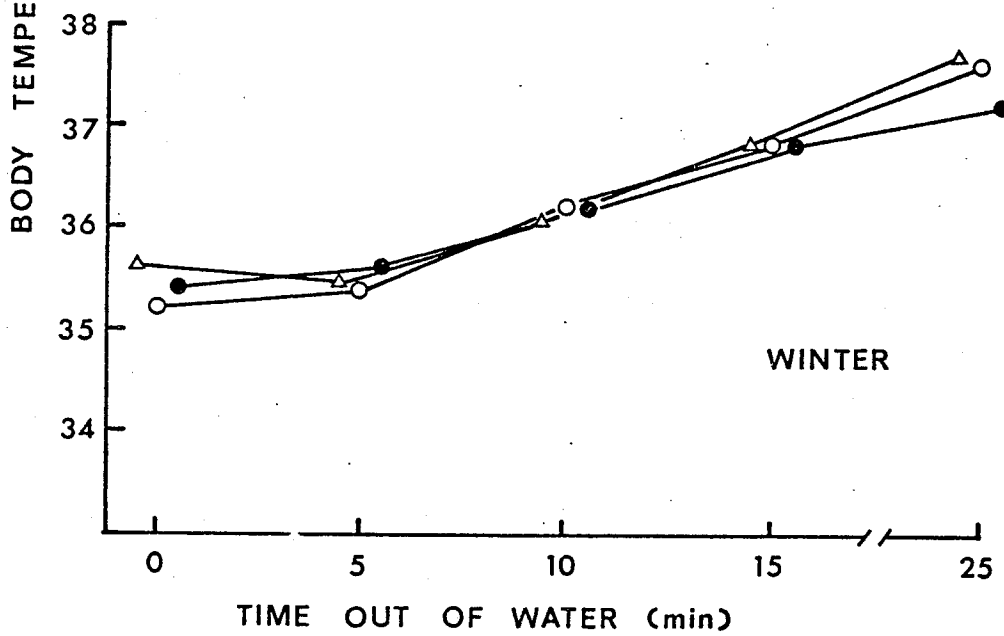
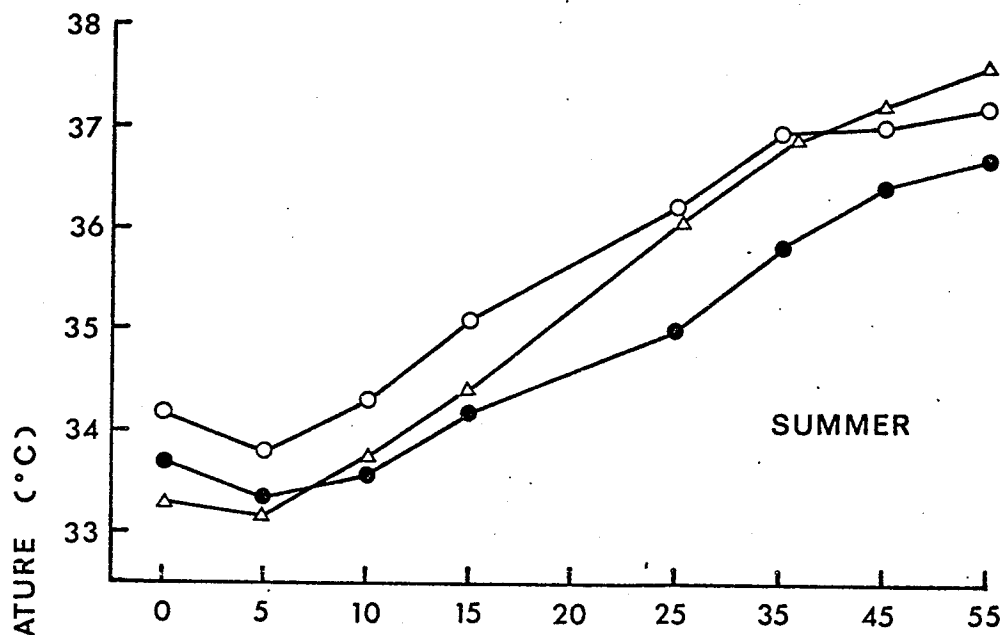


Figure 6. Mean abdominal temperatures of O. zibethicus recorded during rewarming at air temperatures of 0°C, 10°C, and 20 to 23°C, following removal from water at 6°C. Data were obtained from five muskrats in summer (n = 216 observations), and from five muskrats in winter (150 observations).




Air T<sub>a</sub> (°C)

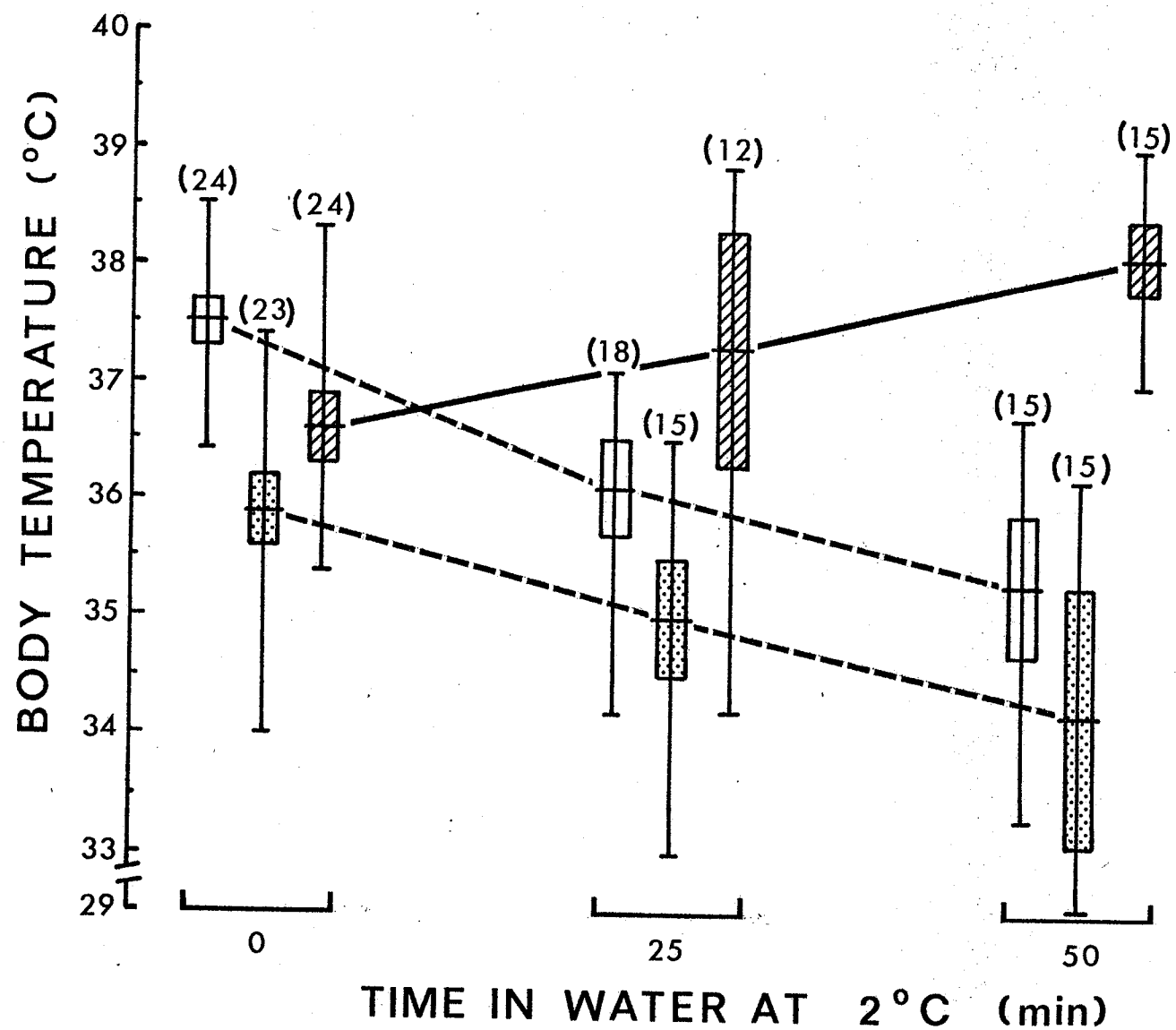
●	-	0
○	-	10
Δ	-	20 to 23



in the abdomen, and overlying skeletal muscle in the MDL region during immersion in cold water (Fig. 7). Covariance Analysis indicated that the Least-Squares regression slope of the IBAT temperature response ( $+ 0.029^{\circ}\text{C}/\text{min}$ ) was significantly different from that of both the abdomen ( $-0.044^{\circ}\text{C}/\text{min}$ ) and the MDL region ( $-0.033^{\circ}\text{C}/\text{min}$ ), respectively ( $F = 84.3$  and  $36.9$ ,  $P < .001$ ).

Figure 7. Subcutaneous (IBAT and MDL region) and abdominal temperature responses of O. zibethicus to prolonged exposure to cold water (2°C) in winter. Horizontal and vertical lines denote means and ranges, respectively; rectangular boxes define the 95 percent confidence limits of the means. Values in parentheses indicate number of observations.

-  - Abdominal temperature (3 animals)
-  - Subcutaneous temperature overlying interscapular brown adipose tissue (IBAT)(3 animals)
-  - Subcutaneous temperature overlying skeletal muscle in the mid-dorsal region (MDL)(2 animals)



## DISCUSSION

### Body Temperature Regulation in Air

The metabolic rate (MR) of individual O. zibethicus over an air  $T_a$  range of 5 to 30°C (Fig. 1A) represents a marked departure from the theoretical model of heat transfer in homeotherms (Kleiber 1975). Activity has been identified as a major source of error in estimating resting MR in small mammals (Hart 1971; Heusner 1971), and this factor may have biased MR determinations between 5 and 20°C in the present study. At lower or higher temperatures, the need for thermal economy or heat dissipation may have precipitated stationary postural adjustments which presumably overrode activity drives. Thus, the thermoneutral zone may actually extend from 10 to 25°C as reported by Hart (1962) and McEwan et al. (1974), but true resting MR at thermoneutrality may have been obtained only at 25°C in single muskrats (Fig. 1A). This hypothesis is consistent with the finding that the mean MR of grouped muskrats (which exhibited minimal activity) between 10 and 20°C was virtually identical with that of single animals measured at 25°C (Fig. 1B).

Alternatively, the apparent plateau in MR between approximately 5°C and 15°C may represent thermoneutrality, whereas the decline in MR at higher temperatures is indicative of heat stress (Fig. 1A). As suggested for the

rock hyrax, Heterohyrax brucei (Bartholomew and Rainy 1971) such a reduction in MR at higher temperatures may occur in response to a decrease in muscle tonus. Although microtines have a poor tolerance to heat stress generally (Chew 1951; Wiegert 1961; Beck and Anthony 1971), behavioral responses for maximizing heat dissipation occurred only at 30°C in the present study. This observation, together with the stability of  $T_b$  at all air temperatures above 15°C argue against the latter hypothesis.

Assuming 25°C is a thermoneutral  $T_a$ , the SMR of O. zibethicus (0.75 cc  $O_2$ /g.h) is 123 percent of the SMR predicted from its weight (880 g; 20 animals) according to the formula:  $cc\ O_2/g.h = 3.8\ W_b^{-0.27}$  (Morrison et al. 1959). Elevated standard metabolic rates appear to be typical of microtines in general. In a summary of 12 studies spanning 8 species of voles, Beck and Anthony (1971) reported SMR values exceeding weight-predicted calculations by 38 to 112 percent. These authors, as well as Packard (1968) have emphasized the adaptive value of an elevated SMR in a group with presumed boreal origins (Hooper 1949). Of perhaps greater significance to O. zibethicus is the relatively shallow slope of thermal conductance,  $C$  (-0.027 to -0.028 cc  $O_2$ /g.h.°C), which is indistinguishable from that (-0.027 cc  $O_2$ /g.h.°C) obtained by Hart (1962). This value of  $C$  is 75 to 78 percent of the weight-predicted calculation based on the formula:  $C = 1.10\ W_b^{-0.505}$  (Herreid and Kessel 1967),



implying that total insulation (pelage + tissue) in the muskrat is excellent at low ambient temperatures.

The  $T_b$  stability observed over broad air  $T_a$  limits (Fig. 3) has also been confirmed in other microtines (Hart and Heroux 1955; Packard 1968; Beck and Anthony 1971). However, this finding is in sharp contradiction to Hart's (1962) observation that rectal  $T_b$  in O. zibethicus declined at all air temperatures below 10°C, and conversely, rose at all temperatures above 20°C. As details pertaining to Hart's (1962) techniques for recording  $T_b$  changes are unavailable, it is not possible to resolve this seemingly major discrepancy in results.

On the basis of present data, it must be concluded that O. zibethicus is capable of precise  $T_b$  regulation over an air  $T_a$  range encompassing the microclimate of this species in nature (Part I). This capability may be largely attributed to an excellent pelage insulation, vasomotor responses that alter peripheral tissue insulation in naked extremities (Johansen 1962), and postural adjustments that modify surface area-to-volume relationships.

#### Body Temperature Regulation in Water

Based on abdominal cooling, muskrats swimming under laboratory conditions appear to be in a negative energy balance (heat loss exceeds heat production) at all water temperatures between 0°C and 30°C in summer, and between

0°C and 25°C in winter (Figs. 4 and 5). These findings are reasonably consistent with Hart's (1962) observation that the rectal  $T_b$  of this species fell at all water temperatures below 20°C.

As in the present study, Hart's (1962) data also reveal that the rate of cooling increases in approximate proportion to decreasing water  $T_a$ . This finding, combined with the observation that the regression coefficient (b) in the linear equation:  $\ln (T_b - \text{Water } T_a) = a + b (\text{time in water})$  is relatively independent of water  $T_a$  (Table 1) suggest that heat production is constant over most water temperatures. However, this deduction contradicts the gradual increase in MR observed by Hart (1962) and Shcheglova (1965) when O. zibethicus was restrained in water at successively lower temperatures.

Based on the assumption that similar MR responses occur in free-swimming muskrats, the present results suggest that pronounced abdominal vasoconstriction may occur during immersion in water. Thus, MR may be adjusted to maintain a constant thoracic-cranial temperature while the vasoconstricted abdomen cools in accordance with the thermal gradient between abdomen and water. The unexpected reduction in abdominal cooling between 10°C and 6°C during summer, and between 6°C and 2°C during winter (Fig. 5) may reflect an increase in heat production at these temperatures, perhaps triggered by a drop in peripheral  $T_b$  below a critical threshold. These conjectures

are speculative, however, and further metabolic studies of muskrats in water are required to verify the relationship between MR and  $T_b$  during swimming.

Contrary to laboratory findings, swimming behavior of O. zibethicus in the field was often accompanied by an elevation of  $T_b$  during summer (Part II). These differences may be partially explained by the restriction of activity in laboratory tests. In addition, the timing of the forced immersion runs in the laboratory may have been out of phase with innate metabolic-activity rhythms, and hence no allowance was made for possible physiological "anticipation" of entry into water.

Compared with other small- to medium-sized mammals studied to date, the muskrat is relatively resistant to deep body cooling in water. Smyth (1973), for instance, noted a poor tolerance to hypothermia in the free-swimming platypus, Ornithorhynchus anatinus. In a study in which experimental animals were immersed to the neck in water at 10°C, Spealman (1946) observed rates of cooling of approximately 1.40°C/min in the laboratory rat, Rattus norvegicus (227 g), 0.49°C/min in the domestic rabbit, Oryctolagus cuniculus (3.59 kg), and 0.16°C/min in the dog, Canis familiaris (27.6 kg). With the exception of the dog, these latter values all exceeded cooling rates of muskrats at a similar water  $T_a$  during both summer (0.17°C/min) and winter (0.09°C/min). Although these results would seem to reflect the insulative

adaptations (see above) and aquatic habits of O. zibethicus, comparisons with values in the literature are complicated by variation in experimental design.

### Seasonal Adaptations to Cold

#### Aggregation Behavior

The slope of thermal conductance for aggregates of 3 O. zibethicus ( $-0.016 \text{ cc O}_2/\text{g.h}$ ) represents a 33 percent reduction from that of single animals ( $-0.024 \text{ cc O}_2/\text{g.h}$ ) measured over the same  $T_a$  range (Fig. 1B). This compares favorably with the 30 to 55 percent reduction in  $C$  noted in groups of 3 to 5 bank voles, Clethrionomys glareolus (Gebczynski 1969), and yellow-necked field mice, Apodemus flavicollis (Fedyk 1971).

Such findings are consistent with theoretical expectations of reduced surface area-to-volume ratio and improved insulation resulting from group aggregation. Moreover, the observation that extrapolated MR fails to intercept the X-axis at  $T_b$  when  $\text{MR} = 0$  (extrapolated value =  $65^\circ\text{C}$ ) indicates a pronounced departure from the linearized model of heat transfer (formerly called Newton's Law of Cooling) described by Kleiber (1975). The results imply that  $C$  does not approach constancy at the lower critical  $T_a$ , but instead continues to decline, possibly as a result of more efficient huddling at lower temperatures.

It should be appreciated that the calculation of  $C$  is of theoretical interest only; the lowest  $T_a$  encountered

by aggregates of muskrats in nature is probably seldom less than  $0^{\circ}\text{C}$  (Part I). At this  $T_a$ , the energy saving resulting from aggregation in the laboratory amounts to only about 13 percent. Of course, the actual number of animals occupying a winter lodge may be at least double that used in the present study (Parts I and II), and hence this latter figure may be an underestimate. On the other hand, the  $T_a$  between adjacent individuals is clearly elevated during huddling, and field studies (Part I) revealed a marked increase in lodge  $T_a$  resulting from group occupation. Thus, the exchange and conservation of heat among the residents of a winter lodge probably represents the major ecological advantage of aggregation behavior in O. zibethicus.

#### Increased Resistance to Cooling

The improved resistance to abdominal cooling during winter that was observed in the aquatic experiments is clearly adaptive to foraging in near-freezing water. This reduction in cooling may be effected through improved pelage, and possibly tissue insulation (vasomotor adaptations) and/or increased capabilities for heat production in winter. Despite the apparent increase in buoyancy observed in muskrats during winter, the oxygen consumption data argue against improved insulation. However, caution must be exercised in extrapolating from thermal conductance measurements in air, to insulative

adjustments in water.

The absence of seasonal differences in thermal conductance confirms the results of Hart (1962), and lends support to Hart's (1956) finding that improvement of the insulative value of the winter pelt is slight in this species (11.9 percent). Comparable results have been obtained in seasonal acclimatization studies of other microtines (Rigaudiere and Delost 1965; Gorecki 1968; Cherry and Verner 1975), as well as the wild Norway rat, Rattus norvegicus (Hart and Heroux 1963). The idea has been advanced (Hart 1962) that O. zibethicus is, to varying degrees, cold-adapted throughout the year, and hence fails to exhibit seasonal changes in insulation. Perhaps the need for a waterproof pelage, combined with occasional exposure to cool, windy conditions during summer foraging (Part II) necessitates a good insulation in summer, as in winter. However, considering the broad annual range of air, and especially water  $T_a$  in Delta Marsh (Part I), one might still expect seasonal differences in the slope of thermal conductance, contrary to present findings.

#### Brown Adipose Tissue (BAT)

The elevation of IBAT temperature in muskrats exposed to cold water during winter infers an active role of BAT in offsetting hypothermia. This is, to my knowledge, the first demonstration of a functional role of BAT during swimming in an aquatic mammal. Results comparable with

those in Fig. 7 were obtained in cold-acclimated hamsters, Mesocricetus auratus, in which Pohl (1965) noted an elevation of subcutaneous IBAT, and concurrent decline in subcutaneous thoracic and lumbar temperatures with decreasing air  $T_a$ .

The strategic location of BAT provides for selective heating of the thoracocervical spinal cord, heart, and great veins returning cooled blood to the thorax from the peripheral circulation (Smith and Roberts 1964). This function would seem particularly adaptive in an aquatic species such as O. zibethicus, which is capable of pronounced cooling in naked extremities (Johansen 1962). In this context, Blix et al. (1975) have commented on the potential significance of BAT in minimizing deep body cooling in diving seals. Warming of spinal thermal receptors by the venous drainage of cervical and interscapular deposits of BAT may also serve to suppress energetically-costly shivering by skeletal muscle in cold (Horwitz and Smith 1971). Again, this role of BAT may be especially adaptive in an aquatic medium where shivering would presumably intensify convective heat loss, resulting in highly inefficient heat utilization. In fact, there was a noticeable reduction in shivering among muskrats exposed to cold water during winter in this study. Brown adipose tissue may also augment the heat production of a muskrat rewarming in a pushup or lodge following foraging activity in cold water (Part II).

A correspondence between BAT mass and capacity for non-shivering thermogenesis has been previously reported (Smith and Roberts 1964; Himms-Hagen 1970), and Aleksiuk and Frohlinger (1971) observed an inverse correlation between IBAT mass and air  $T_a$  in O. zibethicus inhabiting Delta Marsh. Similar field results have been obtained for other microtines (Didow and Hayward 1969; Hissa and Tarkkonen 1969; Sealander 1972), providing further support for an active role of non-shivering thermogenesis in cold adaptation in this rodent subfamily.

Finally, it must be emphasized that IBAT temperatures measured in this study are indicative of a trend only. The superficial position of the IBAT transmitter precluded accurate temperature determination within the tissue itself. Additional studies are needed to determine the metabolic contribution of non-shivering thermogenesis to aquatic thermoregulation in O. zibethicus. This species is one of the largest non-hibernators known to possess brown adipose tissue as an adult, and conversely, it is also one of the smallest aquatic mammals (Irving 1973), and hence one with the greatest potential for cold stress in water.



PART IV

A Note on Winter Movements and Home Range in the  
Muskrat (Ondatra zibethicus)

## INTRODUCTION

To date, a substantial quantity of mark and recapture data have been gathered for Ondatra zibethicus indicating that movements within the summer home range seldom exceed 180 m (Takos 1944; Beshears and Haugen 1953; Wragg 1955; Sather 1958). Based on winter recoveries of animals tagged in late summer or fall, it appears that winter animals seldom move beyond the home range established during the period of open water (Alduous 1946; Fuller 1951; Stevens 1953; Sather 1958). Unfortunately, most of these data have been obtained from winter fur harvests, and difficulties in live-trapping after freeze-up have precluded the accurate delineation of winter home range in this species.

The present study provides insight into the winter movements and home range of O. zibethicus based on the distribution patterns of winter shelters, and on telemetry observations of transmitter-equipped animals. The data reported herein were obtained while conducting field investigations of the microenvironment (Part I) and daily activity and body temperature patterns (Part II) of the muskrat during winter.

## MATERIALS AND METHODS

All observations were made in Delta Marsh, Manitoba, between Dec. 2 and Feb. 24, 1973-74, and between Nov. 6 and Jan. 4, 1974-75. Telemetry studies were conducted on three male and three female subadult and adult muskrats (625 to 900 g) in 1973-74, and on five male subadult and adult animals (700 to 941 g) in 1974-75. Live-trapping methods have been described in Part II.

Within 12 hours of capture, each animal was equipped with an intra-abdominal FM transmitter (Wang 1972), and was released at the site of capture not later than 24 hours after surgery. The continuous tone emitted by each transmitter was received at a specific frequency on the FM band of a transistor radio (Sony AM/FM Cassette-Recorder, Model CF-350 and CF-400). Telemetry instrumentation and monitoring techniques have been described in detail in Part II.

Winter shelter definitions followed Dozier (1948) and Fuller (1951). All distances indicated in the present paper were paced off (estimated accuracy =  $\pm 4$  percent). Daily maximum-minimum air temperatures were available from the University of Manitoba Field Station located within 2.5 km of all study sites. Lodge ambient temperature ( $T_a$ ) was recorded at hourly intervals with a Grant Miniature Temperature Recorder as outlined in Part I.

## RESULTS

Based on a total of 870 observations of 11 muskrats, 50 percent or more of all position determinations for each animal were made within 15 m of its major dwelling lodge. For 10 of the 11 animals, the maximum distance travelled from a dwelling lodge was less than 150 m. The exceptional individual (No. 5) traversed 366 m in early December, 1973, when it abandoned the lodge at which it was trapped and relocated in a neighbouring lodge complex. Once relocated, the movements of this animal were comparable to those of the other individuals studied. The abandonment of the first lodge may have been in response to damage to this structure resulting from trapping efforts.

Most foraging activity occurred within a 5 to 10 m radius of a lodge or pushup, and telemetry revealed that the distribution of winter shelters delineated home ranges fairly accurately. Feeders and pushups were often distributed about a dwelling lodge in a "stepping stone" pattern (Figs. 1 and 2), and telemetry indicated that muskrats usually traversed intervening distances (especially between lodges and pushups) quickly, via direct routes. In contrast, animals travelling along the zone of emergent vegetation frequently moved slowly, stopping intermittently (often > 5 min).

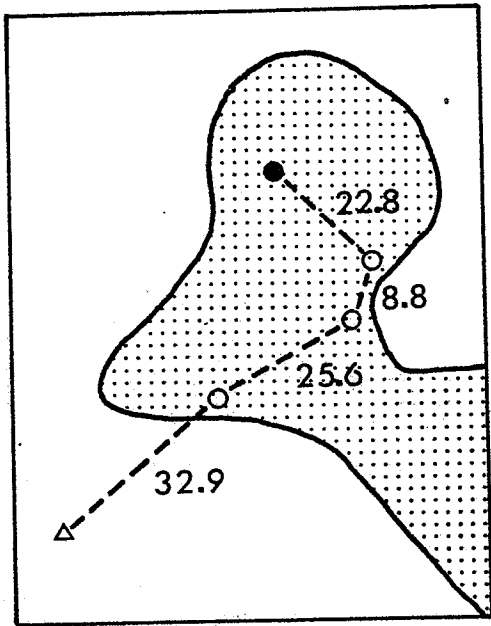
During early winter there was also evidence of inter-

Figure 1. Distribution patterns of winter shelters used by O. zibethicus in Delta Marsh. Numbers indicate distances (m) between associated shelters. Sites II through IV denote the home ranges of the following transmitter-equipped animals:

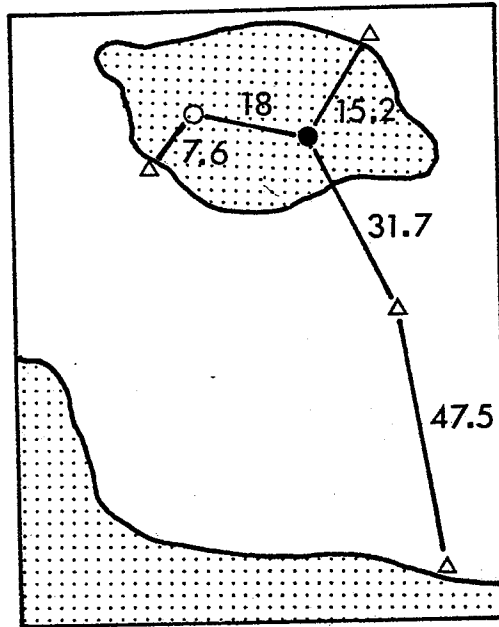
- Site I - Unmarked individuals
- Site II - Nos. 5 (male) and 28 (female)
- Site III - Nos. 3 (female) and 4 (male)
- Site IV - Nos. 1 (female) and 2 (male)

- - Dwelling lodge
- - Feeding lodge
- △ - Pushup
- ▣ - Emergent vegetation (Scirpus spp.)
- - Route verified by telemetry (residents of Sites II and IV)
- ..... - Route verified by telemetry (residents of Site III)
- - Potential route (not verified by telemetry)

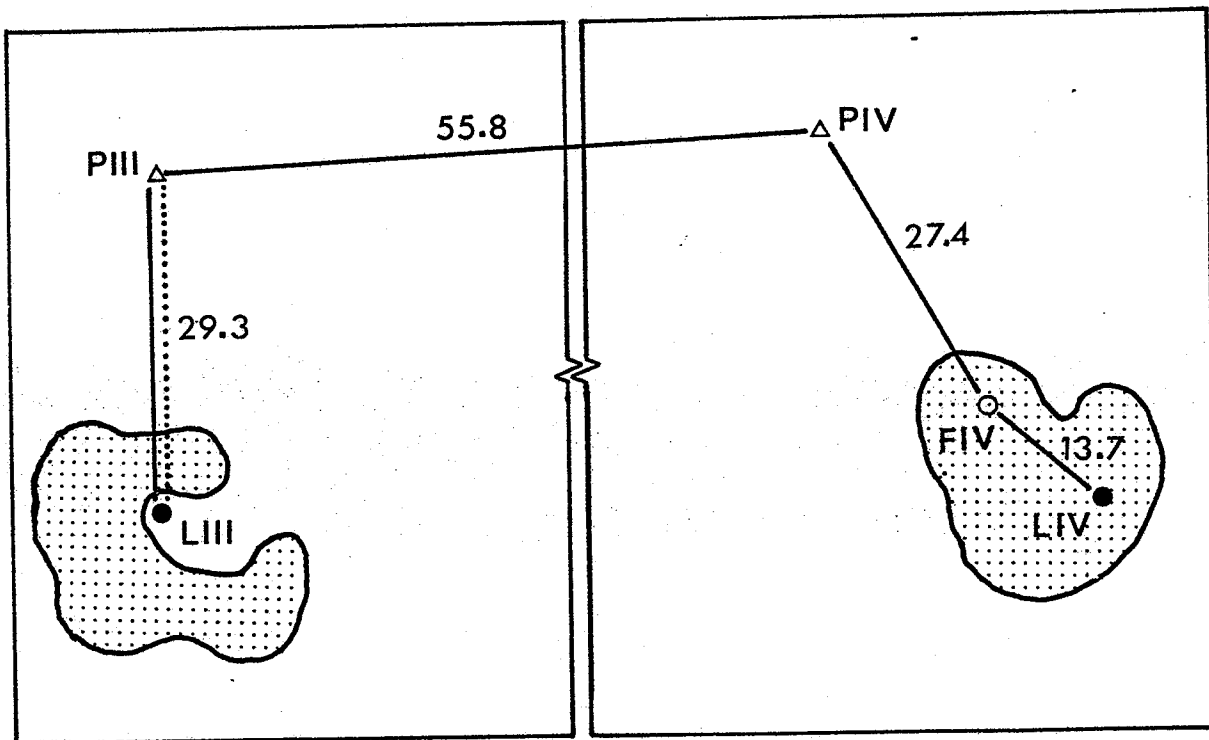
# FORESTER'S BAY



SITE I



SITE II



SITE III

SITE IV

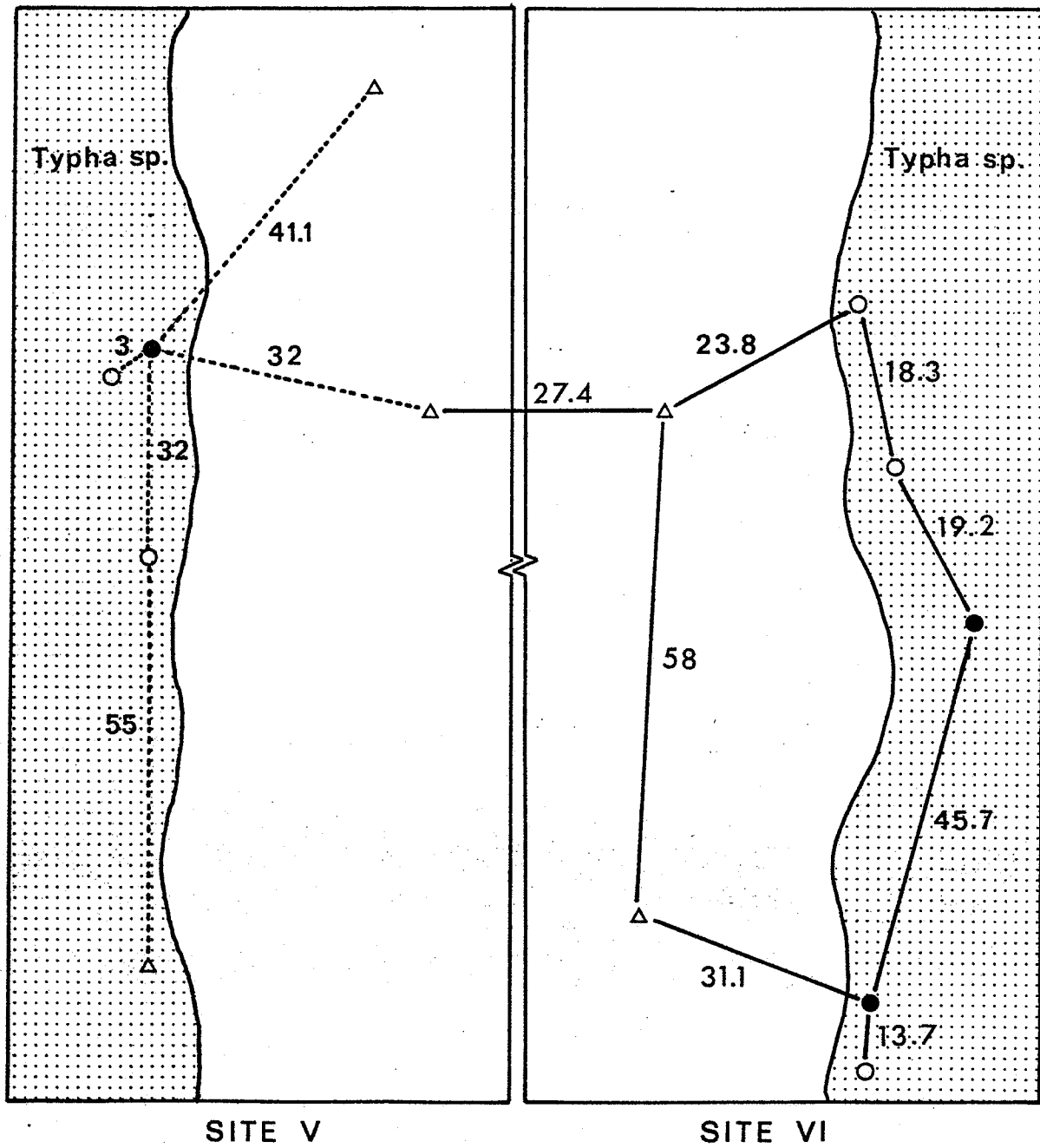
Figure 2. Distribution patterns of winter shelters used by O. zibethicus in Delta Marsh. Numbers indicate distances (m) between associated shelters. Sites V and VI denote the home ranges of the following transmitter-equipped animals:

Site V - No. 9 (male)

Site VI - Nos. 6, 7, 8, 10 (all males)

- - Dwelling lodge
- - Feeding lodge
- △ - Pushup
- ▣ - Emergent vegetation
- - Route verified by telemetry (residents of Site V)
- - Route verified by telemetry (residents of Site VI)





BLIND CHANNEL





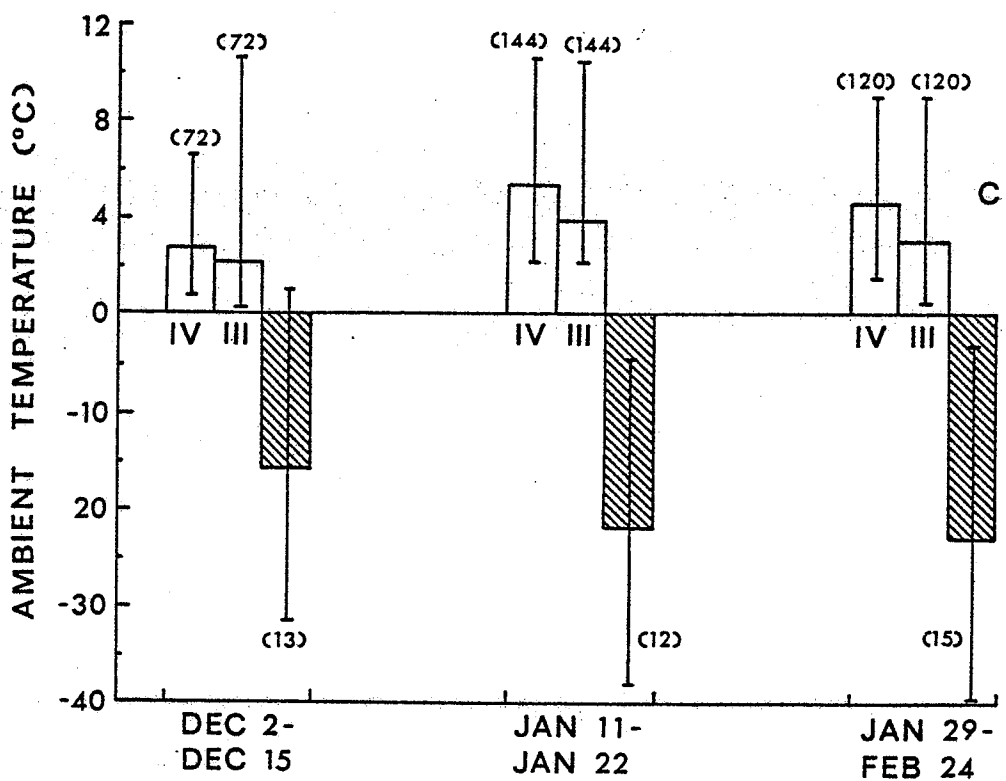
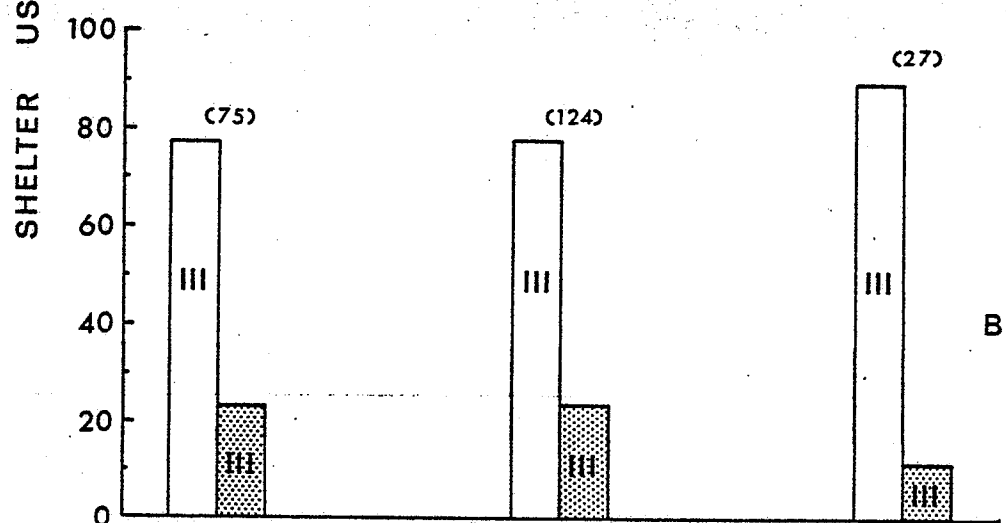
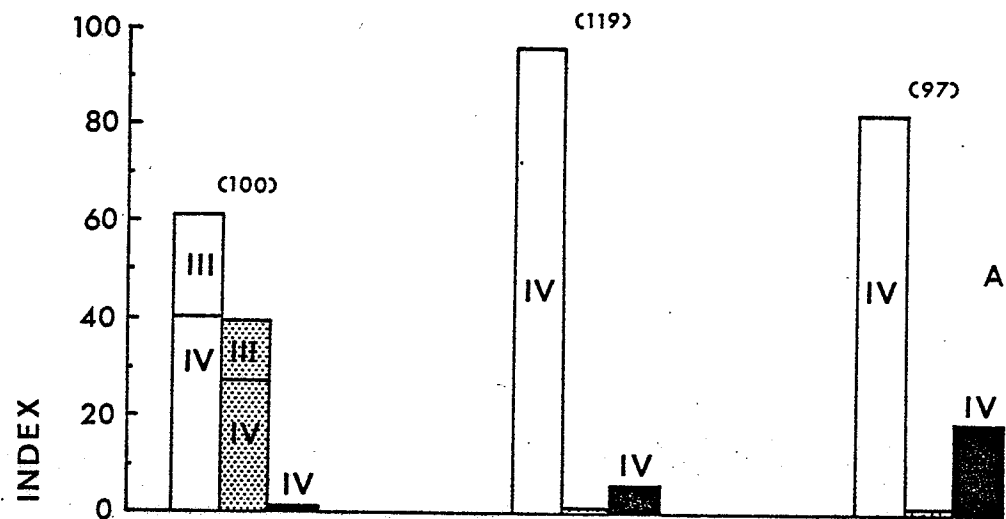
group sharing of pushups, and in one case, of dwelling lodges. Two of the four animals monitored at Site VI during November and December, 1974, for example, were occasionally observed utilizing a pushup associated with Site V (Fig. 2). There was no evidence of inter-group sharing of any other shelters by animals from Sites V and VI. At Sites III and IV, on the other hand, two of the four transmitter-equipped animals (Nos. 1 and 2) utilized dwelling lodges LIII and LIV, and pushups PIII and PIV during the period Dec. 2-15, 1973 (Figs. 1 and 3A). Observed movement between LIII and LIV was always via PIII and PIV, and never directly from one lodge to the other (a distance of 78.6 m). By Jan. 11, PIV had frozen out, and for the remainder of the winter, Muskrat Nos. 1 and 2 were confined to "island IV" with its single dwelling lodge and associated feeder (Fig. 3A). As pushup use by these animals declined, feeder use increased. Pushup PIII remained in use throughout the winter, and the two animals (Nos. 3 and 4) monitored at Site III continued to use this pushup, although here also, there was some indication of decreased pushup, and increased lodge utilization during late winter (Fig. 3B). Increase in lodge use at Sites III and IV (especially Site IV) during January and February is also reflected in slight, but significant (Student's t-test,  $P < .05$ ) increases in lodge  $T_a$ , which occurred despite declining air  $T_a$  (Fig. 3C).

Figure 3. Changes in shelter use by O. zibethicus during winter, as determined from telemetry observations ( $\geq 15$  min apart) of Muskrat Nos. 1 and 2 (A) and Nos. 3 and 4 (B), as well as from lodge temperature changes (C) at Sites III and IV. Numbers in parentheses denote sample size, and in the case of ambient temperature, mean values and ranges (vertical lines) are presented. Lodge temperatures are based on hourly recordings; air temperatures are daily maximum-minimum recordings made at the University of Manitoba Field Station.

-  - Dwelling lodge (LIII and LIV)
-  - Feeding lodge (FIV)
-  - Pushup (PIII and PIV)
-  - Air temperature

Shelter Use Index:

$$\left( \frac{\text{Total observations in shelter}}{\text{Total of all observations}} \right) \times 100$$



## DISCUSSION

As in summer (Beshears and Haugen 1953; Wragg 1955; Sather 1958), the winter home range of O. zibethicus is restricted, with few movements exceeding 150 m, and most foraging activity focused within a 10 m radius of a lodge or pushup. Moreover, calculation of cumulative, linear distances between adjacent shelters depicted in Fig. 1 (range = 90.4 to 128 m) probably provides a fairly realistic estimate of the breadth of winter home range in this species. As suggested in Part I, similarities in the maximum spacing of pushups may reflect optimal, long-range distances for sustained underwater swimming. The rapid swimming often observed between lodge and push-up, as opposed to the slower movement along zones of emergent vegetation, may reflect the prevalence of air spaces in the latter zone (Part I).

It must be emphasized that the delineation of each of the six sites (Figs. 1 and 2) into separate groups is somewhat arbitrary, and nothing is known concerning possible kinship relationships between animals occupying adjacent sites. It is generally believed that a female overwinters with her last litter of young, possibly in association with one or more adult males (Errington 1963). It has also been observed that first litter young often establish themselves within 90 m of the female's home

range (Errington 1963). Therefore, it is entirely possible that kinship ties existed between as well as within adjoining study sites.

The limited evidence indicating inter-group sharing of pushups, and in one case, lodges in early winter (Figs. 1, 2, 3A), as well as the trend for maximal pushup use during this period (Part I), may have important ecological implications. Firstly, inter-group utilization of shelters would enhance the thermal regime within these structures, and in the case of pushups especially, would inhibit ice formation in the plunge hole. Secondly, water levels in Delta Marsh are characteristically shallow (Walker 1965), and in the past, freeze-out has been considered a major source of winter mortality in this marsh (Olsen 1959; McLeod et al. 1951; Errington 1963). In the two winters during which the present study was conducted, shallow portions of the marsh had frozen to the bottom by late January and early February (Part I). There would therefore seem to be strong selective pressure for maximal utilization of peripheral food resources early in the winter when these are most accessible. Such behavior would conserve food reserves in the immediate vicinity of the dwelling lodge until late winter when they would be essential to sustain the animals in the event that ice impeded access to distant pushups. The view is commonly held that muskrats can survive a freeze-out only if they have access to such reserves in proximity to a

lodge or burrow (Hamerstrom and Blake 1939; Errington 1963; Revin 1975).

It is also relevant to note that the net energy gain resulting from foraging at distant pushups would probably decrease as winter advances. Included in the energy expenditure of such activity is the thermoregulatory cost of preparing for, enduring, and recovering from immersion in near-freezing water (Part II), as well as the locomotor energy required to reach and forage in the vicinity of the pushup. As winter advances, cooler lodge, pushup, and water temperatures would tend to elevate thermoregulatory costs. In addition, the animals may have to break through surface ice in the pushup plunge hole in severe weather. As food reserves in the immediate vicinity of the pushup are depleted, the foraging range about the latter must also be increased, reducing foraging efficiency further. All of these added costs for distant foraging during late winter suggest that the progressive reduction in foraging radius observed in this study represents a highly adaptive modification of winter home range.

## SUMMARY AND CONCLUSIONS

The present study provides evidence of behavioral and physiological adaptations of O. zibethicus for optimizing thermal relationships with the natural environment. The maintenance of a favorable microclimate, for example, appears to involve the interaction of a number of diverse behavioral mechanisms. The most obvious of these is the construction of multiple shelters--a behavioral pattern that attains maximal significance during winter. The construction of well-insulated lodges and closely-spaced pushups and feeders during this season provides a stable microclimate moderated by the presence of open water in plunge holes. Thus, the mean temperatures recorded from within these winter shelters were close to, or above freezing ( $-4.6$  to  $11.0^{\circ}\text{C}$ ) in all cases. The lowest  $T_a$  recorded from the winter microenvironment was only  $-9.0^{\circ}\text{C}$ , despite external air temperatures recorded as low as  $-39.0^{\circ}\text{C}$ . Moreover, field and laboratory studies indicated that muskrats are highly gregarious during winter, and group occupation of winter dwelling lodges resulted in mean chamber temperatures ( $3.1$  to  $11.0^{\circ}\text{C}$ ) that closely approached thermoneutrality. In view of the finding that the mean cumulative time per day spent by a muskrat in the winter dwelling lodge was 13.6 hours, these lodge temperatures seem significant in terms of energy conservation.

In contrast, lodge use by adults appeared to be minimal in summer, and these structures were sometimes abandoned in favor of open nests or burrows during this season. It is suggested that the abandonment of summer lodges may occur in response to the high temperatures (25 to 30°C) encountered within these shelters, possibly resulting from fermentative heat production. Burrows provided the coolest, most stable microclimates in summer, with temperatures ranging from 8.5 to 20.5°C.

Aside from shelter construction and huddling behavior, the periodic, labile activity cycle of O. zibethicus may contribute to microclimate stability during winter. Temporal segregation of activity ensures continuous, or nearly continuous occupation of winter shelters by a variable number of animals, and inhibits ice formation in plunge holes. Also, by staggering the use of a finite number of feeding shelters, overwintering animals may avert crowding and stress; hence this aspect of behavior might indirectly facilitate social thermoregulation.

The absence of a strong correlation between daily activity and environmental variables such as air  $T_a$  and wind attests to the buffered winter microenvironment of the muskrat. Seasonally, the strongest correlation between activity and weather occurred in early winter before the advent of a significant snow cover, and in particular, during the period of open water in November. Late fall and early spring were concluded to be the only seasons



when O. zibethicus is likely to be exposed to wind and low air and water temperatures concurrently.

Muskrats demonstrate behavioral mechanisms not only for maintaining an optimal microclimate, but also for minimizing exposure to cold water during winter. This latter function is achieved largely through the closely-spaced, "stepping-stone" arrangement of lodges and pushups, coupled with the rapid transit of animals between these shelters. Also, telemetry studies have indicated that  $T_b$  invariably declines during winter foraging, and muskrats appear to retard this decline by periodically rewarming within pushups and feeders. Similar  $T_b$  responses have been noted among juveniles in summer. It is hypothesized that the need to rewarm periodically during foraging activity in winter may account for the greater mean duration of excursions in this season (83 min) as opposed to summer (55 min).

In addition to the above behavioral mechanisms, muskrats may avoid hypothermia during foraging excursions in winter by elevating  $T_b$  prior to entry into water. Such an elevation, it is suggested, prolongs the endurance capabilities of these animals in cold water. The increase in  $T_b$  observed in this study was related to foraging time, being maximal (mean increase =  $1.2^{\circ}\text{C}$ ) for excursions in excess of 40 min duration. Similar increases in  $T_b$  were not observed during summer.

Laboratory studies of abdominal cooling in water

revealed that muskrats were more resistant to cooling in winter than in summer, at all temperatures tested (6 to 30°C). Furthermore, laboratory investigations indicated that abdominal cooling of muskrats swimming in cold water during winter was accompanied by a concurrent increase in the temperature of interscapular brown adipose tissue. This finding, together with the absence of seasonal differences in the oxygen consumption of muskrats in air (-15 to 30°C), suggest that non-shivering thermogenesis may be more important than insulative adjustments to the winter acclimatization of this species. Brown adipose tissue-mediated thermogenesis may not only retard hypothermia in cold water, but could also contribute substantially to the rewarming of animals within feeders and pushups.

Finally, evaluation of all field and laboratory data collected to date, reinforces the interplay between various group and individual behavioral responses, as well as physiological adaptations, which contribute to thermal homeostasis, energy conservation, and ultimately survival of O. zibethicus.

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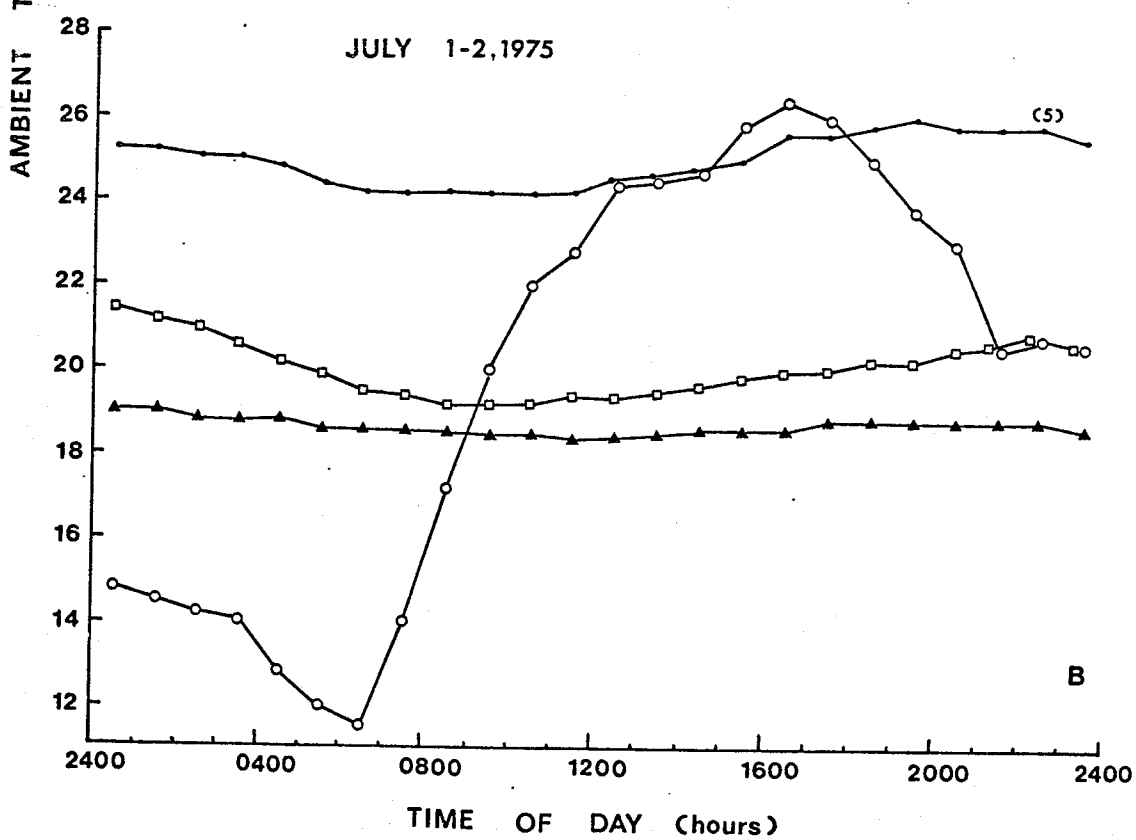
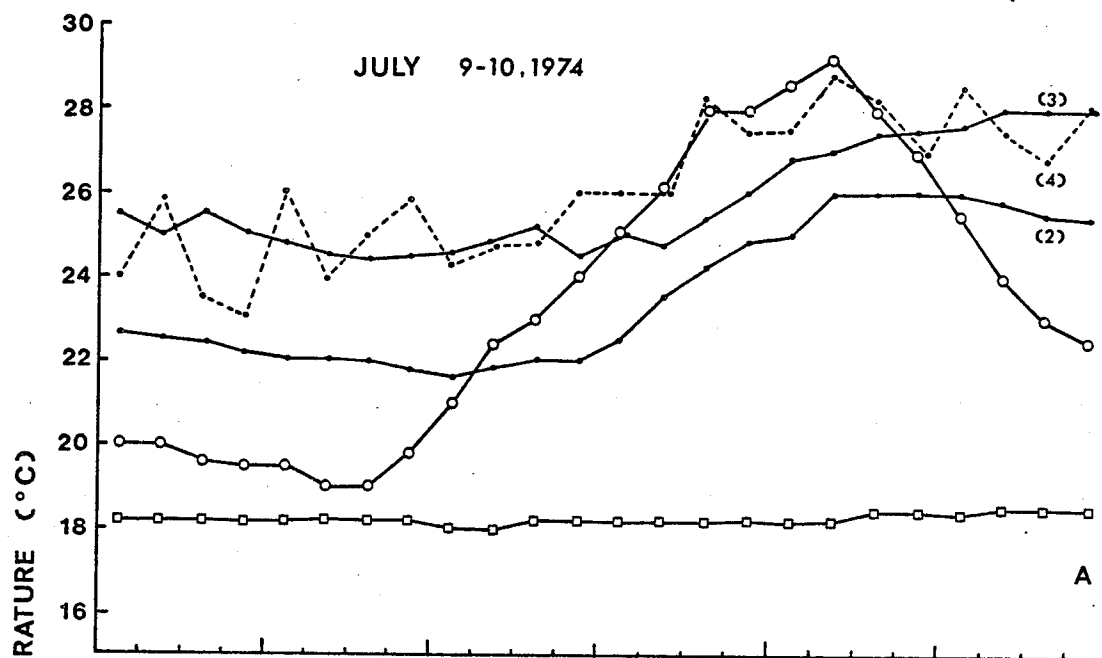
## APPENDICES

Appendix 1A. A representative (randomly selected) 24-hour record of ambient temperature in Delta Marsh in July, 1974. Dashed line indicates a lodge (No. 4) containing a litter of young.

Appendix 1B. A representative (randomly selected) 24-hour record of ambient temperature in Delta Marsh in July, 1975.

- - Air
- - Deep water
- - Dwelling lodge
- ▲ - Shallow burrow

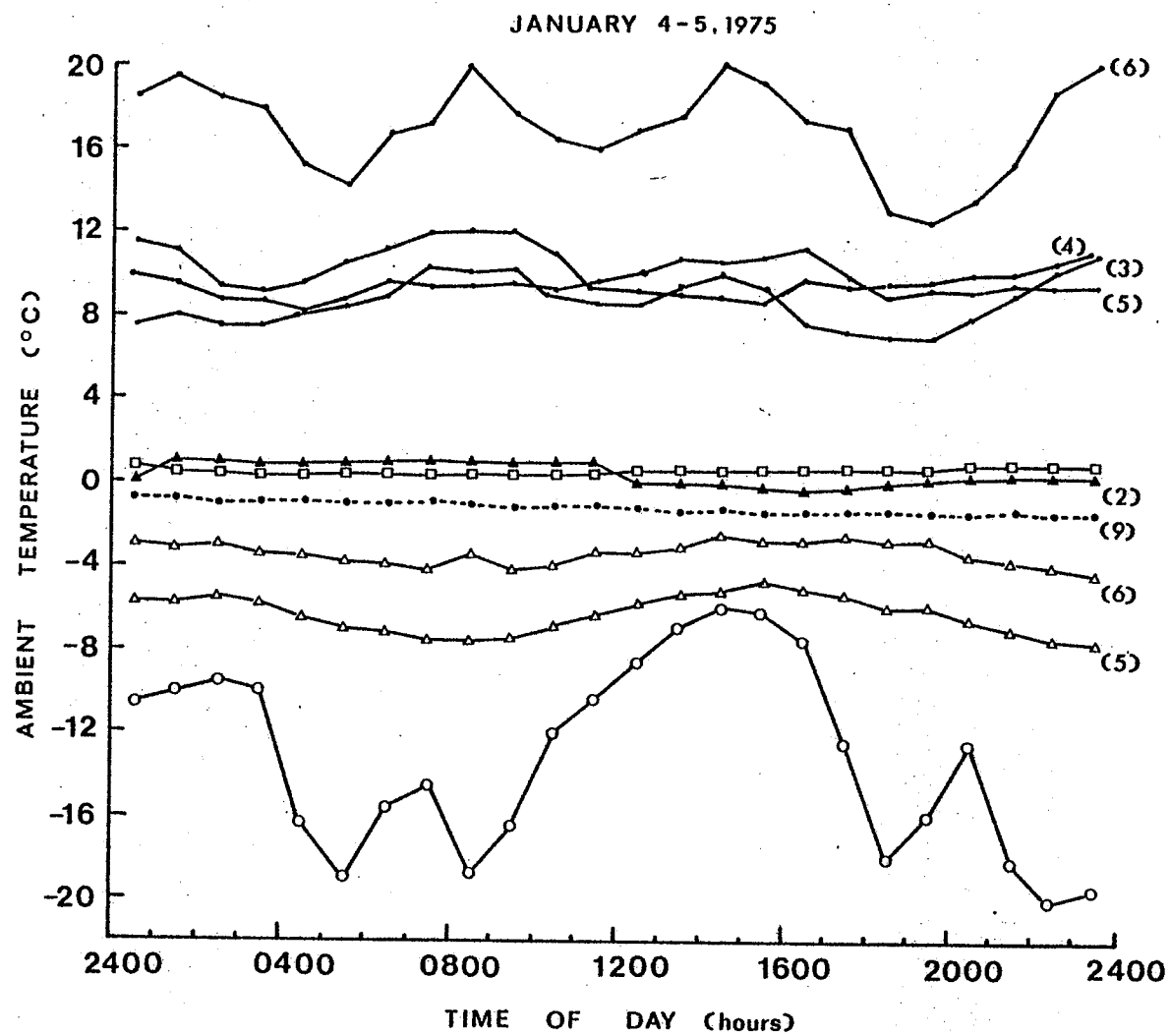
Numbers in parentheses identify dwelling lodges



Appendix 2. A representative (randomly selected) 24-hour record of ambient temperature in Delta Marsh in January, 1975. Numbers in parentheses identify lodges and pushups.

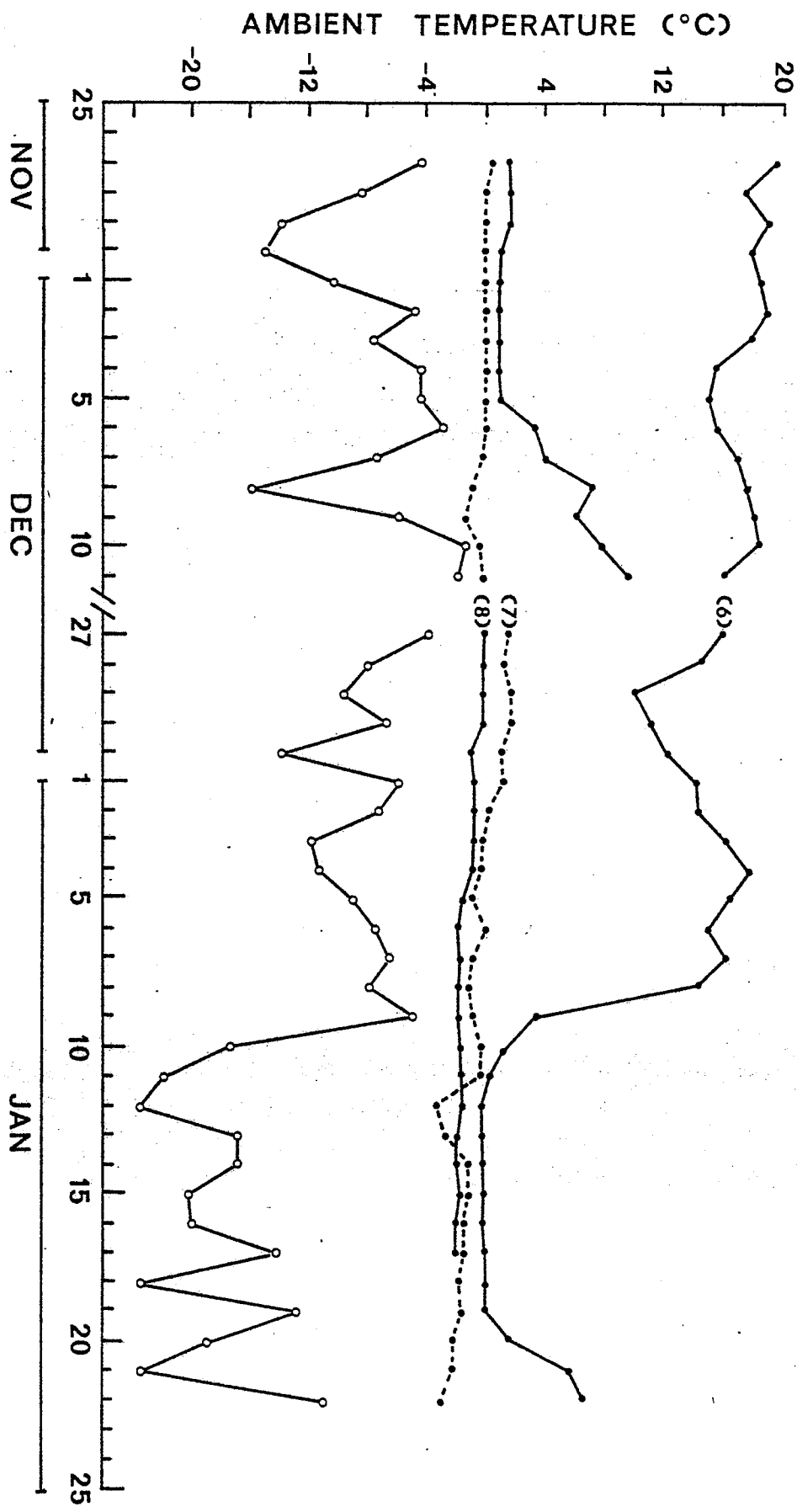
- - Air
- - Water
- - Dwelling lodge
- ▲ - Feeding lodge
- △ - Pushup
- - Abandoned dwelling lodge





Appendix 3. Temporal series of mean daily lodge and air temperatures recorded in Delta Marsh, 1974-75. Each point depicts the mean of 24 recordings made at hourly intervals.

- - Air (Stevenson Screen)
- - Lodge Nos. 6 and 8
- - Lodge No. 7 (abandoned throughout series)



Appendix 4. Summary of sex, body weight, and body temperature data for all muskrats censused at 15 to 240 min intervals, 1973-74

Year	Animal No.	Sex	Weight(g)	Sampling Period	n <sup>a</sup>	Body Temperature (°C)	
						Mean(S.E.)	Range
73-74	1	M	675	Nov.30-Feb.1	125	38.1(.10)	34.4-40.7
73-74	2	M	650	Dec.2-Feb.1	90	37.0(.07)	35.3-38.4
73	3	F	625	Dec.1-Dec.15	48	38.7(.12)	36.0-40.3
73-74	4	F	750	Nov.30-Feb.4	94	-	-
73-74	5	M	900	Nov.18-Feb.1	80	36.1(.13)	33.6-40.3
74	6	M	755	Nov.6-Dec.4	83	38.9(.06)	37.2-40.2
74	7	M	810	Nov.6-Dec.4	90	39.4(.04)	38.8-40.3
74	8	M	700	Nov.6-Nov.18	59	40.6(.06)	39.4-41.7
74	9	M	941	Nov.30-Dec.4	22	40.8(.18)	38.9-42.3
74	10	M	805	Nov.6-Dec.4	76	39.6(.14)	37.1-42.3
74	11	M	755	Nov.6-Nov.30	25	-	-
74	12	M	1100	Jun.18-Jul.19	98	38.4(.07)	36.8-40.4
74	13	M	1016	Jul.9-Jul.30	106	38.4(.08)	37.8-39.1
74	14	M	1055	Jul.8-Jul.30	226	38.5(.07)	37.9-39.1
74	15	F	1150	Jun.20-Jul.25	29	38.9(.11)	37.7-39.8
74	16	M	1175	Jun.18-Jul.19	96	38.6(.05)	37.4-39.8
74	17 <sup>b</sup>	M	500	Jul.19-Jul.30	116	38.7(.05)	37.0-39.6
74	18 <sup>b</sup>	M	452	Jul.19-Jul.30	89	37.7(.06)	36.4-39.3
74	19 <sup>b</sup>	M	456	Jul.19-Jul.30	200	38.4(.08)	37.3-39.0

<sup>a</sup> Number of observations

<sup>b</sup> Juveniles; all others classified as subadults and adults

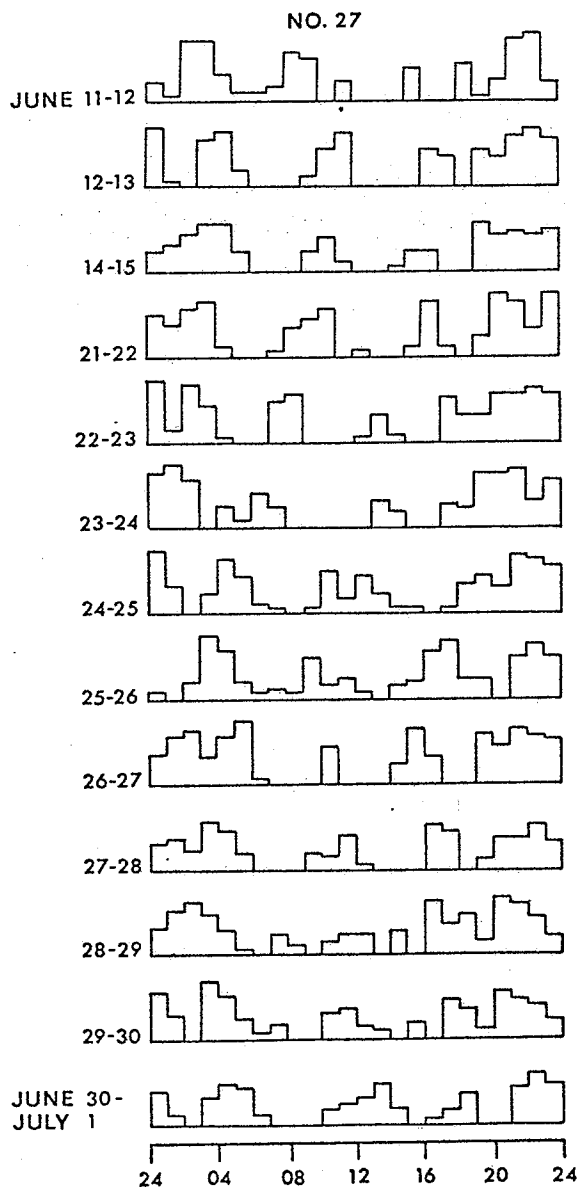
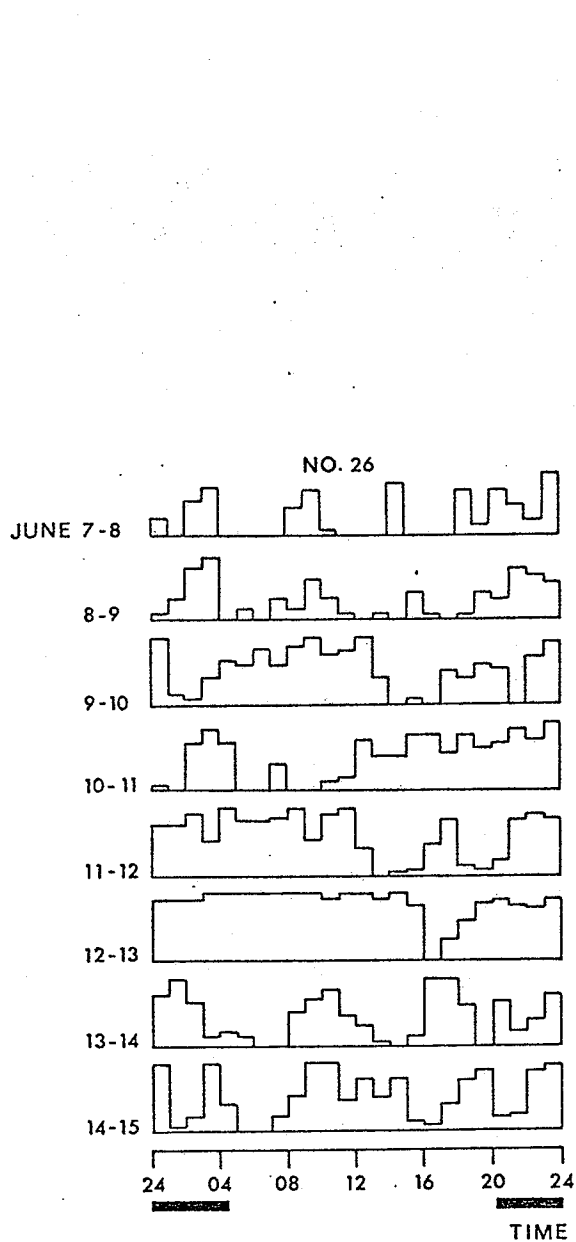
Appendix 5. Summary of sex, body weight, and body temperature data for all muskrats remotely monitored at 5 ( $\pm 0.5$ ) min intervals, 1974-75

Animal No.	Sex	Weight(g)	Sampling Period	n (hours; days)	Body Temperature ( $^{\circ}\text{C}$ )	
					Mean(S.E.) Range	$\bar{X}$ daily amplitude(S.E.) Range
20	M	790	Nov.16-Jan.5	252;11	39.1(.04) 37.5-40.6	2.1(.10) 1.6-2.8
21	F	755	Nov.10-Jan.4	196;10	39.8(.07) 37.8-42.0	2.2(.13) 1.7-2.7
22	F	871	Nov.5-Jan.2	87;8	38.8(.08) 37.4-40.7	2.3(.11) 1.9-2.7
23	M	505	Nov.14-Nov.16	48;2	-	-
24	F	732	Nov.16-Jan.1	96;6	41.4(.12) 39.1-44.5	2.5(.19) 2.2-3.2
25	M	977	Jun.25-Jul.1	144;6	39.2(.05) 38.0-40.4	1.8(.14) 1.4-2.4
26	M	1030	Jun.7-Jun.14	175;8	37.6(.03) 36.6-38.6	1.5(.09) 1.2-1.8
27	M	1085	Jun.11-Jul.11	552;23	37.5(.02) 36.0-39.4	1.8(.10) 0.9-2.6

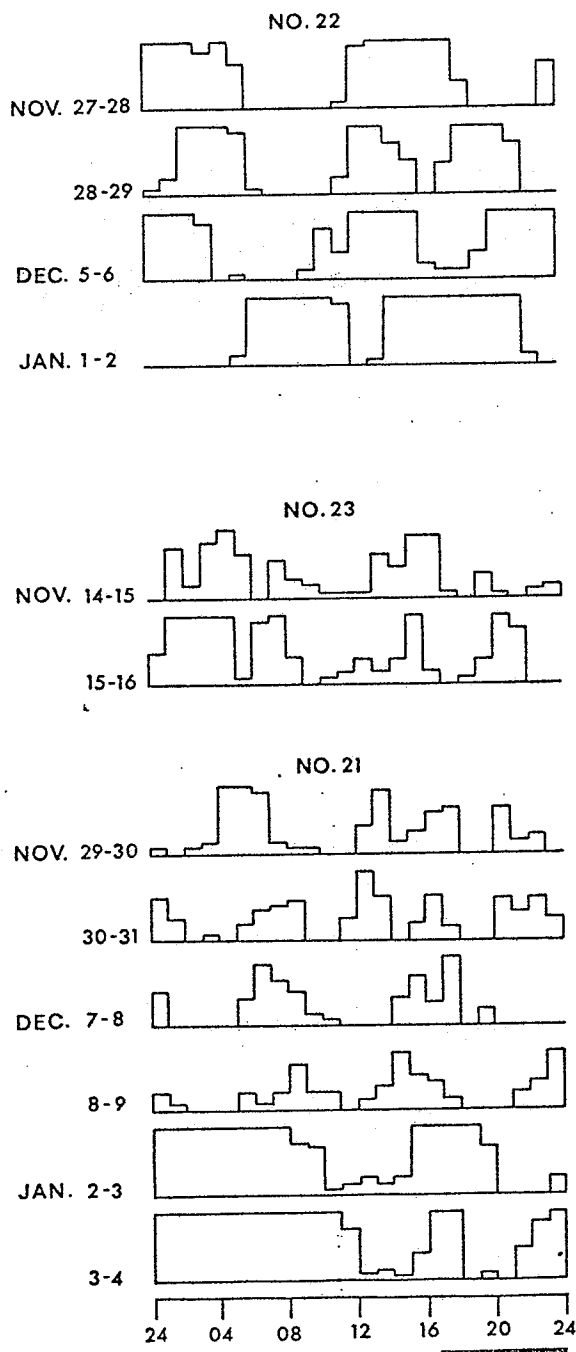
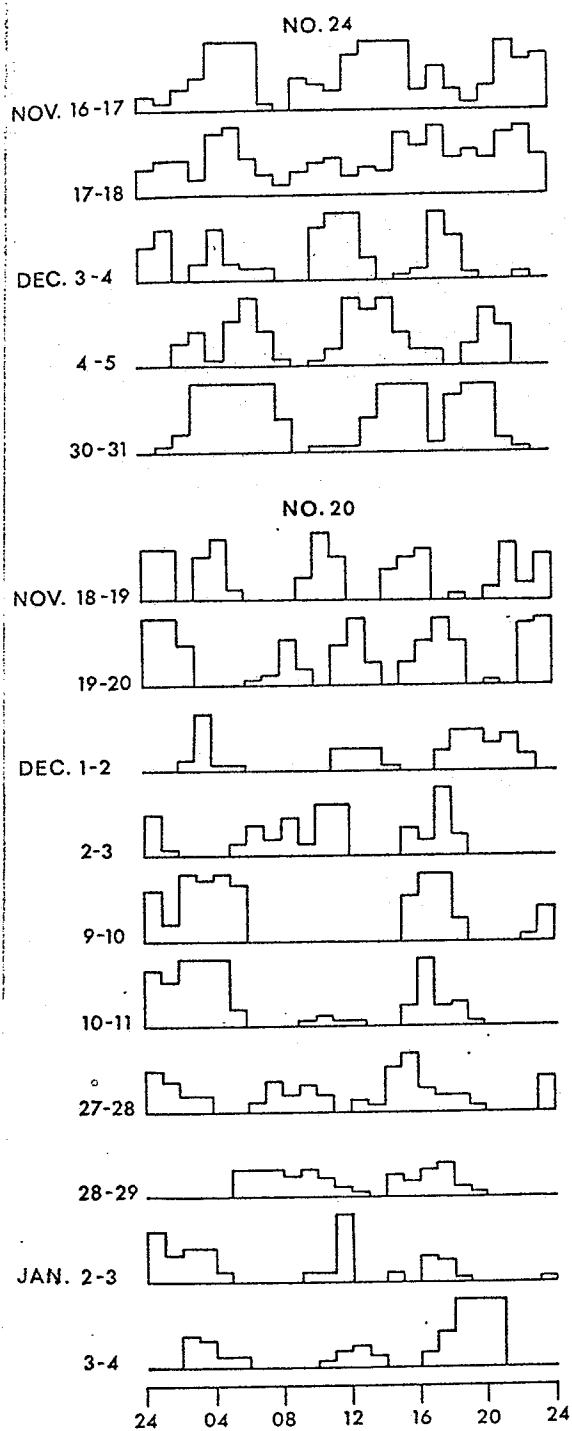
Appendix 6. Daily activity patterns of O. zibethicus remotely monitored at 5 ( $\pm$  0.5) min intervals in summer (A) and winter (B). For each 24-hour period, each bar depicts a mean hourly activity index based on all observations (11 to 13) made within a given hour.

- A - Single lodge-dwelling muskrat (No. 26) monitored June 7-15, 1975, and a single burrow-dwelling muskrat (No. 27) monitored June 11-July 1, 1975
- B - Five muskrats (Nos. 20 to 24, inclusive) occupying Lodge No. 5, and monitored Nov. 14-Jan. 5, 1974-75
- - Period of darkness (sunset to sunrise)

A



B

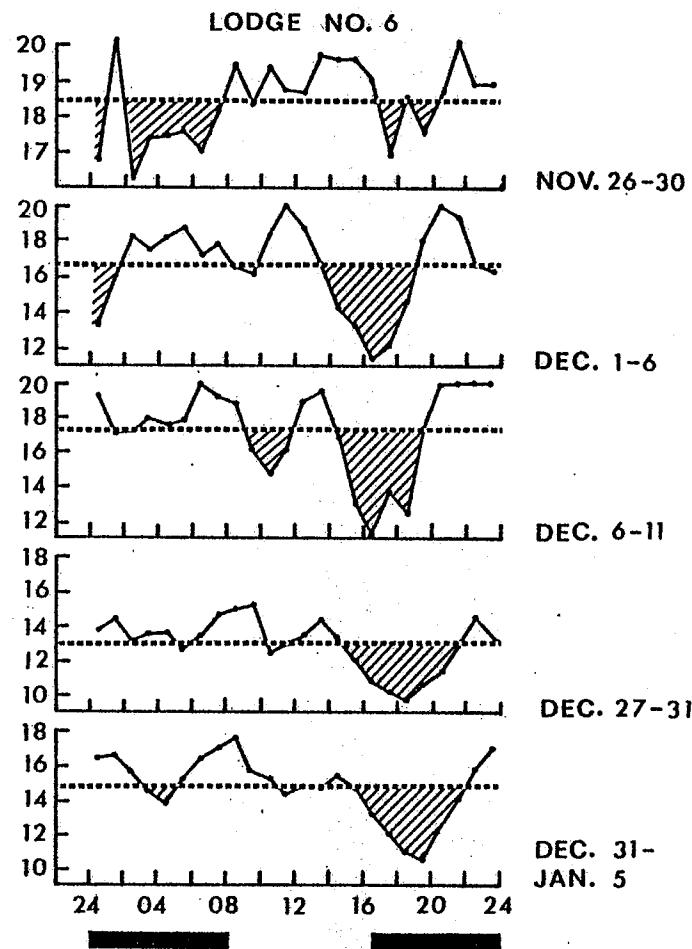
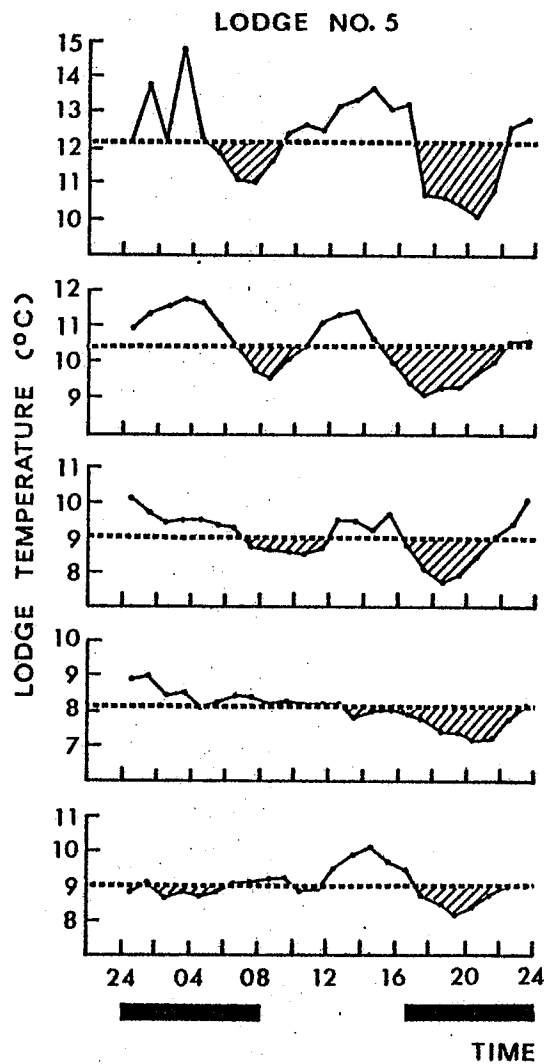


TIME OF DAY (hours)



Appendix 7. Changes in the group activity patterns of O. zibethicus occupying Lodge Nos. 5 and 6 between Nov. 26, 1974, and Jan. 5, 1975, as determined from hourly recordings of lodge temperature. For each 4- or 5-day observation interval, each point depicts the mean of 4 or 5 hourly recordings (averaged across days). Periods of presumed maximal activity away from the lodge are indicated as negative deviations (hatched areas) from the overall, 24-hour mean (dashed line).

■ - Period of darkness (sunset-sunrise)



## Appendix 8. Care of Muskrats in Captivity

In addition to the holding conditions outlined in Part III, two other methods were tried in the preliminary phase of the study. The first involved placing animals in large wire mesh cages (35 x 35 x 91 cm) equipped with wooden nest boxes, food troughs, and water bottles. These cages were located in a walk-in environmental chamber held at 15 to 20°C, with a photoperiod of 9L:15D. In the absence of open water, eye, and in some cases, nose and tail infections developed in a few animals after 1 to 2 weeks in captivity.

A superior method involved locating a large circular fibreglass tank (diam = 1.22 m; ht = 0.91 m) in a walk-in environmental chamber (Air  $T_a$  = 20°C; Photoperiod = 16L:8D). This tank was filled with water to a depth of 30 cm, and an "artificial lodge" installed in the center. The latter was constructed from a 5-gallon metal drum. A right-angle furnace elbow duct (diam = 15 cm) was soldered to a circular hole cut in one side of the drum just above water level, providing an underwater entrance. A wire mesh (0.6 cm) ramp was soldered to the inside of this duct, and was continuous with a wire mesh floor fixed to the inside of the drum, 6 to 8 cm above water level. Food was provided in the form of apple, carrot, and cattail, Typha latifolia. This latter set-up was used to house a transmitter-equipped female (No. 7) that gave birth and nursed a litter of seven young within the above lodge during June, 1974.

Appendix 9. A comparison of the metabolic rate (MR) of 8 O. zibethicus after 1 to 15 days in captivity (Trial I), with the MR after 12 to 18 days in captivity (Trial II)

Animal No.	$T_a$ (°C)	Trial I		Trial II		Time interval (days)	MR-difference
		Date	MR <sup>a</sup>	Date	MR		
1	8	Feb.22	1.39	Mar.10	1.43	16	+0.04
2	8	Feb.23	1.11	Mar.10	1.56	15	+0.45
3	8	Feb.24	1.22	Mar.10	1.33	14	+0.11
4	15	Jan.21	1.12	Feb.7	1.12	17	0.00
5	15	Jan.20	0.87	Feb.7	1.23	18	+0.36
6	15	Jan.25	0.73	Feb.6	0.95	12	+0.22
8	20	Feb.21	0.98	Mar.11	1.00	18	+0.02
9	20	Feb.21	0.87	Mar.11	0.91	18	+0.04
10	20	Jul.12	0.76	Jul.29	1.07	17	+0.31
11	20	Jul.12	0.86	Jul.29	0.69	17	-0.17
Mean <sup>+</sup> S.E. (range)			0.99 <sup>+</sup> .06 (0.73-1.39)		1.13 <sup>+</sup> .07 (0.69-1.56)		+0.14 <sup>+</sup> .05 (-0.17-+0.45)

<sup>a</sup> (cc O<sub>2</sub>/g.h)

Appendix 10. Aggregation responses of O. zibethicus  
in the laboratory at an air  $T_a$  of  $5^\circ\text{C}$



Example of close aggregation



Example of loose aggregation

Appendix 11. Rectal and intra-abdominal temperatures (°C) of five O. zibethicus<sup>a</sup> (2 females, 3 males) under light sodium pentobarbital anaesthesia, September, 1973

	Rectum (12 cm)	Lower abdomen	Mid- abdomen	Upper abdomen
Mean(S.E.)	38.0(.30) <sup>b</sup>	37.6(.26)	38.0(.34)	38.7(.16)
Range	36.8-38.9	36.8-38.6	37.4-39.0	38.0-39.2
n	8	7	4	8

<sup>a</sup> All measurements were made with a YSI No. 402 Tele-Thermometer probe. For intra-abdominal determinations, the probe was inserted through a 4 mm incision in the body wall.

<sup>b</sup> The mean rectal  $T_b$  of eight non-anaesthetized animals at room  $T_a$  was also 38.0°C.