

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°C , whereas temperatures recorded from within lodges, burrows, and pushups varied from -9 to 30°C . The range of mean temperatures (3 to 25°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°C (range = 11 to 35°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°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°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°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°C . Body temperature was independent of air temperature between -20°C and 30°C , but body cooling in water occurred at all temperatures below 30°C in summer, and 25°C in winter. Cooling rates in summer exceeded those in winter ($P < .01$) at all water temperatures tested (6 to 30°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: ± 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; Boccock (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°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.

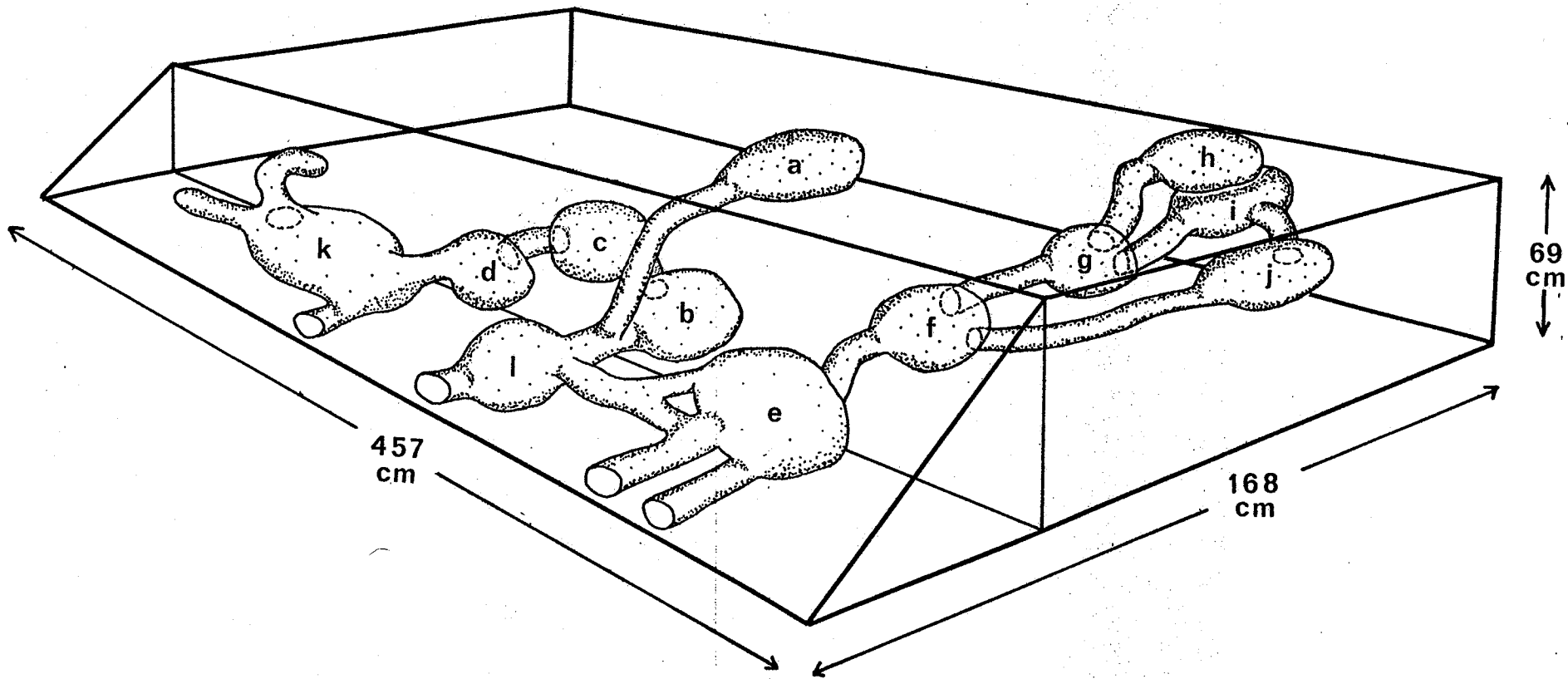


Table 1. Chamber measurements of Burrow System No. 1

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

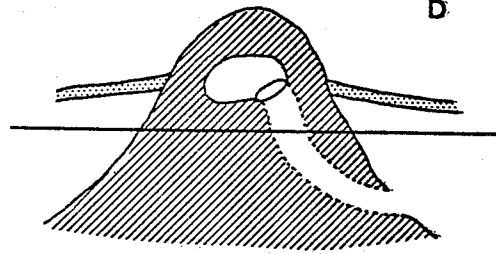
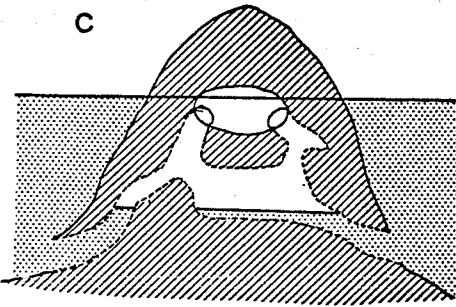
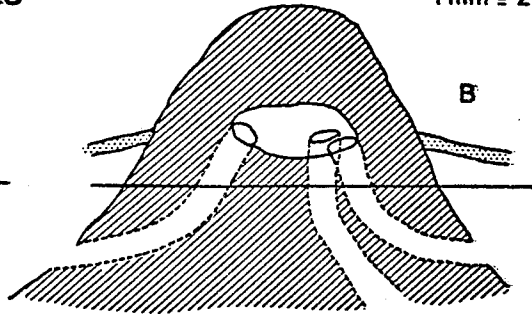
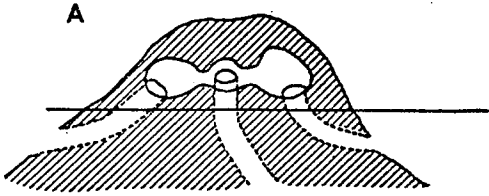
 - Structure composed of vegetation

 - Ice

Solid horizontal line - Water surface

LODGES

1 mm = 2.5 cm



PUSHUPS

1 mm = 0.5 cm

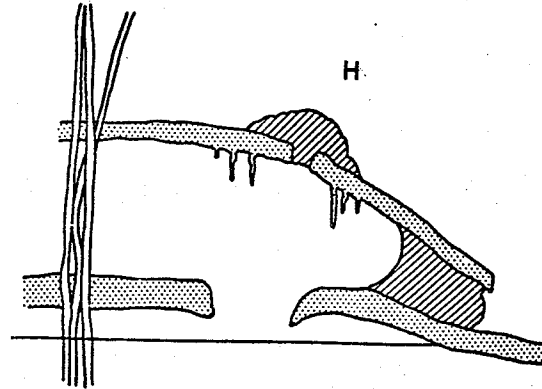
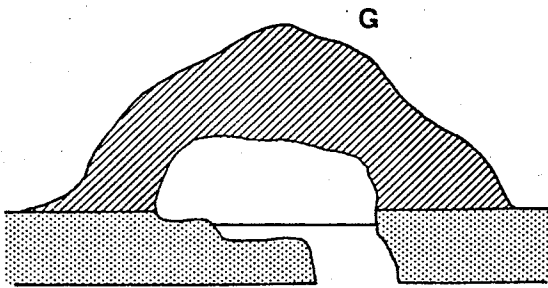
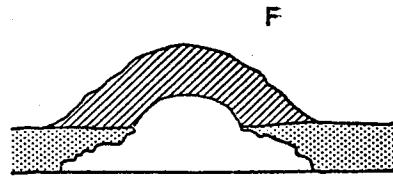
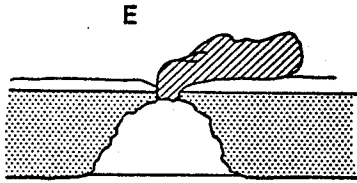


Table 2. Summer and winter lodge measurements ^a

Variable	Summer Dwelling Lodges	Winter Dwelling Lodges	Winter Feeders
<u>External</u>			
Length	145(6.6) ^b 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

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

^b 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)^a

Thermistor site	Month(year) monitored	n (days)	Mean hourly		Daily Amplitude	
			T _a (S.E.)	Range	Mean(S.E.)	Range
<u>Dwelling Lodge</u>						
No.1	J,J,A,(74) ^b	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 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 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 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 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

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

^b 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

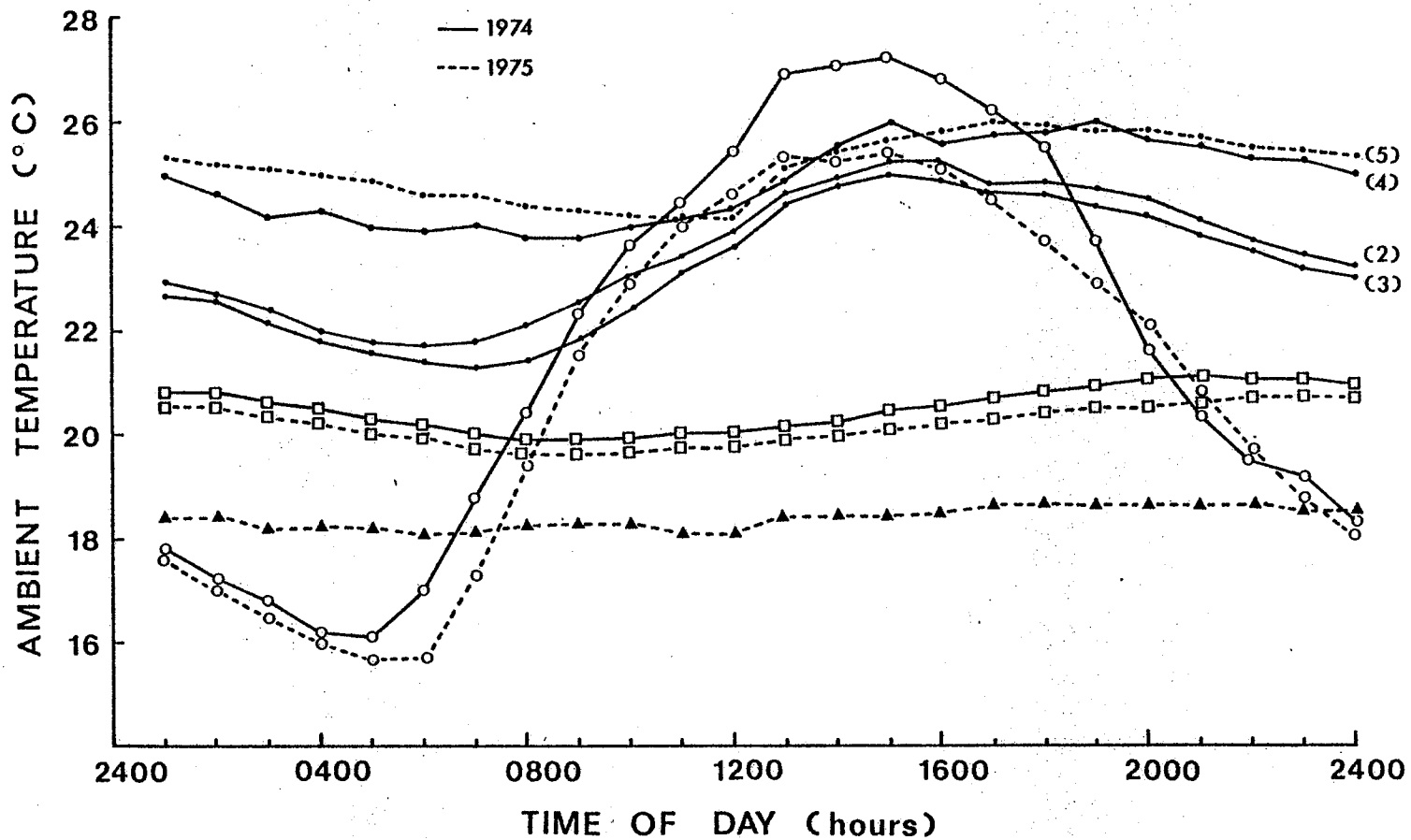
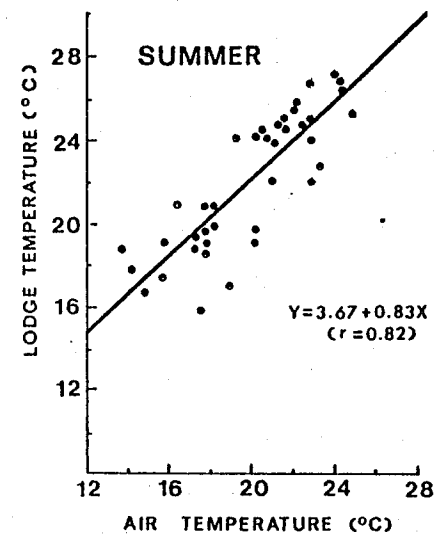
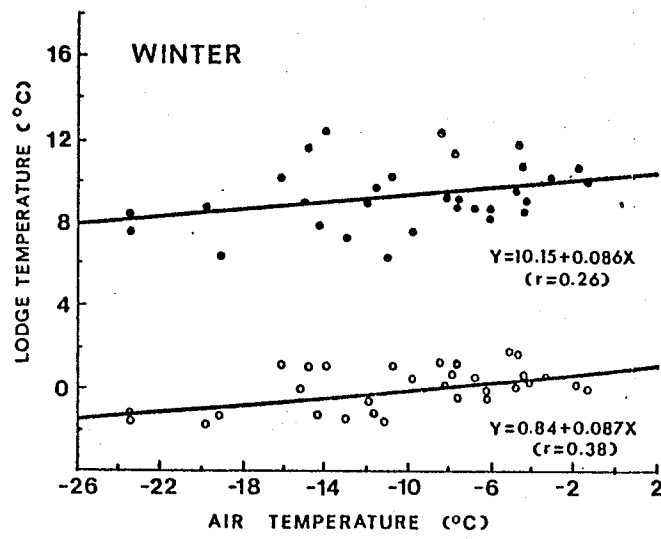
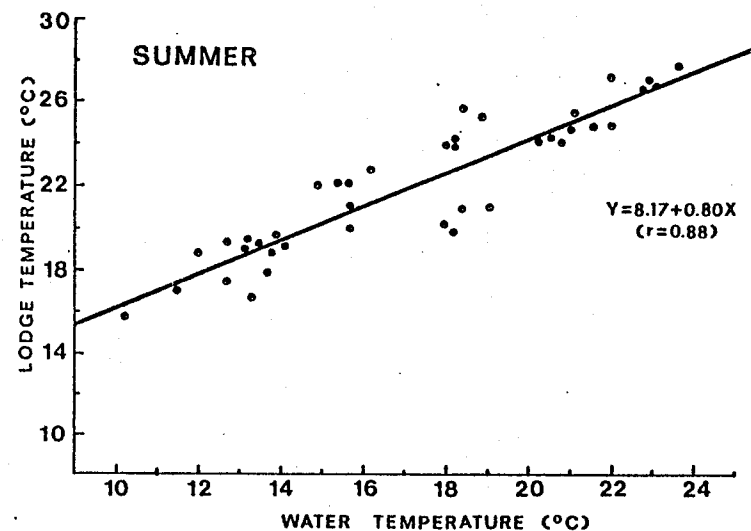
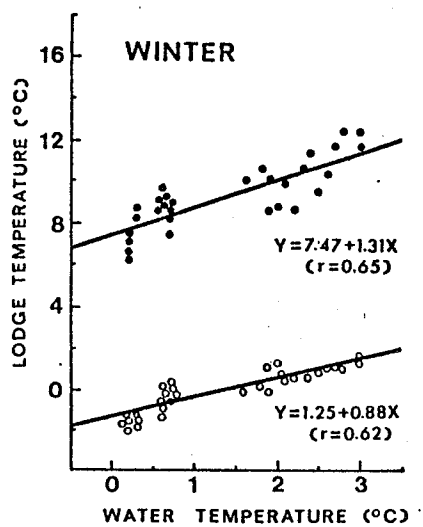


Figure 4. Regression analysis of mean daily dwelling lodge T_a in relation to air and water T_a , summer and winter. Values are based on hourly temperature recordings in Lodge Nos. 1 and 2 in summer (June 1-July 30; $n = 44$ days), and Nos. 3 and 4 (occupied) and Nos. 7 and 9 (abandoned) in winter (Nov. 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)^a

Thermistor site	Months(year) monitored	n (days)	Mean hourly T _a (S.E.)	Range	Daily Amplitude		
					Mean(S.E.)	Range	
<u>Dwelling</u>							
<u>Lodge</u>	No.1	D,J,F,(73/74) ^b	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 ^c	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 ^c	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 ^c	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

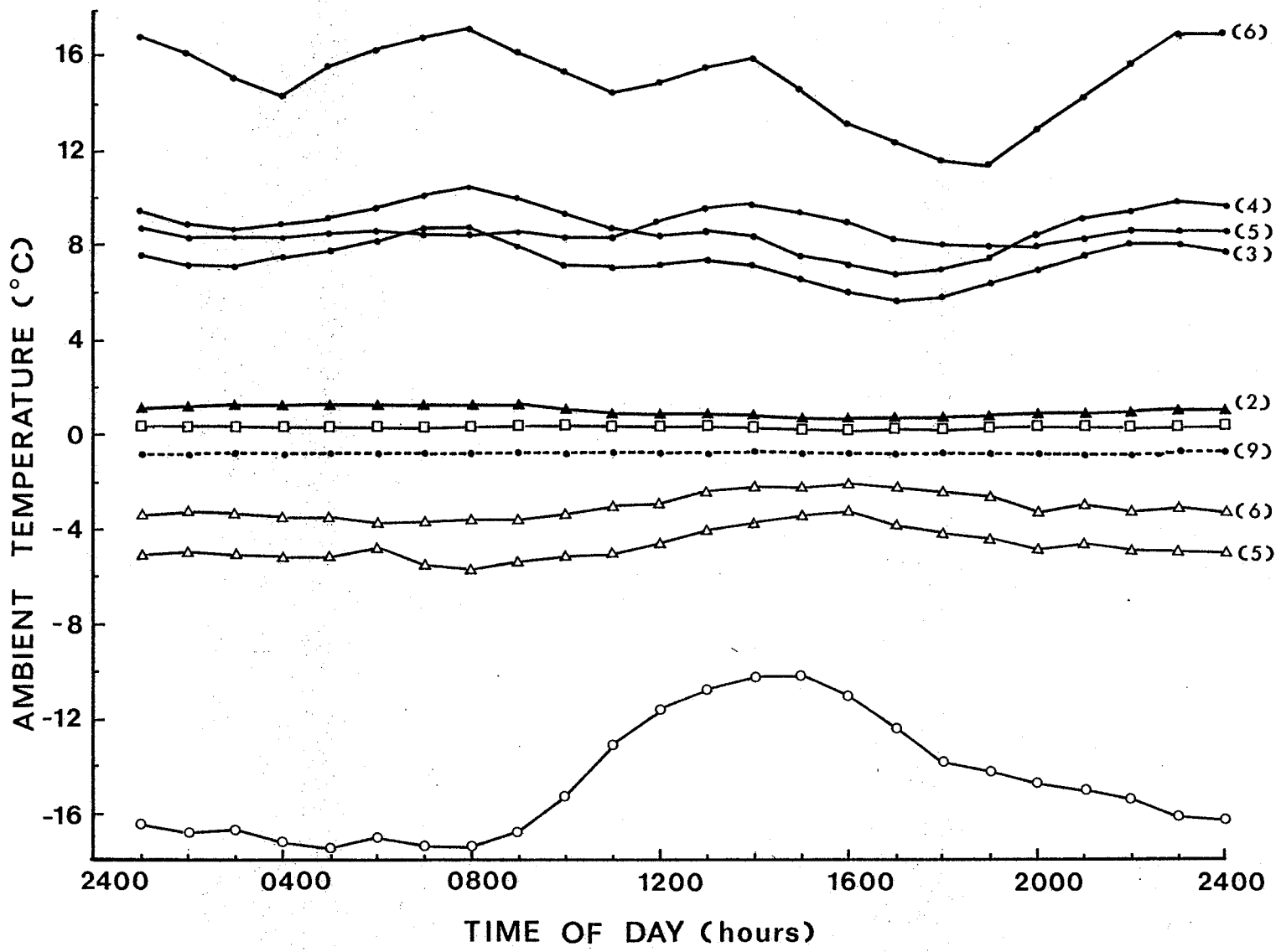
^a Major observation intervals: Dec. 12-15, Jan. 13-21, Feb. 9-23, 1973-74; Nov. 15-Dec. 11, Dec. 27-Jan. 23, Feb. 14-18, 1974-75

^b Abbreviations: November-N, December-D, January-J, February-F

^c 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



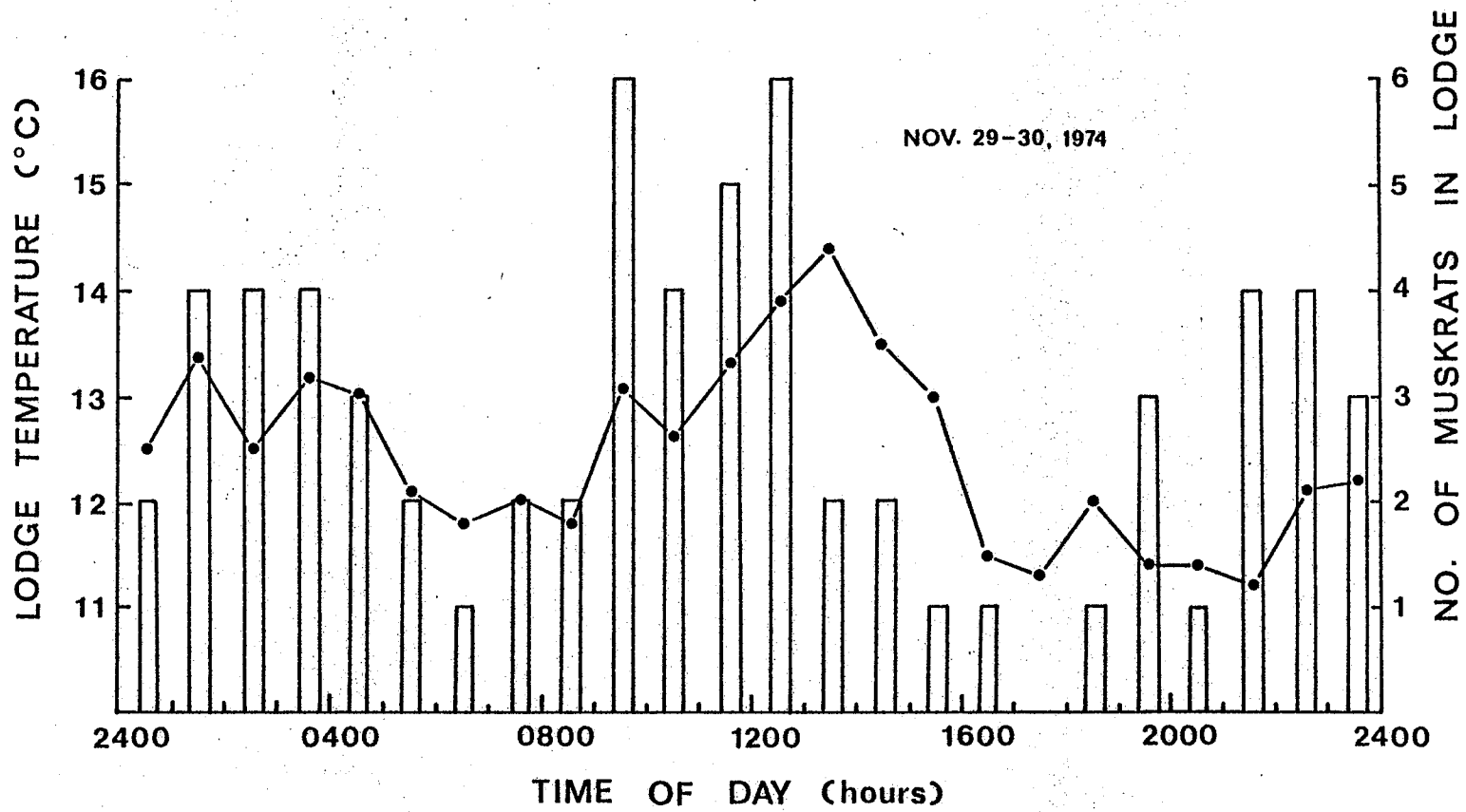
air T_a monitored simultaneously. As in summer, the mean daily temperatures within two occupied (Nos. 3 and 4) and two abandoned (Nos. 7 and 9) lodges were significantly correlated with water T_a ($r = +0.65$, and $+0.62$, respectively, $P < .01$) in winter (Fig. 4). Seasonal regression comparisons for 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.

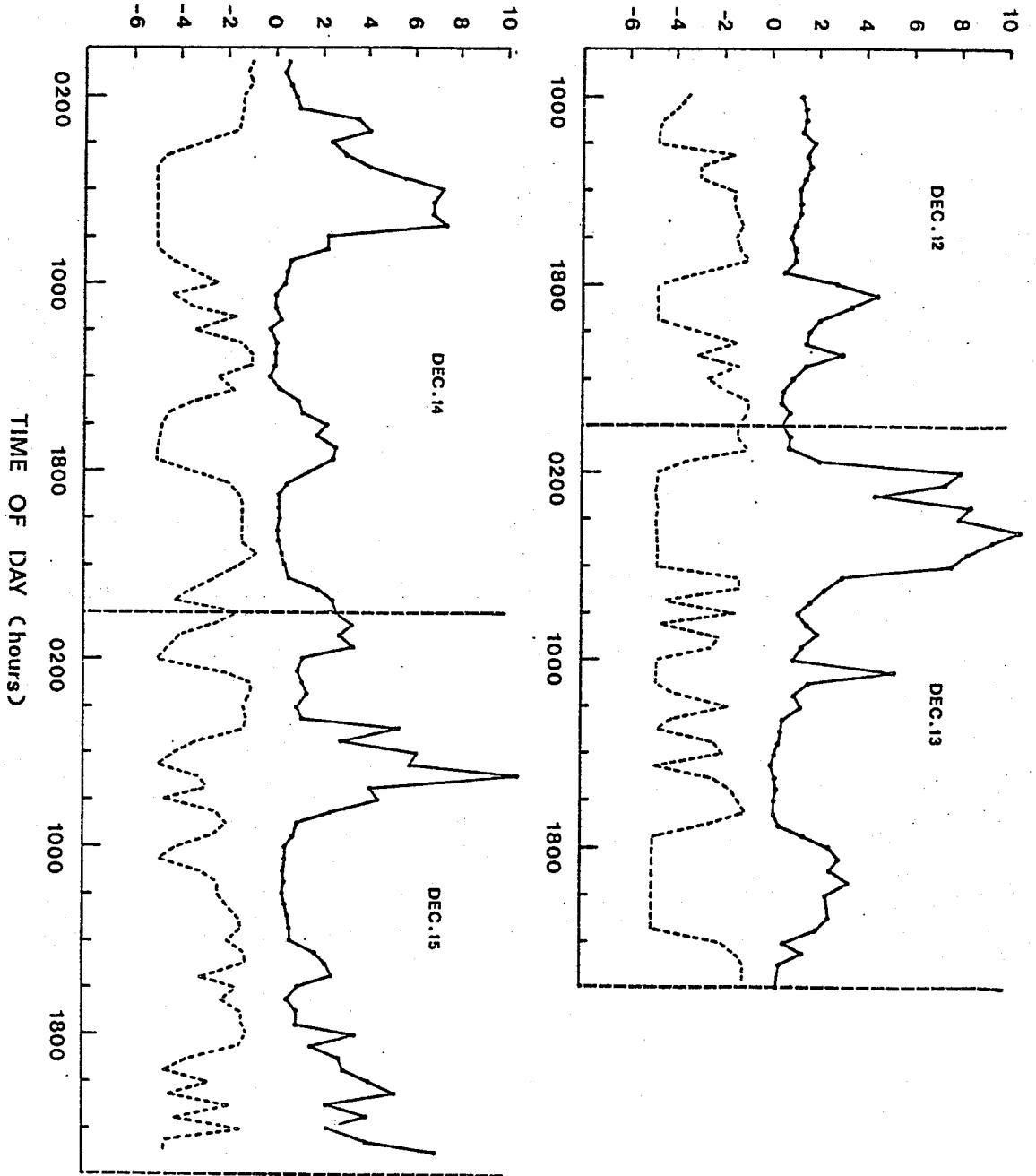
In a few cases, the occupied/abandoned status of dwelling lodges appeared to change through the winter, such that presumed abandoned lodges became occupied, and vice versa (Appendix 3).

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°C .

AMBIENT TEMPERATURE (°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°C) established from laboratory metabolic studies (Hart 1962; McEwan et al. 1974). In fact, lodge T_a in July often approached 30°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°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 ± 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 ± 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 (± 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_p . 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,b₁,b₂,b₃,...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: (Total observations per hour in which animal is active away from lodge or burrow / Total of all observations per hour) x 100
- ▣ - Hourly index of activity ≥ 25 m away from lodge or burrow: (Total observations per hour in which animal is active ≥ 25 m away from lodge or burrow / Total of all observations per hour) x 100
- - Period of darkness (sunset to sunrise)

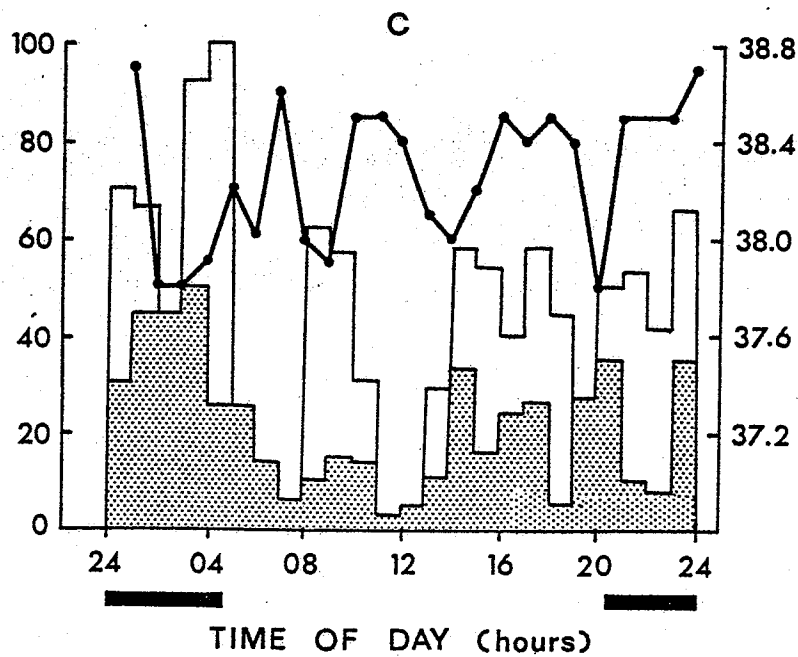
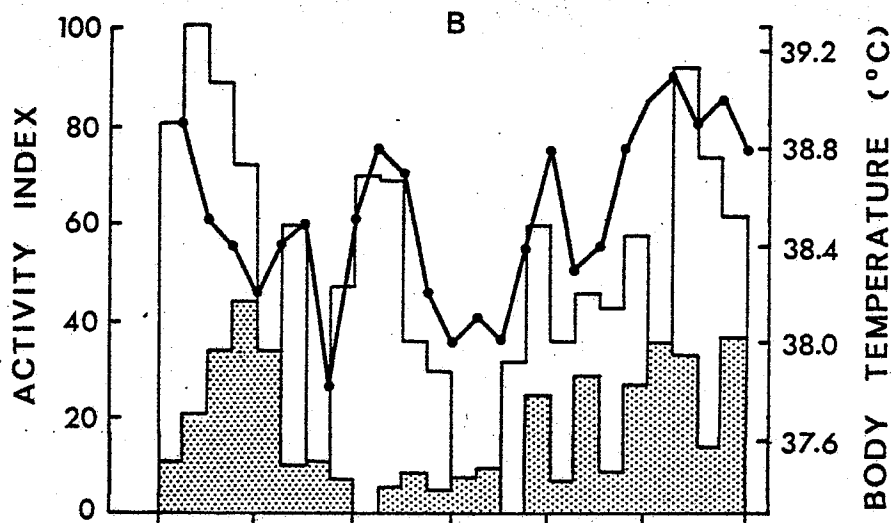
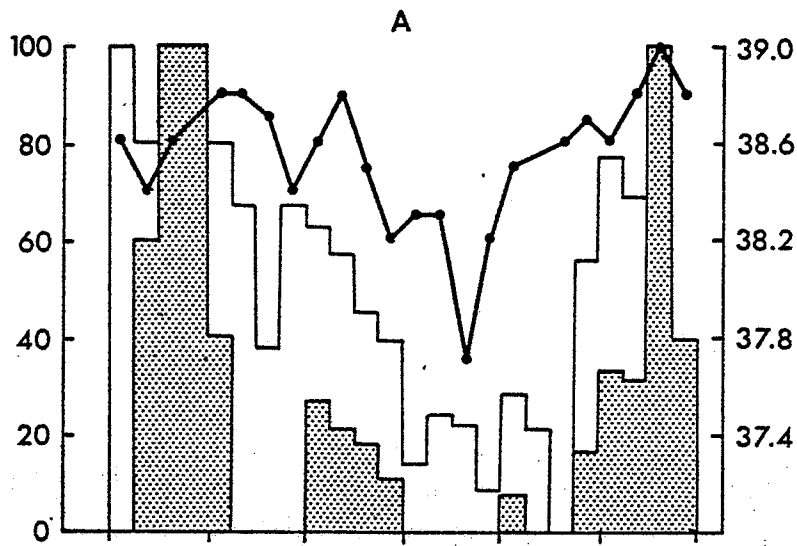


Figure 2A. Representative daily activity patterns of two burrow-dwelling, adult O. zibethicus (Nos. 25 and 27) remotely monitored at 5 (\pm 0.5) min intervals in summer, 1975 (n = 14 days). For each 24-hour period, each bar depicts a mean hourly activity index based on all observations (11 to 13) made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

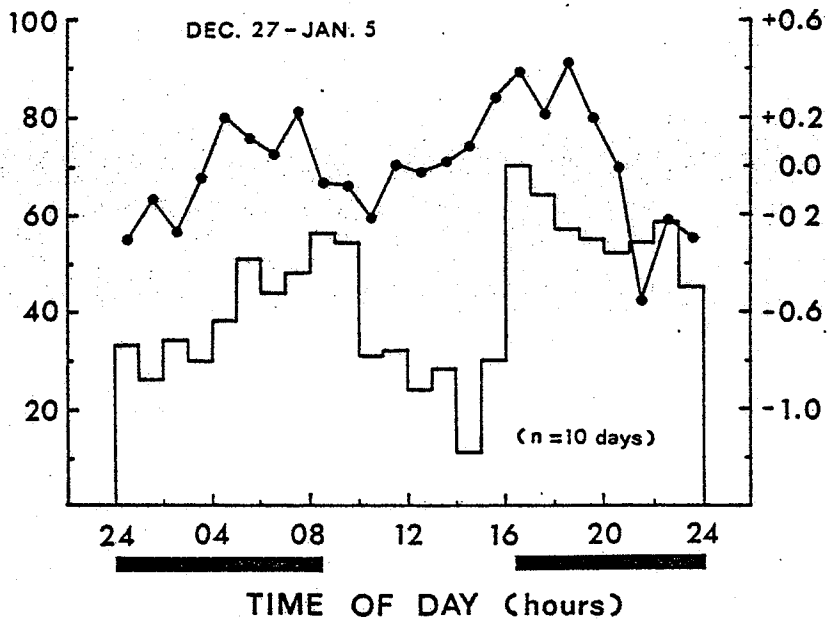
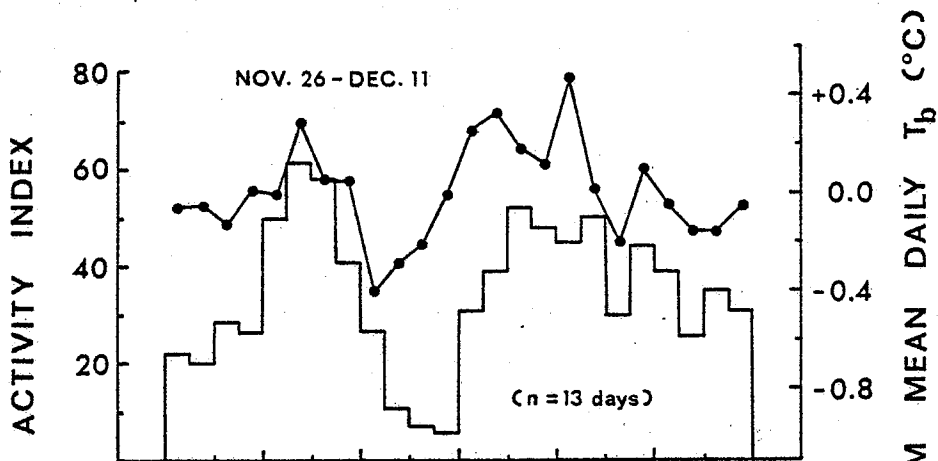
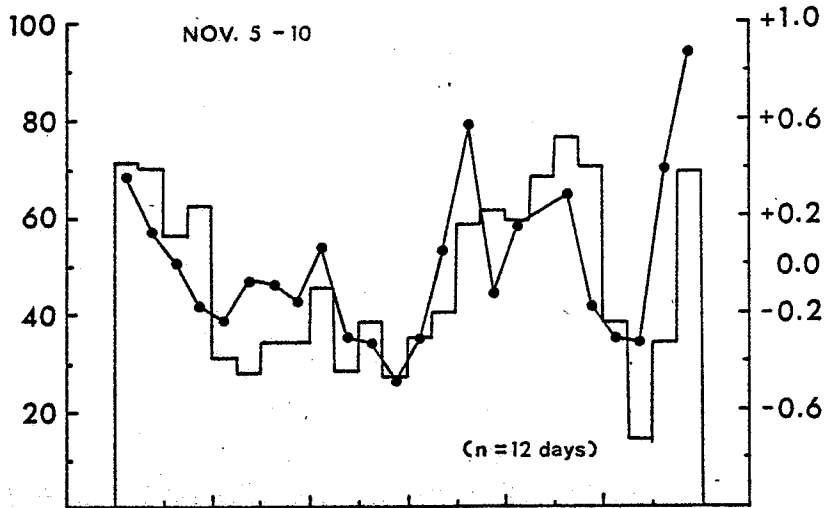
As in summer, muskrats in winter tended to be periodically active throughout the day (Figs. 3, 4, and 5). However, there was less evidence of bimodality in the frequency distribution of major activity bouts during the latter season (Fig. 4B). Maximal levels of activity generally occurred in late afternoon 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)

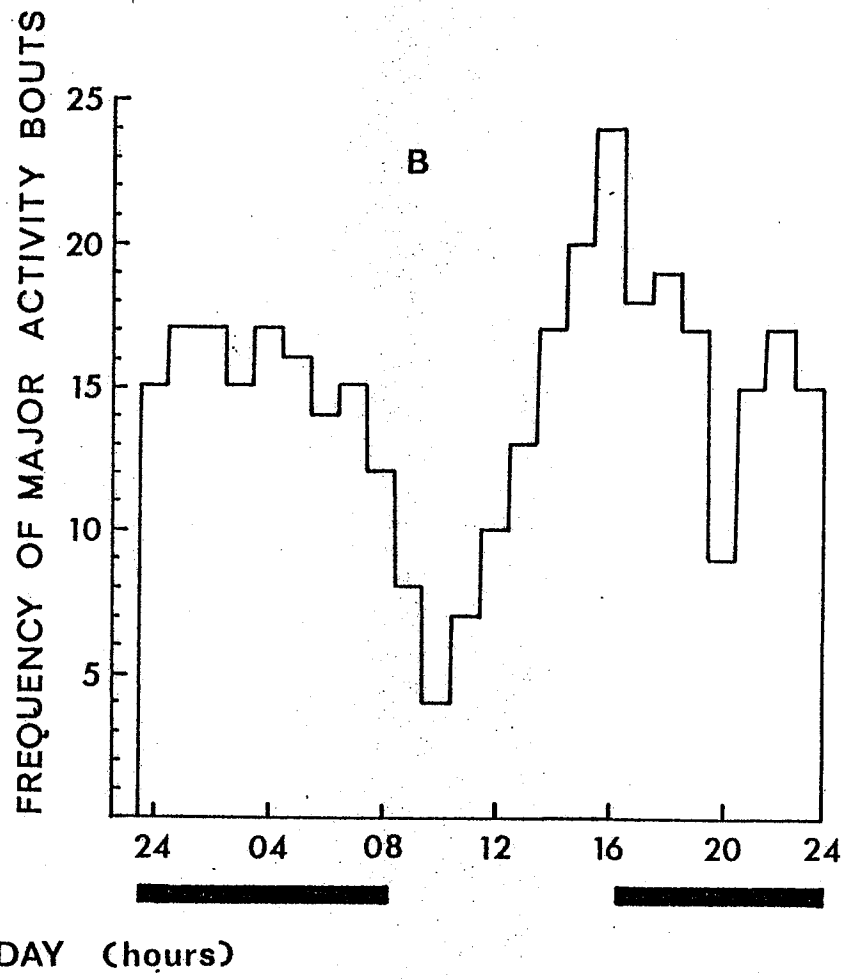
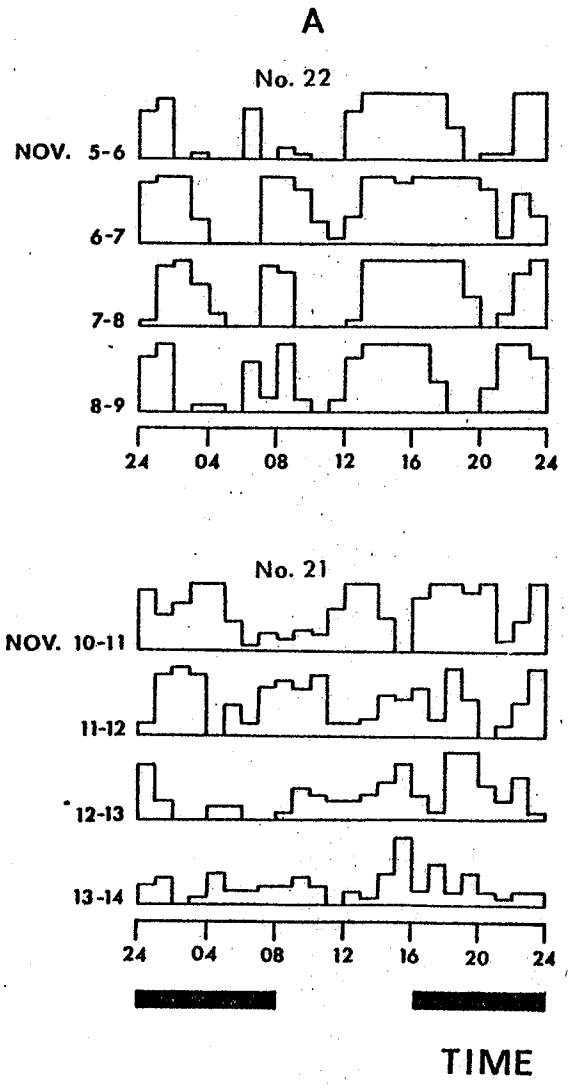


DEVIATION FROM MEAN DAILY T_b ($^{\circ}\text{C}$)

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)

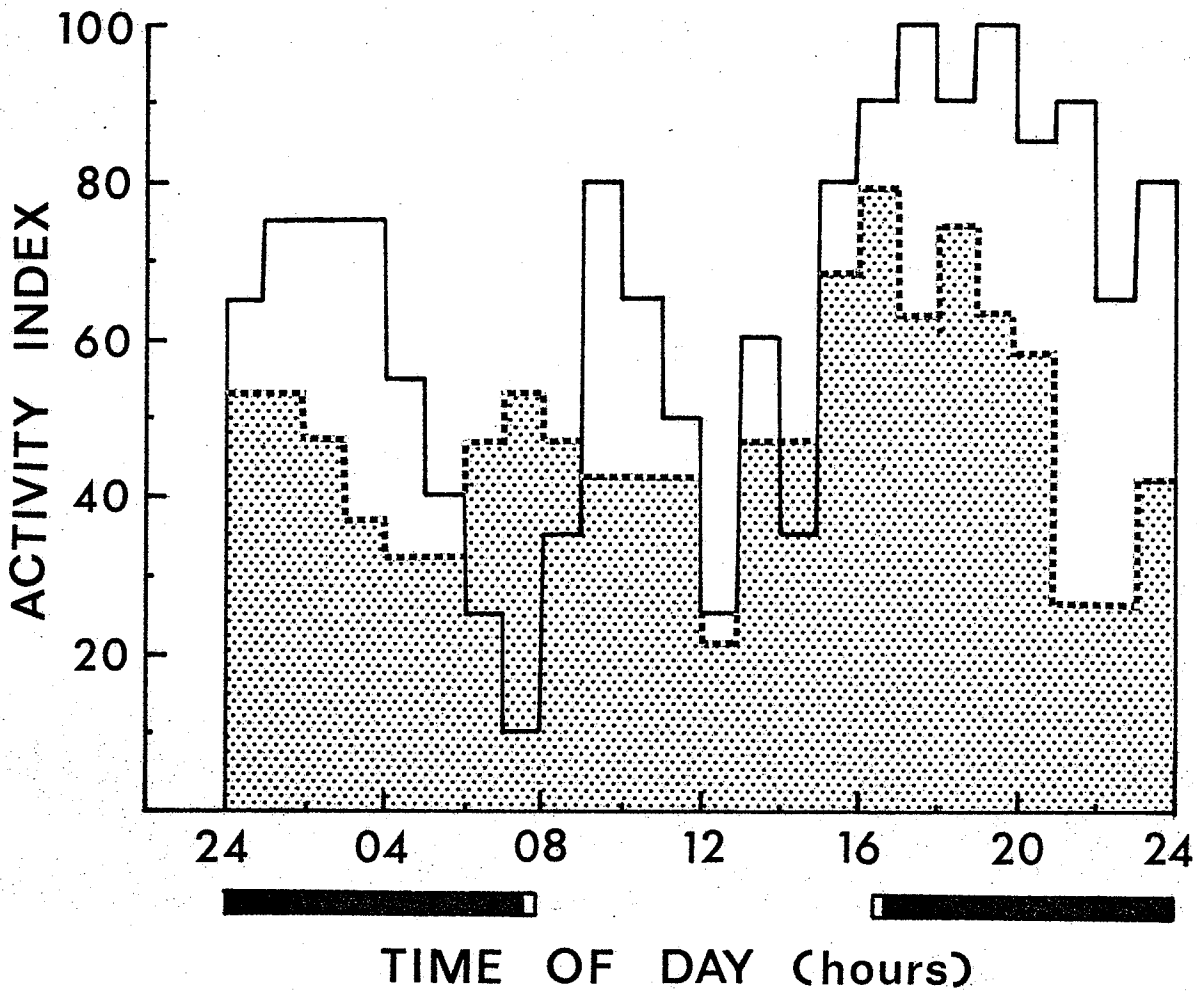


Figure 6. Changes in the daily activity pattern of a group of O. zibethicus occupying Lodge No. 4 between Nov. 20, 1974, and Jan. 21, 1975, as determined from hourly recordings of lodge T_a . For each 4- or 5-day observation interval, each point depicts the mean of 4 or 5 hourly recordings (averaged 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

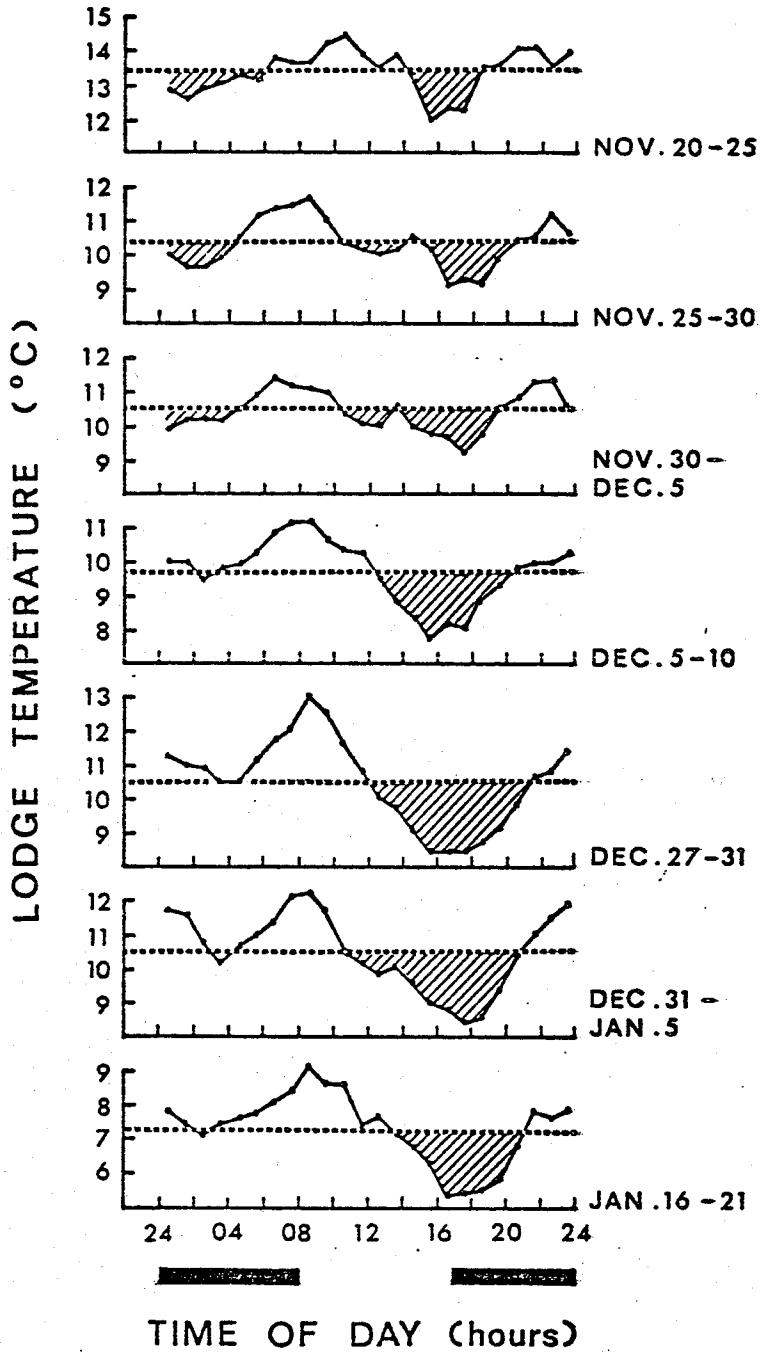


Table 1. Activity variables of *O. zibethicus* remotely monitored at 5 (\pm 0.5) min intervals per 24-hour period in summer, 1975

Animal No.	Sampling Period (n days)	Time in lodge or burrow per day in hours	Excursions		Hourly Activity Index	N/D Ratio	STC ^a in hours
			Freq. per day	Dur. in min			
25	June 25- July 1 (6)	12.6(.64) ^b 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 ^c (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

^a Short-term cycle of activity and rest

^b Mean (standard error)
Range

^c 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 ^a in hours
			Freq. per day	Dur. in min			
20	Nov. 16- Jan. 5 (11)	17.6(.63) ^b 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

^a Short-term cycle of activity and rest




^b Mean (standard error)
Range

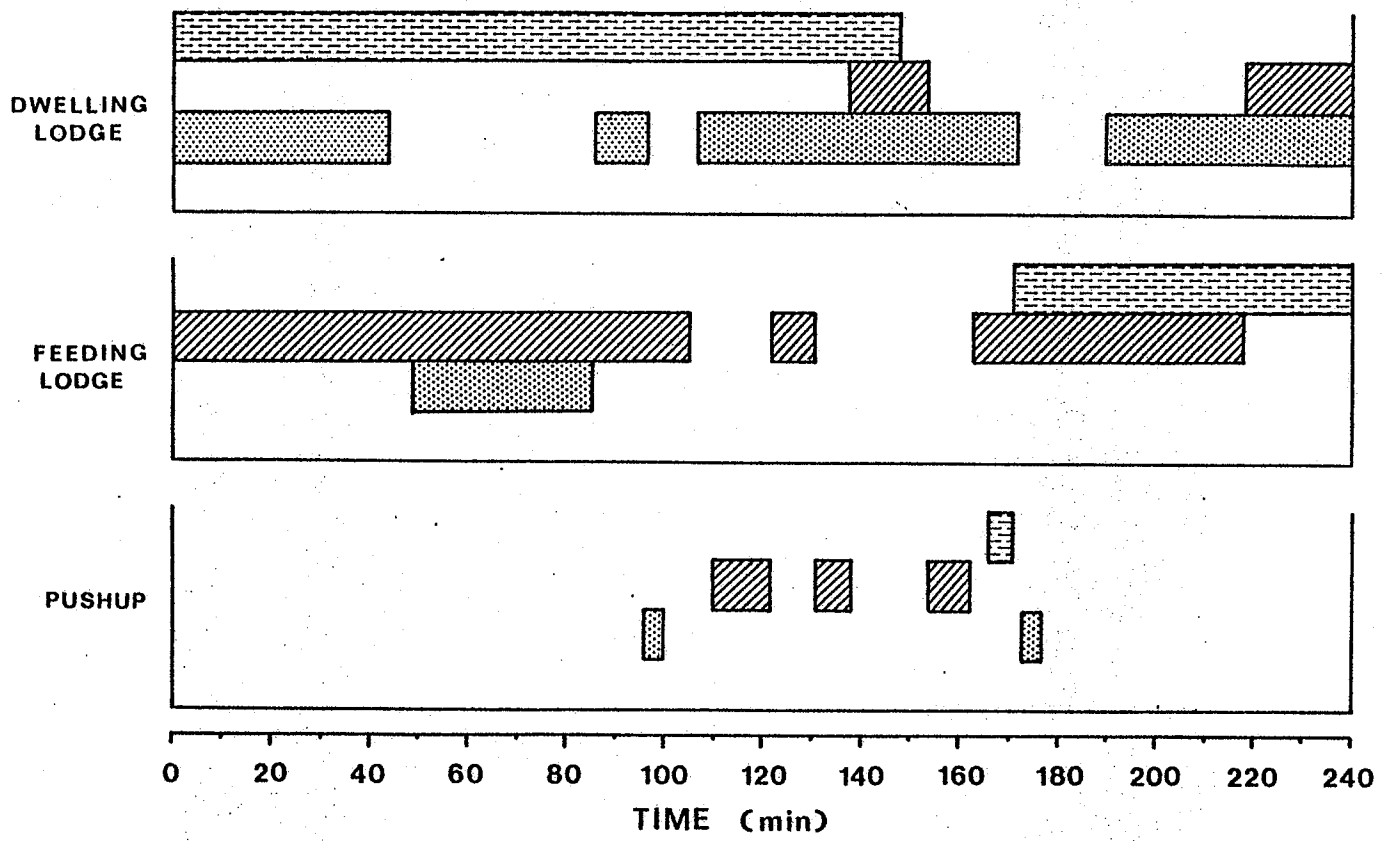
Day-to-day variation in the activity patterns of individual animals is apparent in both summer (Fig. 2A) and winter (Fig. 4A). Inter-individual variation is also suggested by these data, and is clearly evident in Fig. 7. This figure indicates that temporal variation in activity within an overwintering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

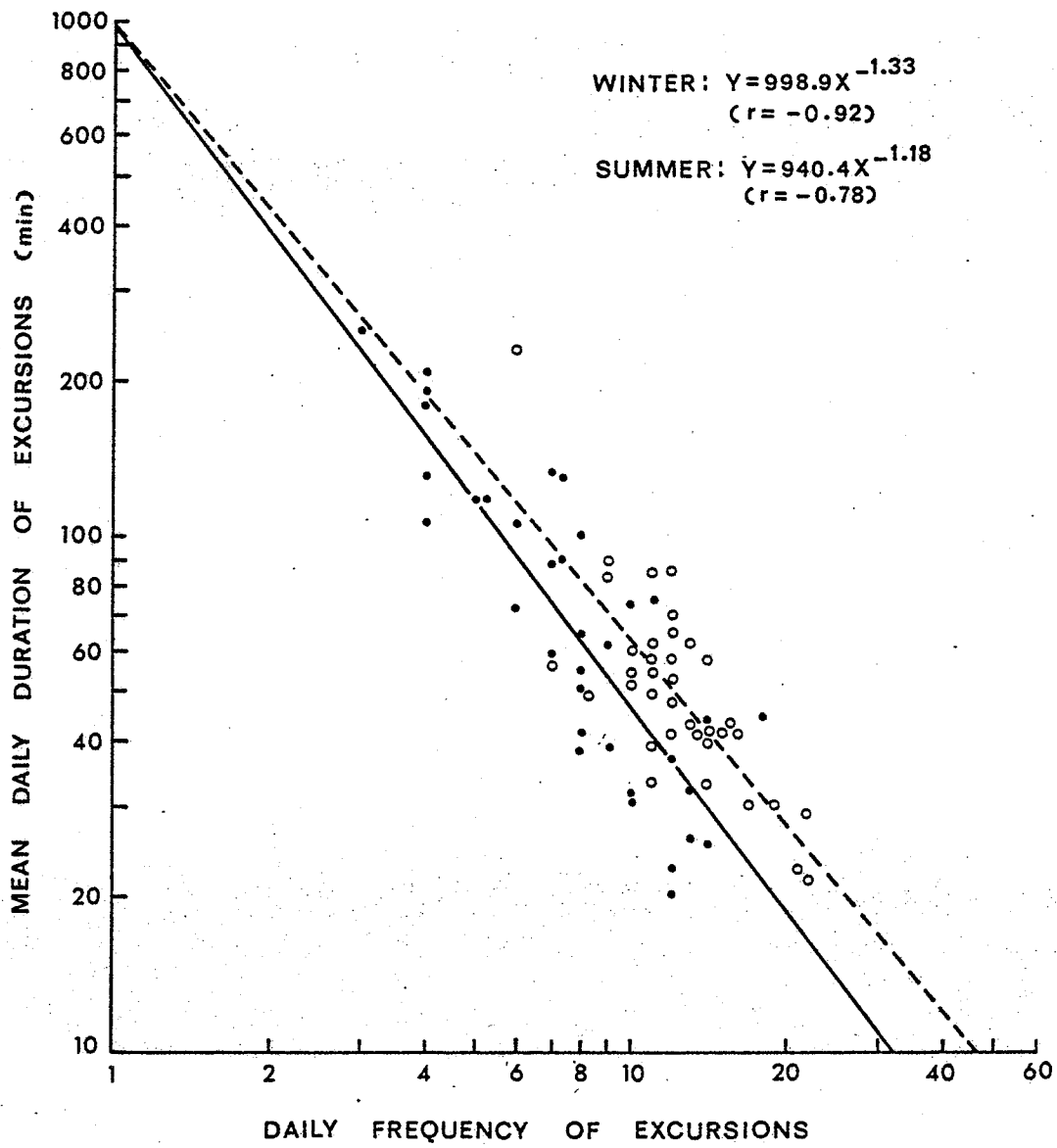


Table 3. Least-Squares regression analysis of activity in relation to environmental variables in summer (June 11-July 11, 1975)

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

^a

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 ^a (N; days)	r	t-value
Mean daily air T _a (°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

^a 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).

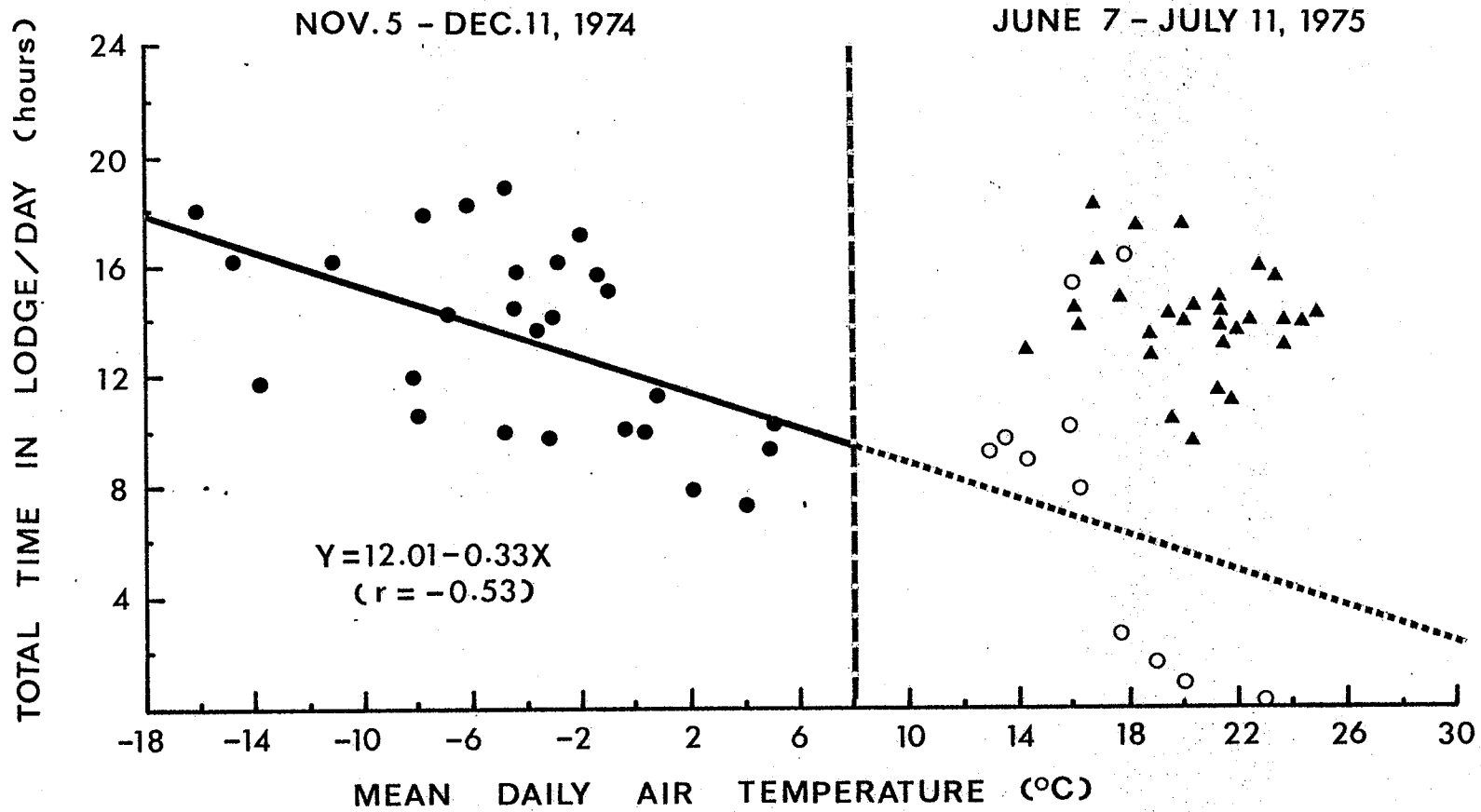
Although sample size was limited, the period of open water (Nov. 5-15) was also characterized by an increase in time spent in the lodge with increasing wind speed ($r = +0.56$, $P > .05$). During this same period, there was an increase in the frequency ($r = -0.47$, $P > .05$) and concurrent decrease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

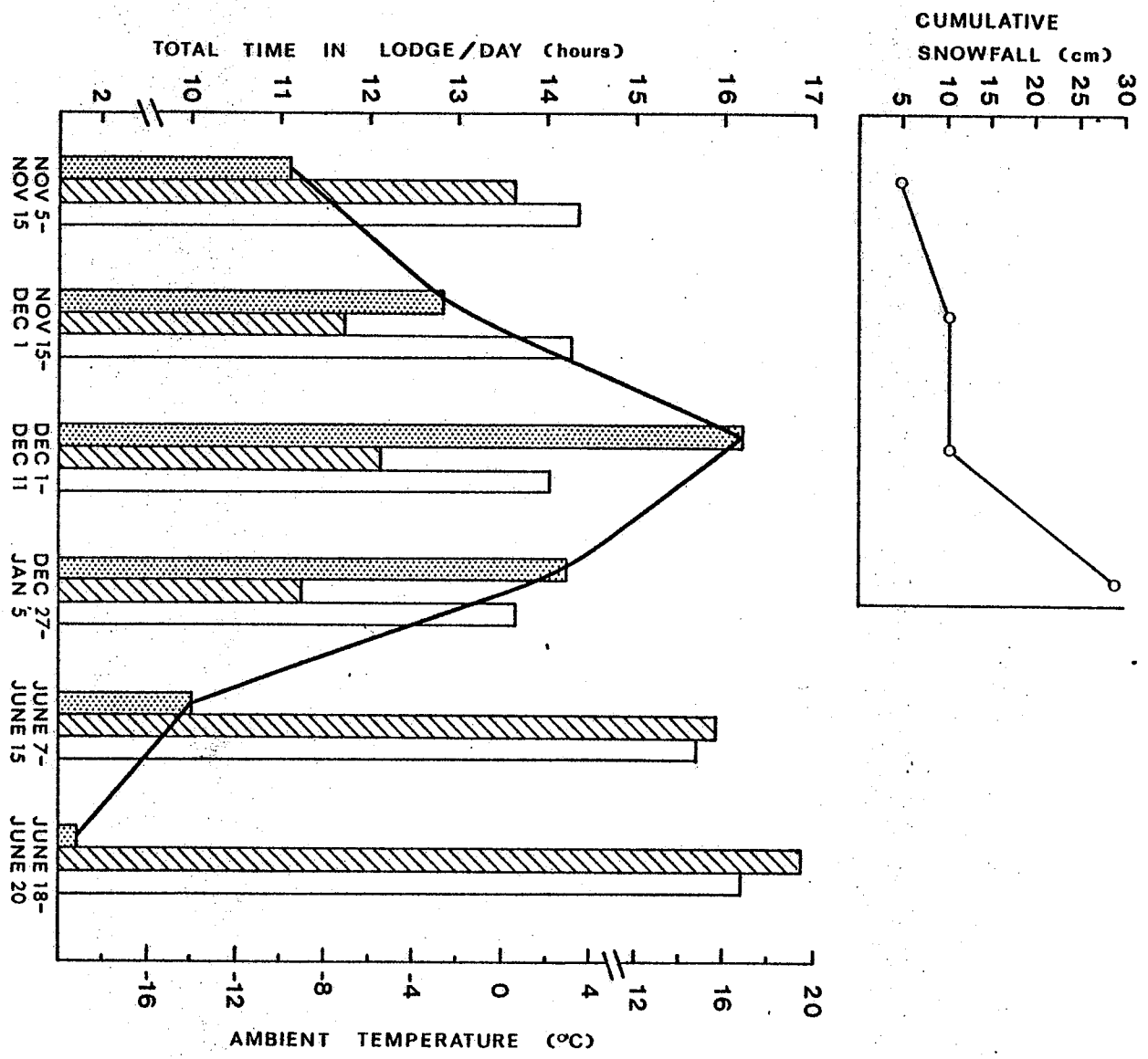


Table 5. Least-Squares regression analysis of the relationship between mean hourly body temperature (Y) and hourly activity index (X) for O. zibethicus censused at 15 to 240 min intervals, June-July, 1974

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 ^a 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

^aAll adults except No. 15

* P < .05

** P < .01

Table 6. Least-Squares regression analysis of the relationship between mean hourly body temperature (Y)^a 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 ^{**}	368	Y=-0.18 + 0.75X
21	-	-	-	-	-	-	+0.40	6.02 ^{**}	279	Y=-0.27 + 0.83X
22	-	-	-	-	-	-	+0.38	3.82 ^{**}	203	Y=-0.19 + 0.76X
24	-	-	-	-	-	-	+0.30	3.46 ^{**}	312	Y=-0.21 + 0.52X
25	+0.71	8.49 ^{**}	71	+0.56	5.64 ^{**}	71	+0.64	10.0 ^{**}	143	Y=-0.45 + 1.10X
26	+0.46	3.02 ^{**}	35	+0.36	2.25 [*]	35	+0.41	3.72 ^{**}	71	Y=-0.17 + 0.46X
27	-0.27	2.32 [*]	71	+0.23	1.95	71	+0.01	0.13	144	Y=-0.01 + 0.02X

^a 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.

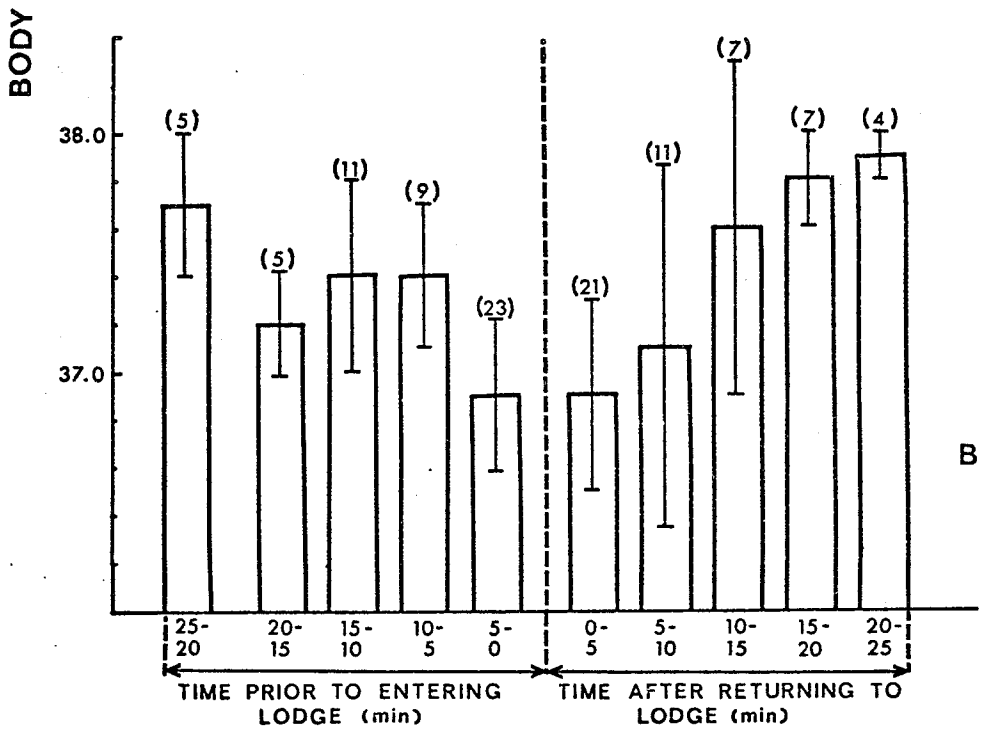
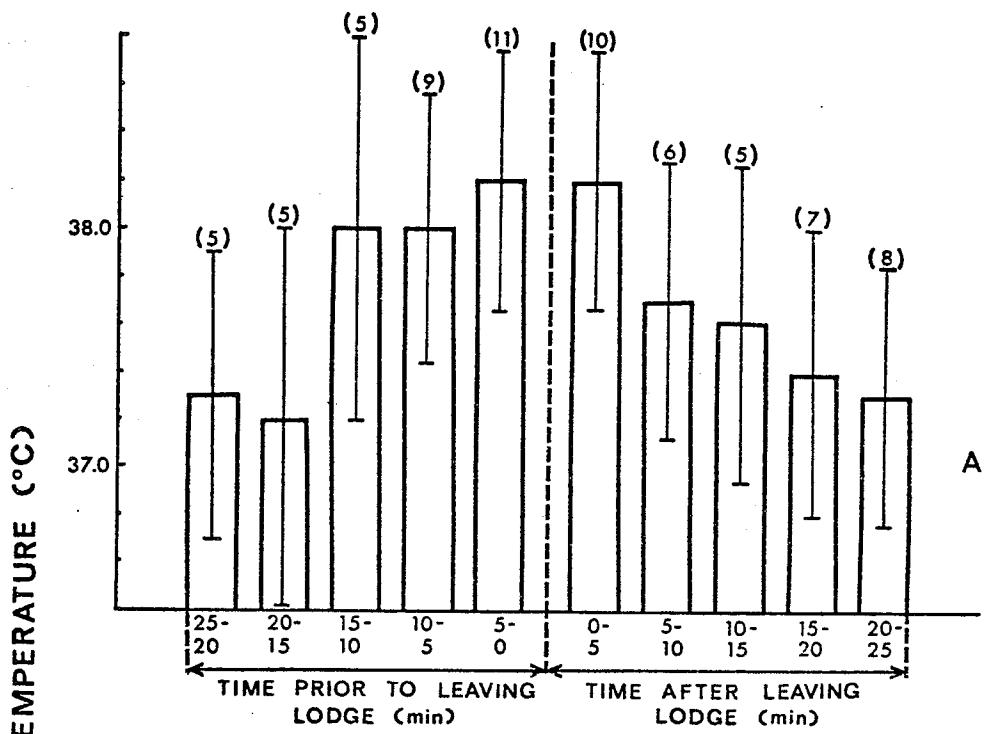
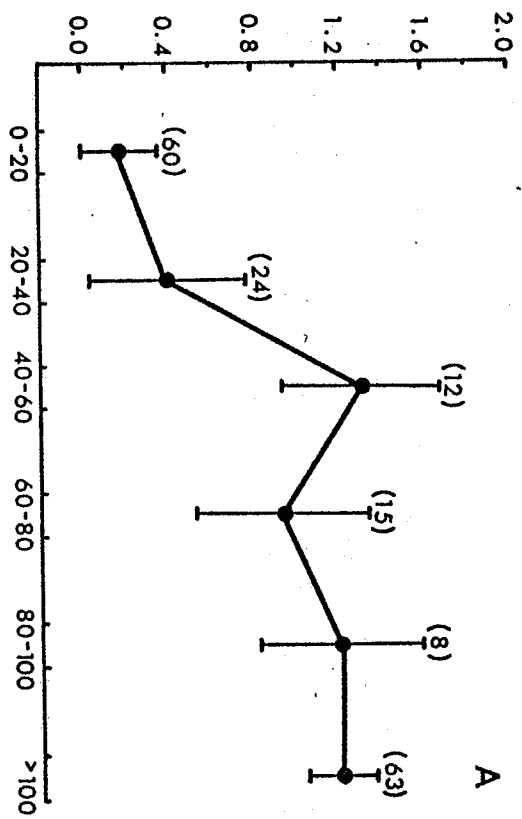


Figure 12. Mean body temperature changes in O. zibethicus (Nos. 20, 21, 22, 24) associated with the duration of foraging excursions away from Lodge No. 5, Nov. 26-Dec. 11, 1974. Vertical lines denote the 95 percent confidence limits of the means; values in parentheses indicate the number of observations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

DEVIATION FROM MEAN DAILY
 T_b AT DEPARTURE ($^{\circ}\text{C}$)



EXCURSION ΔT_b ($^{\circ}\text{C}$)
 (DEPARTURE T_b - RETURN T_b)

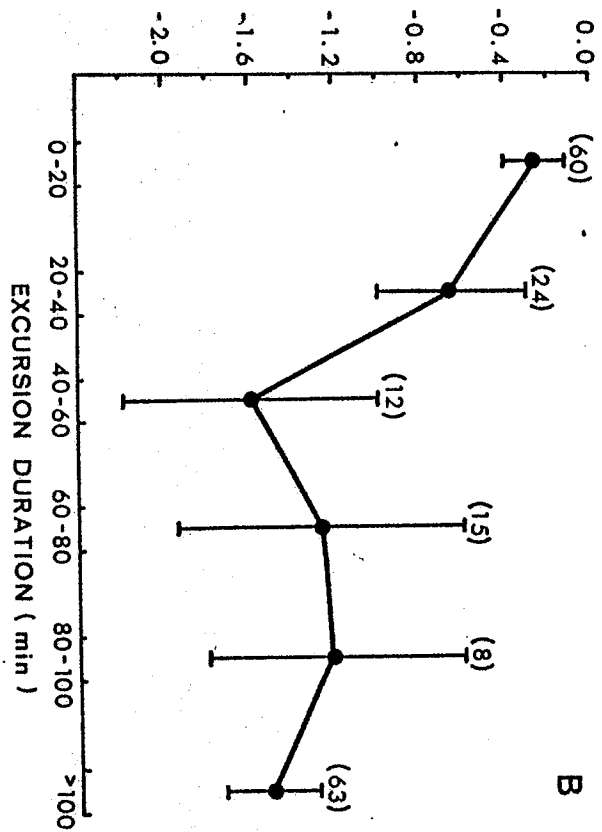
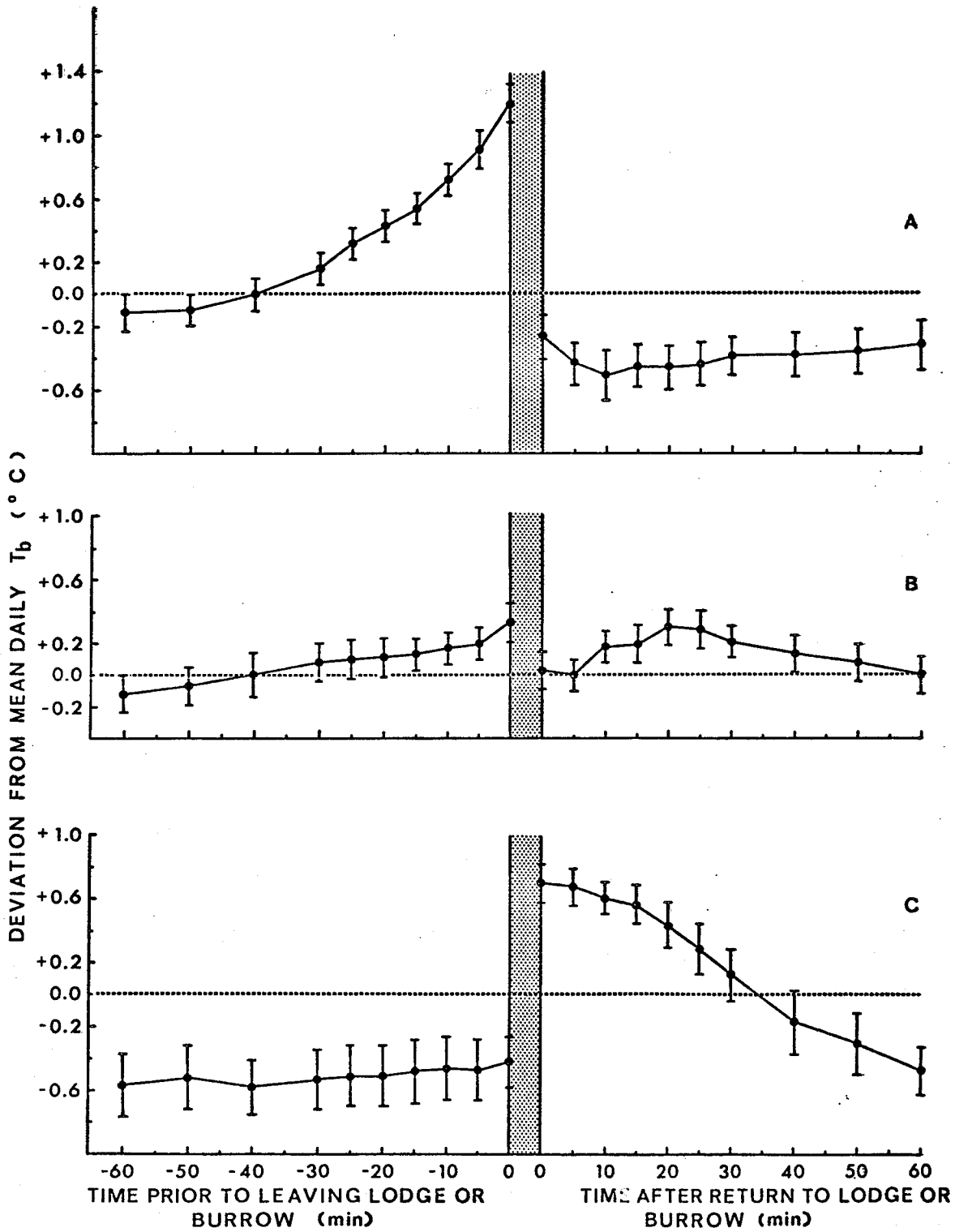


Figure 13. Mean body temperature changes in O. zibethicus during one hour immediately preceding, and during one hour immediately following major excursions (≥ 40 min duration) away from the lodge or burrow. Body temperature data are presented as deviations (\pm) from daily means. Vertical lines denote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



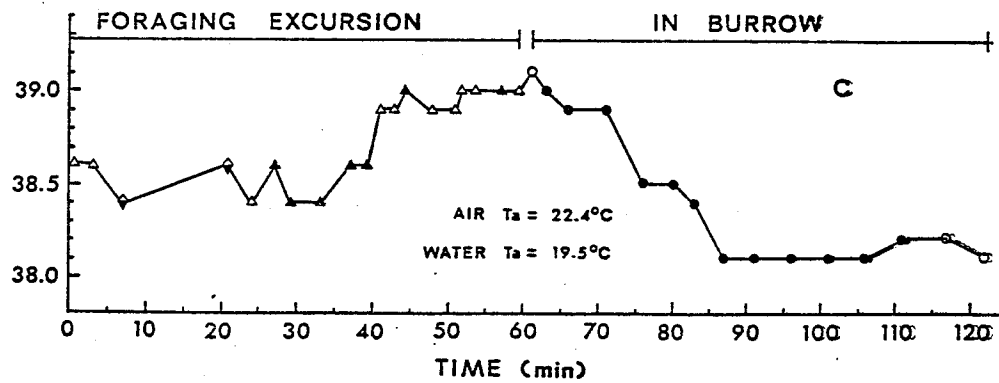
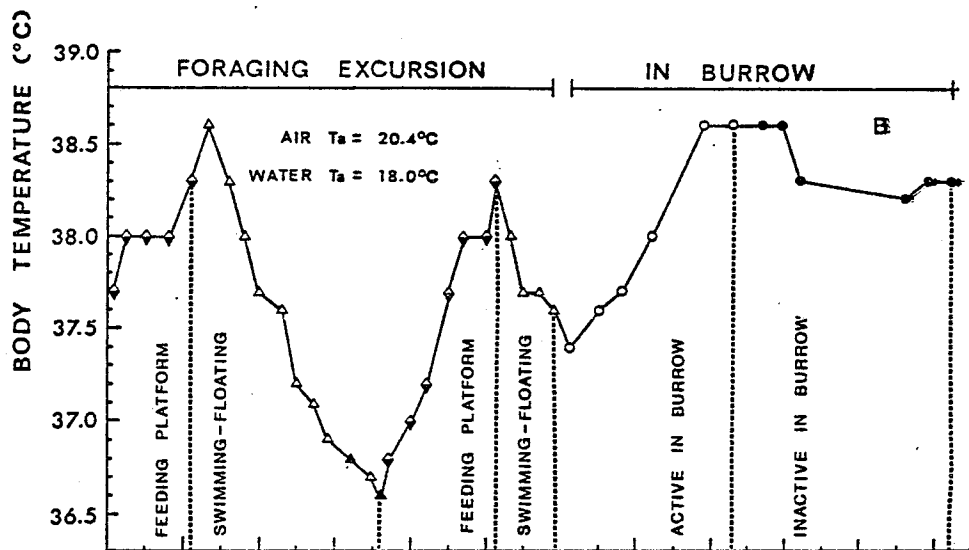
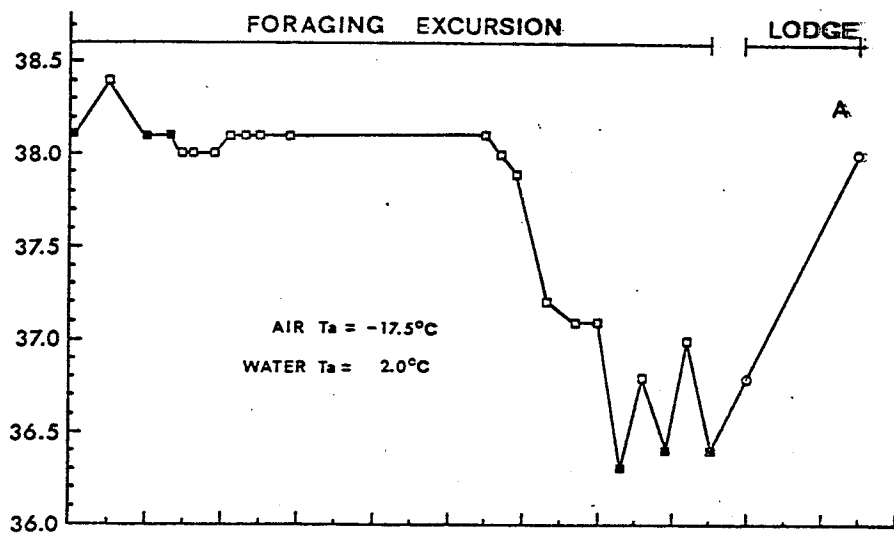
Considering only those excursions ≥ 40 min duration, a curvilinear increase in T_b was observed during the last 60 min prior to exit from the winter lodge (Fig. 13A). This increase attained a mean maximum value of 1.2°C immediately prior to exit from the lodge. In summer, only a slight rise in T_b ($< 0.5^\circ\text{C}$) 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°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

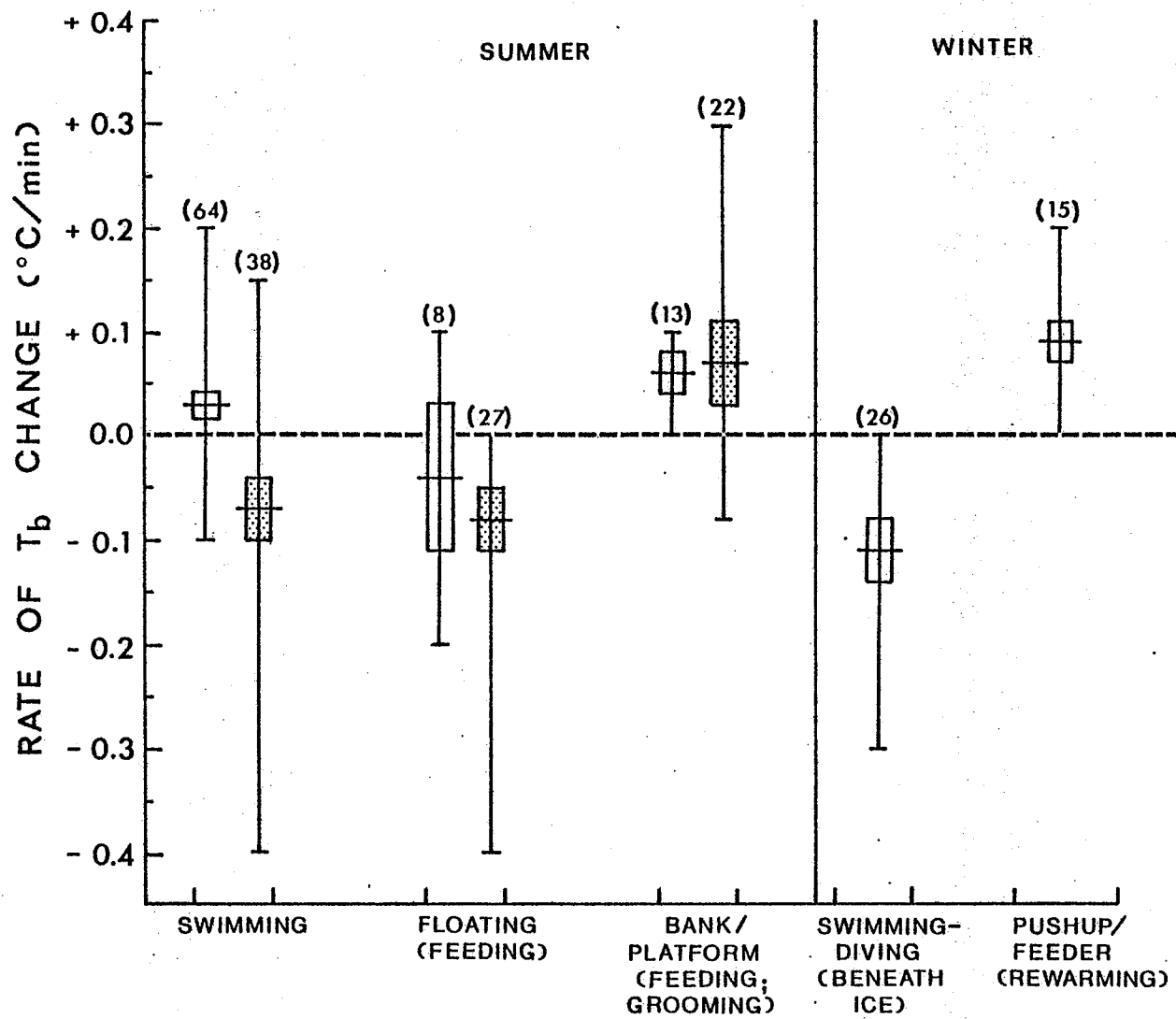



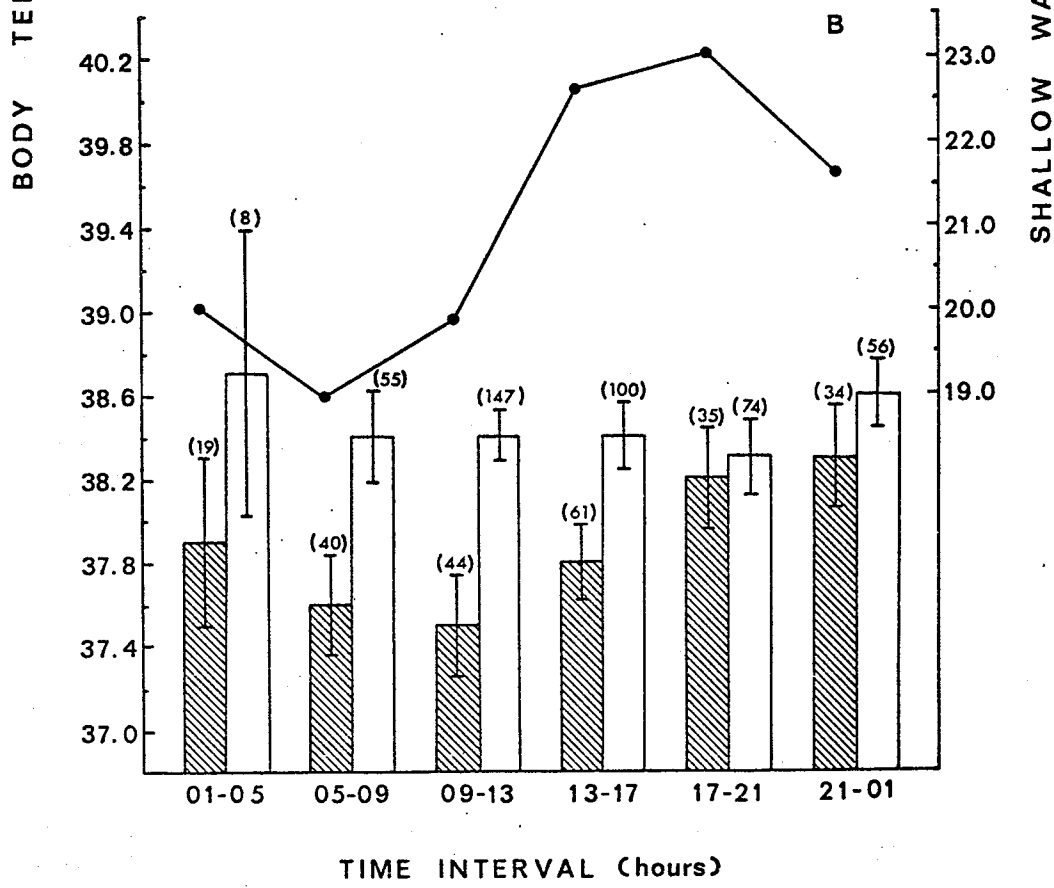
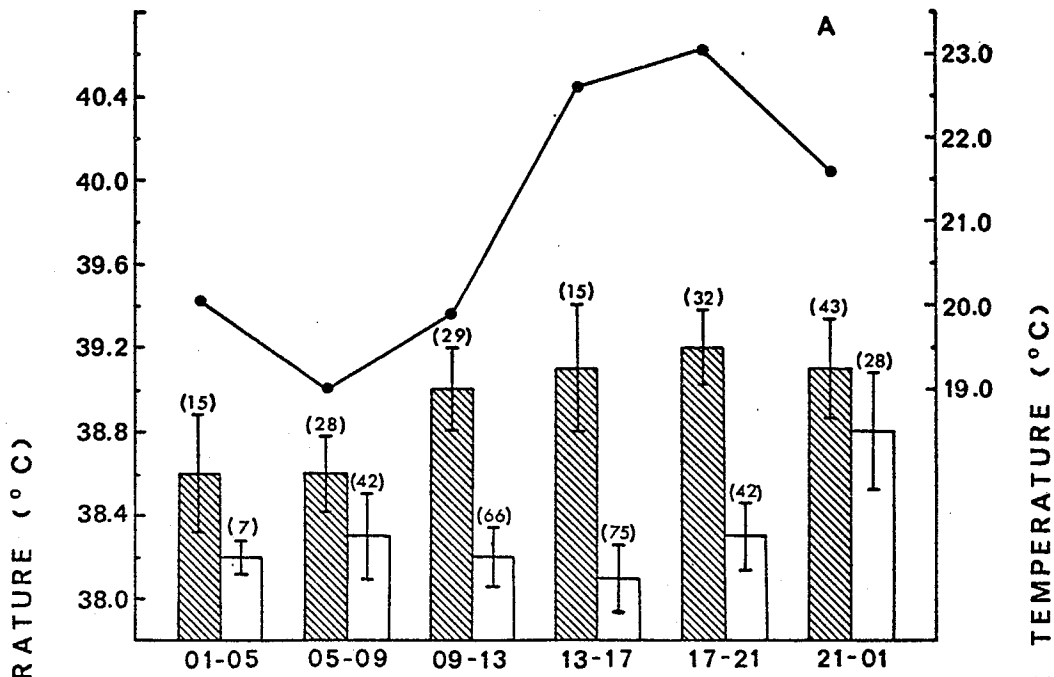


Figure 16A. Mean body temperatures of adult O. zibethicus (Nos. 13, 14) during periods of swimming, and during periods of inactivity within the burrow, in relation to time of day and shallow (3 to 20 cm) water T_a , July 8-29, 1974. Vertical lines denote the 95 percent confidence limits of the means;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

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



TIME INTERVAL (hours)

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