

Bioenergetics and thermoregulation of beavers (*Castor canadensis*)

by

Alvin P. Dyck

A thesis
presented to the University of Manitoba
in fulfillment of the
thesis requirement for the degree of
Master of Science, Zoology
in
Faculty of Graduate Studies

Winnipeg, Manitoba

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MASTER OF SCIENCE

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Abstract

Seasonal changes in microenvironment, daily activity pattern, and precision of body temperature (T_b) control were investigated in free-living beavers (*Castor canadensis*) inhabiting a boreal environment. The construction and group occupation of lodges provided the animals with year-round access to a thermoneutral microclimate. Thermal benefits were achieved at the expense of only limited disturbance to the respiratory gas concentrations inside the lodge, despite the large metabolic mass of the resident animals. Before freeze-up, the gaseous composition and mean lodge temperature (T_L) of occupied and unoccupied lodges were similar. Following freeze-up, mean CO_2 accumulation, O_2 depletion, and T_L were significantly higher in occupied houses. Mean monthly T_L consistently exceeded mean monthly air and water temperature. During the open-water season, water temperature (T_w) accounted for 90% of the T_L variation in occupied lodges. Following freeze-up, none of the meteorological or physical variables measured was a significant predictor of T_L .

The abdominal body temperature (T_b) of kits and adults averaged about 37.0°C throughout the year, with no evidence of seasonal hypothermia. During the open-water season, both age groups demonstrated a daily T_b rhythm characterized by a gradual increase in T_b between 0600h and 1800h, followed by a general decline during the nocturnal active period. During the ice-bound season, there was no evidence of a distinct daily T_b rhythm in either age group. Before and after freeze-up, both age groups exhibited a 0.22-0.64°C increase in mean T_b during the 3-h period immediately preceding the first excursion from the lodge. Aquatic activity almost invariably resulted in a decline in T_b , which usually continued for 5-15 min after beavers returned to their lodge or burrow. This was usually followed

by a period of rewarming prior to subsequent excursions. Kits exhibited a mean (\pm SE) rate of cooling in 1-9°C water ($0.11 \pm 0.02^\circ\text{C}/\text{min}$) which was 2.8 times greater than that of adults under similar conditions. Kits appeared to compensate for their greater susceptibility to aquatic cooling by spending less time in cold water than adults.

The T_b of captive beavers (≥ 1.5 years old) living in a simulated winter microhabitat averaged $36.5 \pm 0.02^\circ\text{C}$, with a mean daily amplitude of $1.2 \pm 0.4^\circ\text{C}$. The beavers exhibited a distinct 24-h rhythm in metabolic rate, with a mean, average daily metabolic rate of 2.87 ± 0.03 W/kg. This estimate of the cost of free existence was 1.5 times the resting metabolic rate previously reported for beaver. Mean hourly metabolic rate was strongly correlated with mean hourly immersion time in all animals tested. Total daily energy expenditure averaged 3880.59 ± 586.15 kJ/day. Based on current estimates of the energy content and digestibility of forage cached prior to freeze-up, it is unlikely that the winter energy requirements of this species can be met solely from the submerged food cache.

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Symbols and Abbreviations used in the Text

ADMR average daily metabolic rate

BMR basal metabolic rate

ΔO_2 oxygen decrement

FMR field metabolic rate

T_a ambient temperature

T_b body temperature

TL lodge temperature

TNZ thermoneutral zone

T_w water temperature

RMR resting metabolic rate

RQ respiratory quotient

W body weight

General Introduction

Animals that inhabit cold northern environments are often faced with formidable thermoregulatory challenges, which in winter may be compounded by reduced energy and nutrient availability. Problems of maintaining thermal balance are especially critical in small-bodied birds and mammals with high mass-specific energy requirements, large surface area-to-mass ratios, and limited capacities for improving insulation. These animals mitigate thermal stress largely through a combination of behavioral avoidance of extreme cold and physiological mechanisms that retard heat loss (MacArthur and Aleksik 1979; Pauls 1979; Wolff and Durr 1986; Feist and White 1989). Of particular interest, are species of non-hibernating mammals that encounter a broad spectrum of macroclimatic conditions by virtue of their geographic distribution. An excellent example is provided by the beaver, *Castor canadensis*. It is the largest North American rodent, with a range that extends from the Gulf of Mexico to the Mackenzie delta and northern Yukon (Hall 1981). At high latitudes, the formation of ice precludes onshore activity in winter, yet beavers regularly forage in near-freezing water throughout the ice-bound season.

Compared to the wealth of information available regarding the ecology, behavior and management of this prominent fur-bearer (see Naiman et al. 1986; Novak 1987), relatively few bioenergetics and thermoregulatory studies of this species have been undertaken (e.g., Novakowski 1967; Aleksik and Cowan 1969a, 1969b; MacArthur 1989a; Smith et al. in press). Results of several of these studies have suggested that beavers enter shallow torpor during periods when resources are scarce in winter. For example, Novakowski (1967) found that the winter food caches were usually insufficient to meet the energy requirements of colony members, assuming

that beavers remained euthermic throughout the winter. Furthermore, Aleksasuk and Cowan (1969a, 1969b) inferred a winter metabolic depression from a cessation of growth, aphagia, low thyroid activity and apparent behavioral paralysis in captive northern beaver kits subjected to complete darkness. In addition, Smith et al. (in press) reported a significant, 1.0°C decline in the mean daily T_b of three free-ranging adult beavers during winter, but noted that a single kit maintained an elevated T_b during the same period. Interestingly, MacArthur (1989a) found that the rectal T_b of a single captive beaver kit (< 6 months old) was generally lower and less stable than the abdominal T_b of older animals. Thus, age-related differences in the precision of T_b regulation in free-living beavers require further investigation. It appears that, despite a large body size, beavers are sensitive to immersion hypothermia (MacArthur and Dyck 1990), which suggests that behavioral strategies for T_b regulation may be critical to these animals in nature.

Knowledge of the lodge microenvironment, including gas composition and temperature of the nest chamber, is essential to developing an understanding of the energetic and thermoregulatory requirements of this species. There are few records of lodge and burrow temperatures for northern populations of *C. canadensis* (Coles 1967; Stephenson 1969; Buech et al. 1989), and almost nothing is known about the seasonal variation in the respiratory gas composition of these shelters (Novak and Cook 1972).

The present study investigates behavioral and physiological aspects of temperature regulation in free-ranging beavers, and also examines the thermoregulatory performance and metabolic requirements of beavers held in a simulated winter microhabitat. Part I addresses seasonal variation in the microclimatic conditions experienced by beavers existing in a boreal

environment. This phase of the study included monthly monitoring of air, water, and lodge temperatures, as well as O_2 and CO_2 levels in both occupied and unoccupied lodges. Part II investigates the possible occurrence of seasonal hypothermia in this species and also examines the precision of T_b regulation, including the role of behavior, in adult and juvenile beavers. Finally, using microclimate data collected in Part I, my objectives in Part III were to simulate winter field conditions in the laboratory to estimate daily energy requirements, and evaluate temporal patterns in metabolic rate, T_b and aquatic activity of captive beavers. Estimates of the cost of free existence were used in energy budget calculations to predict metabolic costs and food requirements of overwintering beavers in nature.

Part I

**Seasonal variation in the microclimate and gas composition
of beaver lodges in a boreal environment**

Introduction

The construction and occupation of burrows, dens or lodges are fundamental behavioral strategies by which small mammals minimize thermoregulatory costs in northern environments (Glaser and Lustick 1975, MacArthur and Aleksuk 1979, Wolff and Durr 1986, Buech et al. 1989). However, thermal benefits accrued from such behavior may be offset by the physiological stress posed by CO₂ accumulation and O₂ depletion in these shelters (Maclean 1981). Disturbance in microenvironmental gas composition should be most acute in large-bodied or communally nesting species, especially those at high latitudes where gas exchange may be impeded by frozen substrates (Withers 1978).

The beaver, *Castor canadensis*, provides an excellent model for investigating this problem. It is the largest North American rodent with a range extending from the Gulf of Mexico to the Mackenzie delta and northern Yukon (Hall 1981). A family group, usually consisting of the adult breeding pair together with a variable number of two-year olds and yearlings (see Novak 1987), typically occupy either a bank den or a lodge constructed of branches and mud. In northern regions, severe winter temperatures may cause lodge walls to freeze through most of their depth. These factors, together with the increased time spent in the lodge following freeze-up (Potvin and Bovet 1975; Lancia et al. 1982; Smith et al. in press), suggest that there could be pronounced annual variation in the gaseous composition of beaver lodges at northern latitudes. Preliminary data reported by Novak and Cook (1972) suggest that the respiratory gas concentrations of beaver lodges deviate little from ambient air. This seems improbable, given that Huenecke et al. (1958) and MacArthur (1984) documented sharp increases in the CO₂ levels of muskrat (*Ondatra zibethius*) lodges in winter. Previous

studies of beaver lodges in New Hampshire (Coles 1967), Algonquin Park, Ontario (Stephenson 1969), and northern Minnesota (Buech et al. 1989), all suggested that lodge temperatures usually fall within the thermoneutral zone of this species (MacArthur 1989a). However, all of these studies also reported minimum lodge temperatures that were below the lower critical temperature (0-2°C) previously established for beaver (MacArthur 1989a).

The first objective of this study was to quantify the seasonal variation in gaseous composition of beaver lodges in a Manitoba boreal forest. A second objective was to examine daily and seasonal fluctuations in lodge temperature, in order to describe the thermal microenvironment of this species, as well as identify the primary physical factors that affect lodge temperature at these latitudes. Such information provides a necessary foundation for subsequent bioenergetic and thermoregulatory studies of beaver living in a boreal environment (Parts II and III).

Study area

Research was conducted in the Canadian Shield of southeastern Manitoba near the town of Pinawa (50°10' N, 96°3' W). The climate of the region is classified as cool continental, with average annual temperature extremes ranging from -40.2 °C to 33.1°C. Mean annual rainfall and snowfall are 43.0 cm and 131.7 cm, respectively (Whiteshell Nuclear Research Establishment, climatological records). Beaver lodges were located throughout the region on numerous ponds and ditches, and on the Winnipeg River between Sylvia and Margaret lakes. The study area is typical boreal forest, dominated by black spruce (*Picea mariana*) and aspen (*Populus tremuloides*). Emergent vegetation at lodge sites was primarily cattail (*Typha* spp.), whereas willow (*Salix* spp.) was predominant along seasonally flooded shorelines.

Methods

Lodge gas and microclimate analyses

Lodge gases and accompanying microclimate data were collected at monthly intervals from 14 lodges in the Pinawa region during the period 3 June 1988 through 14 March 1989. For comparative purposes, limited data were also gathered from two occupied lodges in Delta Marsh (50° 11' N, 98° 23' W) on 26 March 1990. All measurements were gathered between 0800 and 1400 h, and each lodge was classified as occupied or unoccupied, based on observations made at the time of sampling. Criteria used to establish the occupancy status of a lodge included: presence or absence of beaver nearby, vocalizations or splashing sounds emanating from the lodge interior, signs of recent foraging activity along shore, fresh construction on a nearby dam, lodge, or food cache and, in winter, the appearance of frost crystals above the lodge "chimney".

When a lodge was sampled for the first time, the nest chamber was located by penetrating the wall with a steel spear (9-mm diameter) or an 85-cm drill bit (8-mm diameter) mounted on a cordless power drill. Wall thickness was estimated by measuring the point at which a sudden loss of resistance was detected with the spear or drill. A 750- to 900-cm length of stainless steel tubing (1-cm ID) was sealed at one end with tape, and the taped end of this access pipe was pushed through the opening in the lodge wall until it extended into the nest chamber. A 1-m long sampling tube (6-mm ID, 28-ml volume), also taped at the distal end, was then fed into the access pipe until it contacted the tape seal of the outer pipe. A 9-cm length of Tygon tubing connected to a three-way stopcock was attached to the sampling tube immediately after both tape seals were punctured with a

metal plunger (5-mm diameter). A 60-ml plastic syringe was attached to the three-way stopcock and approximately 180-ml of lodge gas were drawn through the sample tube and discarded. Two, 60-ml aliquots of lodge gas were then drawn into separate syringes, which were immediately sealed and set aside for subsequent O_2 determinations. All syringes were lubricated with silicone grease prior to sampling, in order to minimize diffusion (MacArthur 1984). After the second sample was drawn, the three-way stopcock was removed and quickly replaced with a Dräger colorimetric indicator tube specific for CO_2 (range: 0.1-6.0 % by volume). A one-way Dräger hand-pump was used to draw a standard volume of chamber gas through the indicator tube and the % CO_2 was read directly from the scale on the Dräger tube. Following gas sampling, the Tygon tubing was removed from the sample tube and a copper-constantan thermocouple was threaded into the nest chamber. Lodge temperature (T_L) was measured to the nearest $0.1^\circ C$ with a Sontec Model BAT-12 digital thermometer. Following T_L measurement, the sample tube was removed while the access pipe remaining in the lodge wall was sealed and camouflaged with loose branches. Ambient air temperature (T_a) in the shade, and shallow water temperature (T_w) were also measured at each lodge site.

The O_2 concentrations of gas samples were determined within 4-5 h of collection, using a Beckman OM-14 polarographic oxygen analyzer. Water was removed from the gas prior to injection into the analyzer by passing each sample through a small column of indicating drierite (anhydrous $CaSO_4$). Oxygen decrement (ΔO_2) was calculated by subtracting the % O_2 in the nest chamber from the value for ambient air (21.0 %).

Automated lodge temperature measurements

Hourly measurements of T_L , T_W and T_a were recorded at two lodge sites from 28 August 1988 through 4 June 1989. A Type U Grant thermistor probe protected in a sealed brass tube (5mm ID) was permanently installed within the nest chamber at the level of the resting platform. A similarly protected thermistor probe was secured to a post next to the lodge to measure T_W approximately 30 cm below water level. A third, shielded thermistor probe recorded T_a 1 m above ground level at the lodge site. All three temperatures were recorded hourly by a Model 1201 Grant Squirrel data logger housed in a weather-proof box located at the lodge site. Data collection was interrupted periodically to allow for manual or computer-assisted downloading of stored recordings.

Variations in T_L were examined in relation to T_W , T_a , wind speed (km/h), net radiation flux (total incoming radiation - total outgoing radiation in W/m^2), and lodge wall thickness (including snow depth in winter). Air and water temperatures were recorded at the lodge site; all other meteorological data were obtained from an official weather station situated within 11 km of all lodge sites (Environmental Research Branch WNRE).

Statistical analysis

Analysis of variance (ANOVA) and Fisher's LSD test were used to evaluate seasonal variations in lodge temperature and gas composition. Two-sample comparisons of means were made with Student's t -tests or paired t -tests. Stepwise regression was used to determine variables which were important in explaining observed variation in lodge temperature. Mean values are presented with ranges or ± 1 SE.

Results

Seasonal variation in lodge gas composition

Table 1-1 summarizes the physical characteristics of the 14 lodges monitored in this study. Ten of the 14 lodges were classified as occupied, while the remaining 4 lodges appeared to be abandoned, although these were all located in the vicinity of occupied houses. Surprisingly, there was no evidence of seasonal variation in either CO₂ concentration ($F_{1,8} = 0.67$, $P = 0.73$) or O₂ decrement ($F_{1,7} = 0.85$, $P = 0.56$) in occupied lodges (Fig 1-1). Lodge gas concentrations were highly variable, with monthly variation in CO₂ levels ranging from 0.32% (0.03-0.35% CO₂) in February, to 1.77% (0.03-1.8% CO₂) in December. Minimum CO₂ and maximum O₂ levels recorded from beaver lodges corresponded to normal ambient air (0.03% and 21.0%, respectively). The highest CO₂ concentration (1.8%) was recorded in December from an occupied lodge (No. 6) constructed almost entirely of mud and lacked any obvious chimney or vent. This "mud house" was the only one of its kind in the Pinawa study area and consistently demonstrated the highest CO₂ accumulation and O₂ depletion. Only during the month of June did another lodge (No. 2), known to contain kits, demonstrate a higher % CO₂ (0.45%) and Δ O₂ (0.45%) than the mud lodge (CO₂ = 0.18%; Δ O₂ = 0.18%). Lodges similar in construction to No. 6 typically occur in marsh habitats where beaver have limited access to woody vegetation and, consequently, construct houses primarily from mud and aquatic plants. It was therefore not surprising that the CO₂ levels of the two occupied lodges (Nos. 15 and 16) sampled in Delta Marsh during March 1990 (0.79% and 1.5%, respectively) were consistent with the measurement of No. 6 (0.82%) sampled at the Pinawa site in March 1989.

Table 1-1: Physical characteristics of lodges monitored during 1988-1990.

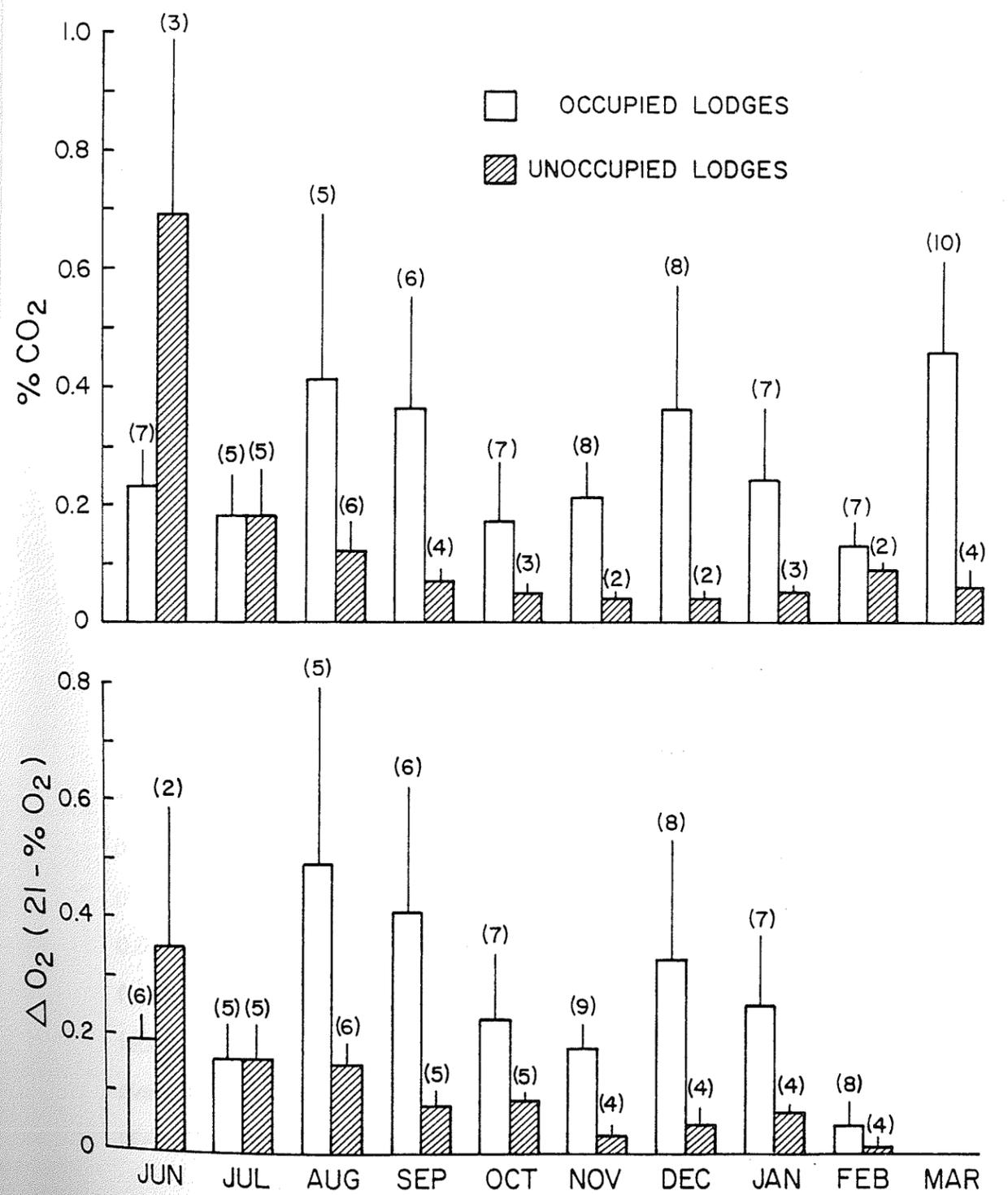
Lodge No.	Lodge Site	Circumference	Height	Wall Thickness	Sampling Period
1 *	onshore	12.0 m	1.1 m	73 cm	Jun 88-Mar 89
2 *	onshore	----	----	30 cm	Jun 88-Oct 88
3	island	18.6 m	1.2 m	52 cm	Jun 88-Mar 89
4 *	island	12.5 m	1.0 m	45 cm	Jun 88-Mar 89
5	onshore	12.6 m	0.8 m	40 cm	Jun 88-Mar 89
6 *	onshore	13.0 m	1.2 m	80 cm	Jun 88-Mar 89
7 *	onshore	----	----	43 cm	Jun 88-Mar 89
8 *	onshore	13.7 m	1.4 m	70 cm	Jul 88-Jun 89
9	island	20.2 m	1.3 m	48 cm	Jul 88-Mar 89
10	onshore	11.0 m	0.9 m	32 cm	Jul 88-Mar 89
11 *	onshore	----	----	66 cm	Sep 88-Mar 89
12 *	onshore	15.4 m	1.0 m	32 cm	Sep 88-Mar 89
13 *	onshore	14.4 m	1.2 m	28 cm	Nov 88-Mar 89
14 **	island	11.1 m	1.2 m	30 cm	Aug 88-Nov 88
15 ***	onshore	16.5 m	1.3 m	67 cm	Mar 26, 1990
16***	bank	----	2.0 m	55 cm	Mar 26, 1990

* occupied lodges

** monitored for temperature only (automated hourly recordings)

*** lodges sampled at Delta Marsh

Figure 1-1. Seasonal variation in mean CO₂ concentration and mean O₂ decrement ($\Delta O_2 = 21.0 - \% O_2$ in chamber) of occupied and unoccupied lodges. Vertical lines indicate ± 1 SE; values in parentheses denote number of lodges sampled.



Mean monthly % CO₂ ($0.69 \pm 0.30\%$) and Δ O₂ ($0.35 \pm 0.24\%$) of unoccupied houses were higher in June than during any other month sampled (Fig. 1-1). For these houses, mean CO₂ concentrations ($0.18 \pm 0.07\%$) were about six times the normal ambient level (0.03%) in July, then dropped to four times ambient in August ($0.12 \pm 0.05\%$), and remained close to two times ambient ($0.05-0.07 \pm 0.02\%$) for the remainder of the sampling period (September through March). Mean Δ O₂ declined over the summer months from $0.35 \pm 0.24\%$ in June, to $0.15 \pm 0.04\%$ in August, becoming negligible in fall and winter ($0.0-0.09 \pm 0.02\%$).

From mid-August through mid-March, % CO₂ and Δ O₂ were consistently higher in occupied, than in unoccupied lodges (Fig. 1-1). To facilitate statistical comparisons between occupied and unoccupied lodges, data were pooled to create two datasets, one including all measurements prior to freeze-up (June-October), the other, all measurements after freeze-up (November-March). Before freeze-up, there was no difference ($P > 0.05$) between occupied and unoccupied houses in either mean % CO₂ or mean Δ O₂. After freeze-up, however, the mean CO₂ level was significantly higher in occupied ($0.30 \pm 0.06\%$, $n=40$), than in unoccupied lodges ($0.05 \pm 0.01\%$, $n=13$) ($t = 3.87$, $df=40$, $P=0.0004$). The mean Δ O₂ of occupied lodges ($0.2 \pm 0.06\%$, $n=32$) also exceeded that of unoccupied houses ($0.04 \pm 0.01\%$, $n=16$) following freeze-up ($t = 2.74$, $df=32$, $P=0.01$). The CO₂ level of occupied lodges in winter correlated with lodge wall thickness, which included the overlying snow cover, ($r^2 = 0.31$, $df=62$, $P=0.012$), but not with T_L ($r^2 = 0.06$, $df=66$, $P=0.61$), or the thermal gradient, $T_L - T_a$ ($r^2 = -0.002$, $df=62$, $P=0.99$).

Seasonal variation in lodge temperatures

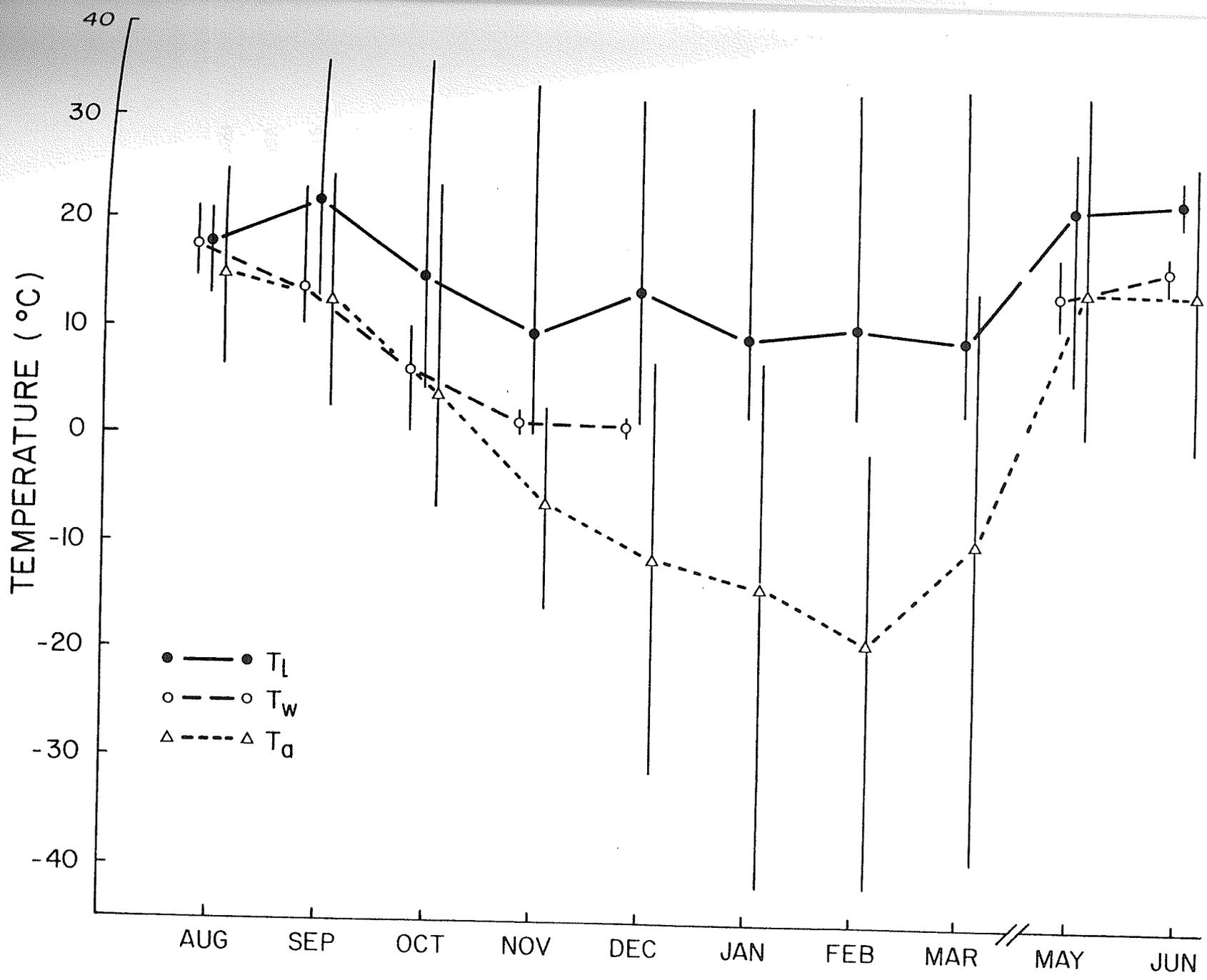
Prior to freeze-up, mean T_L was similar ($P > 0.05$) in occupied ($17.1 \pm$

1.35°C, n=30) and unoccupied lodges (16.3 ± 1.82°C, n=24) censused at monthly intervals. After freeze-up, however, mean T_L was significantly higher ($t = -6.05$, $df=61$, $P=0.0001$) in occupied (2.7 ± 0.42°C, n=41), than in unoccupied (-1.3 ± 0.43°C, n=21) lodges. The lowest T_L recorded from an occupied lodge was -0.04°C, measured in Lodge No. 1 during February, whereas the minimum T_L recorded from an unoccupied lodge (No. 10) during the same month was -6.0°C. Maximum temperatures for both occupied and unoccupied lodges were recorded in June (25.6°C and 28.7°C). Air temperatures measured outside the lodge at the time of the monthly sampling (Table 1-1), ranged from -15.3°C to 33.5°C.

Automated hourly measurements of T_L , T_W and T_a were recorded from a single occupied lodge (No. 14) during the period 28 August 1988 through 22 November 1988, after which this lodge was abandoned by the beaver family in favour of lodge No. 8, situated approximately 500 m away. This relocation was confirmed by monitoring the movements of two radio-implanted members of this family group (see Part II). Automated temperature recordings were resumed on 23 November 1988 at lodge No. 8 and measurements of this lodge continued until 4 June 1989. Ice damage of the T_W probe precluded T_W measurements from January through March at this site.

Mean monthly T_L of lodge Nos. 8 and 14 consistently exceeded mean monthly T_W and T_a (Fig 1-2). The annual variation in T_a at these sites was 73.8°C (-41.4 to 32.4°C), compared to a T_L range of only 37.0°C (1.4 to 35.6°C). Since the T_L thermistor was installed in the nest chamber at the level of the resting platform, it is likely that animals inside the lodge periodically came in contact with the probe. This could explain the regular occurrence of T_L values > 30.0°C in 7 of the 10 months sampled (Fig 1-2).

Figure 1-2. Mean monthly lodge (closed circles), water (open triangles), and ambient air (open circles) temperatures at lodge sites Nos. 8 and 14 (see text). Vertical lines denote range.



During fall and winter, daily T_L fluctuations in lodge Nos. 8 and 14 exhibited regular peaks and troughs with a periodicity close to 24 h (Figs. 1-3 and 1-4). In early autumn, daily variation in T_L generally reflected changes in T_a (Fig 1-3). The apparent daily periodicity in T_L also corresponded closely to the duration of the light-dark cycle, with T_L minima usually coinciding with periods of darkness (Fig 1-3). In winter, periodicity was still apparent in the T_L data, but now with less evidence of synchrony between T_L and T_a (Fig 1-4). Despite a substantial drop in minimum daily T_a from approximately -10.0°C on Feb 11-13 to -40.0°C on Feb 15-17, daily minimum T_L remained constant at 3.0 - 5.0°C (Fig 1-4). Mean hourly T_L of lodge No. 8 ranged from 8.0 to 12.0°C during the period 9 January 1989 through 28 March 1989. In all seasons, daily peaks in T_L usually coincided with the presence in the lodge of at least one of the two above-mentioned, radio-tagged beavers. In spring, there was no clear evidence of periodicity in T_L , despite often dramatic fluctuations in outside T_a (Fig 1-5). In several instances (e.g., May 15-16), T_a was as much as 10.0°C higher than T_L .

Monthly census data from occupied lodges (Table 1-1) were used in an attempt to identify variables that could account for the observed fluctuations in T_L . Stepwise regression analyses were run on T_L data collected before and after freeze-up. Before freeze-up, T_w was the only significant variable ($F_{1,27} = 256.49$, $P=0.0001$), accounting for 90% of the variation in chamber temperature of occupied lodges. Following freeze-up, none of the five variables tested was a significant predictor of T_L .

Figure 1-3. Daily fluctuations in water (dashed line), ambient air (dotted line), and nest chamber (solid line) temperature of lodge No. 14 during September.

SEPTEMBER 1988

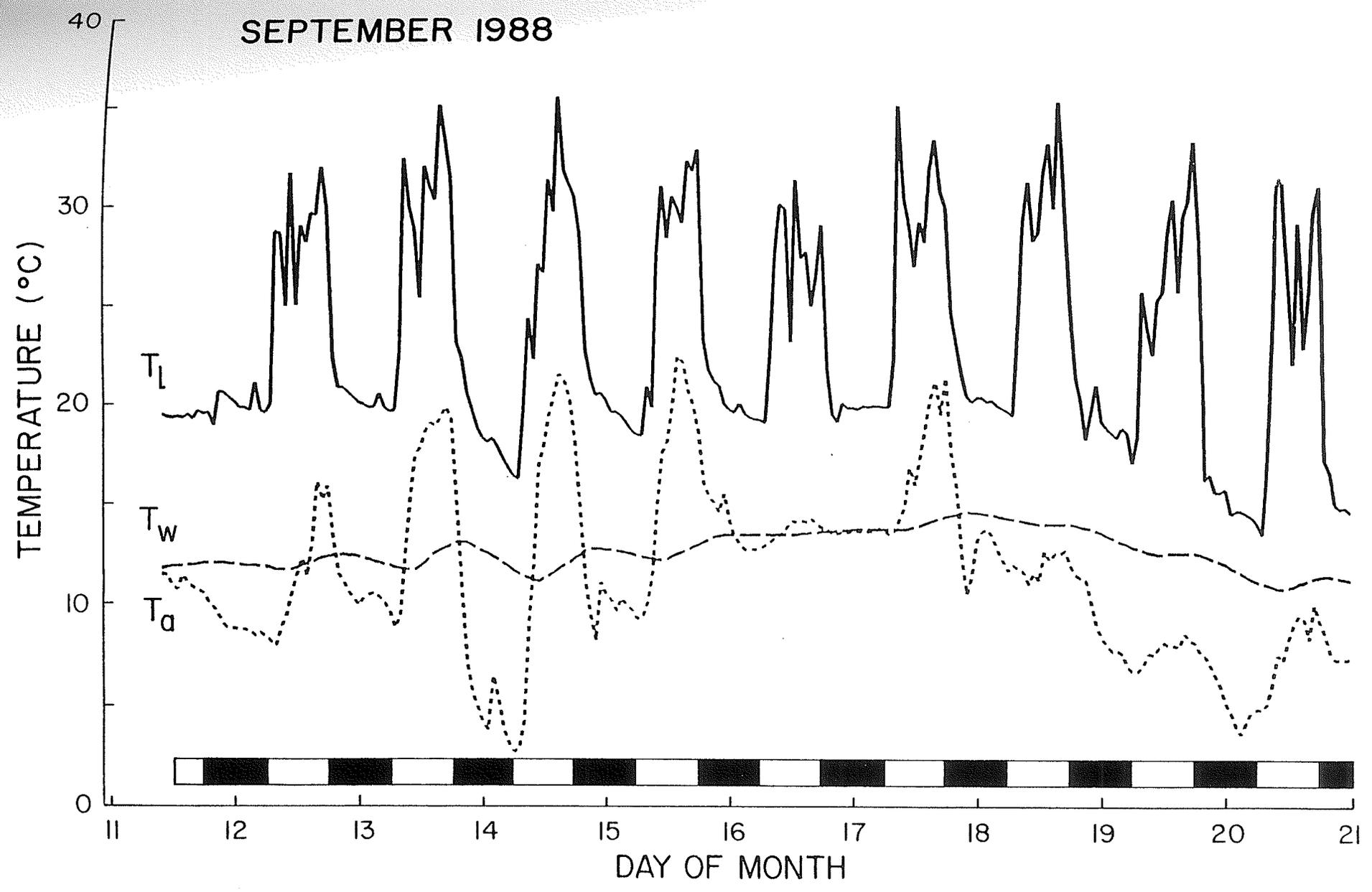


Figure 1-4. Daily fluctuations in ambient air (dotted line) and nest chamber (solid line) temperature of lodge No. 8 during February.

FEBRUARY 1989

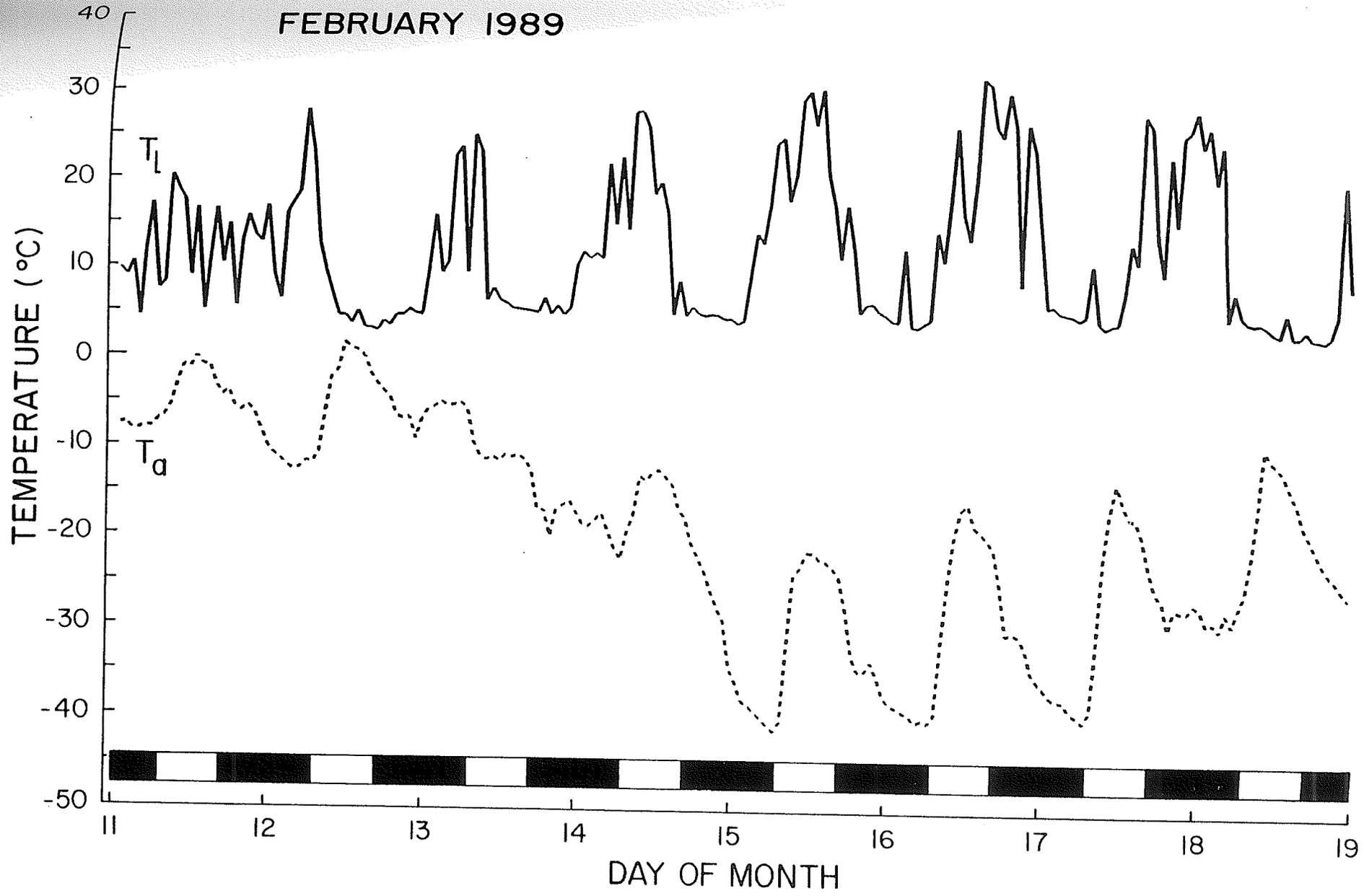
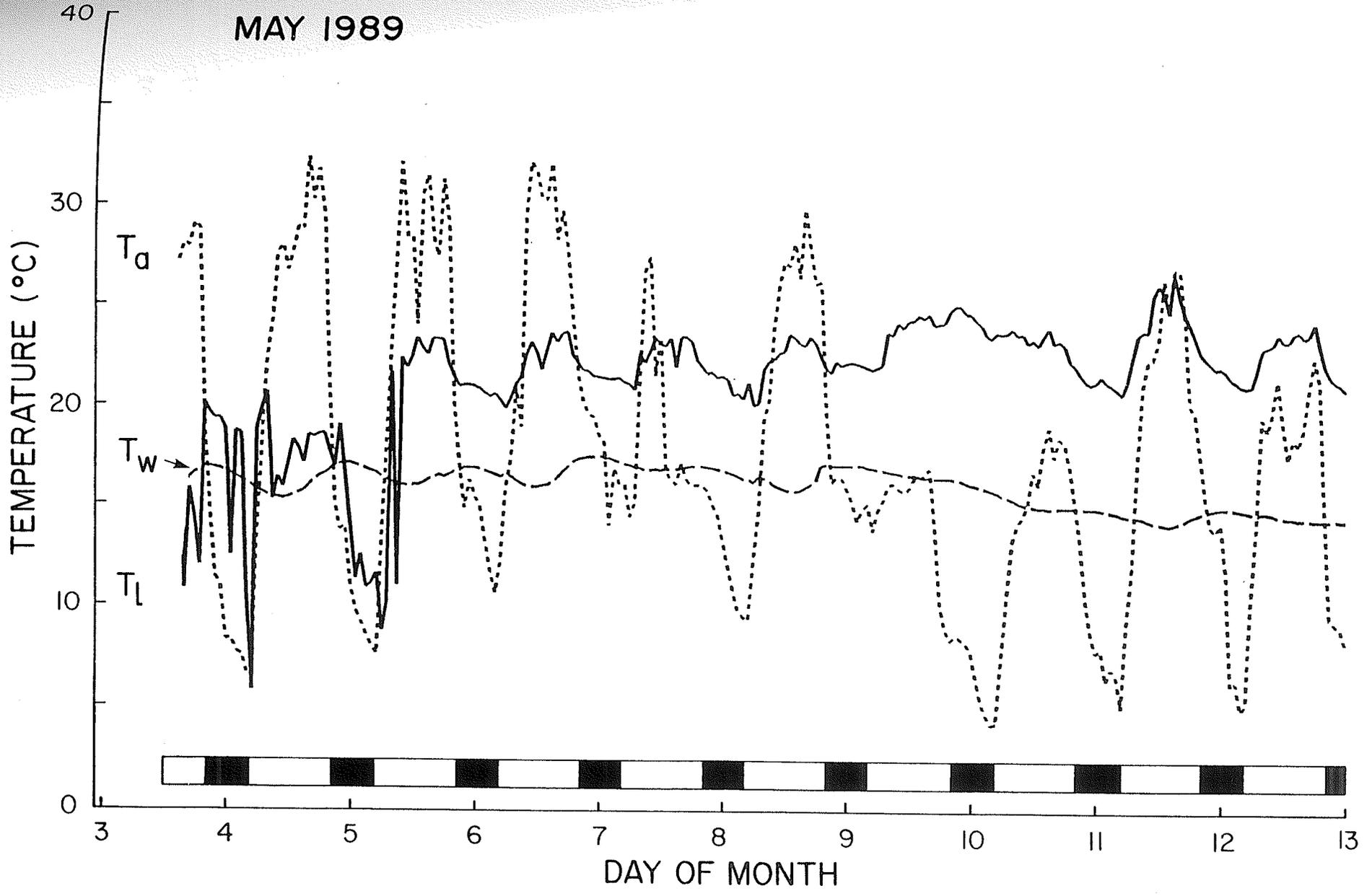


Figure 1-5. Daily fluctuations in water (dashed line), ambient air (dotted line), and nest chamber (solid line) temperature of lodge No. 8 during May.



Discussion

The low CO₂ levels (maximum=1.8%) and absence of any obvious seasonal variation in respiratory gas concentrations of chamber air, suggest that occupied beaver lodges remained well-ventilated throughout the year. To date, the only other study of CO₂ concentrations in beaver lodges was conducted by Novak and Cook (1972) in southern Ontario during March. They reported a mean CO₂ level of 0.11% (n=15 lodges), which is considerably lower than the mean value of 0.46% that I recorded for the same month. These authors determined that the turnover rate for CO₂ in one beaver lodge was 60 min, based on the amount of time required for CO₂ concentrations in the house to return to pre-test levels (0.03%) following an experimental increase in lodge CO₂ to 0.28%.

Gas exchange between the nest chamber and the external environment takes place primarily through a vent located at the apex of the lodge where the wall is usually thinnest and the use of mud for construction is minimal (Bailey 1926, Coles 1967). In the present study it was noted that as freezing of the lodge wall progressed in early winter, the vent remained open, presumably due to thermal warming by the resident animals. On winter sampling days when T_a dropped below -20.0°C and winds were calm, plumes of steam were often observed rising above active lodges. In all occupied lodges sampled, the vent remained unfrozen throughout winter, whereas the walls of unoccupied lodges froze completely. In contrast, muskrat lodges do not have a vent and walls gradually freeze through most of their depth as winter progresses (MacArthur 1984). Huenecke et al. (1958) and MacArthur (1984) documented a buildup of CO₂ in muskrat lodges that peaked at 5.0-10.0% in late winter-early spring.

Despite the presence of a vent, active beaver lodges still demonstrated

significantly higher CO_2 and ΔO_2 levels than abandoned houses in winter. Factors identified that influence the composition of respiratory gases in animal burrows (Maclean 1981) and muskrat lodges (MacArthur 1984), including the absolute metabolic rate of the occupants, moisture levels, and substrate porosity, may also have contributed to the increased CO_2 accumulation and O_2 depletion in active beaver lodges after freeze-up. If it is assumed that a beaver lodge contains four animals, each with a mean weight of 18.0 kg, an RQ of 0.92 and a resting metabolic rate at thermoneutrality of 0.32 L O_2 /kg/h (MacArthur 1989a), then the cumulative CO_2 production and O_2 consumption of this family group corresponded to 23.13 L CO_2 /h and 25.15 L O_2 /h, respectively. These respiratory demands, together with the restriction of outside activity following freeze-up (Part II), undoubtedly contributed to the observed seasonal changes in the gaseous composition of active beaver lodges. Considering the metabolic mass of a beaver family in winter, it is remarkable that seasonal changes in lodge gas concentrations were not more pronounced.

Results of this study suggest that the type of material used in constructing lodges may also influence respiratory gas concentrations in the nest chamber. The highest CO_2 levels (1.5- 1.8%) were recorded from lodge Nos. 6 and 15 which were constructed almost exclusively with mud, clay and compacted aquatic vegetation. These structures likely presented a greater barrier to diffusing gases than the walls of the other, more typical lodges sampled, which consisted of a matrix of branches interspersed with mud. The thickness of lodge walls (including snow cover) may also influence the gaseous composition of lodges, given that a significant, albeit weak, correlation was found between CO_2 level and wall thickness. It is important to note, however, that even the maximum CO_2 concentrations

recorded in this study would probably have little physiological effect on the lodge occupants, since beaver are apparently insensitive to CO₂ concentrations of up to 10% (Irving 1938). At CO₂ concentrations below 10%, Irving (1938) detected no changes in the ventilation rate, heart rate, blood pressure and peripheral circulation of anesthetized beavers.

Before freeze-up, problems in confirming the occupancy status of lodges (especially in summer), as well as changes in shelter use could have accounted for the lack of significant differences in gas concentrations between active and inactive lodges. During spring and summer, there is little fresh construction on dwelling lodges, as beavers concentrate on foraging and caring for their young. In areas where several lodges were located on the same waterway, the lack of fresh construction sign on any of the lodges made it difficult to identify which lodges were occupied. Also, the use of secondary shelters (e.g., bank dens) increases in summer, when animals spend a greater proportion of their time away from the main lodge (Coles 1967). This contrasts with the situation in winter, when all members of a colony reside in a primary shelter.

Results of the seasonal microclimate studies attest to the thermal buffering capacity of beaver lodges at northern latitudes. The annual variation in the T_L of occupied lodges in this study (-0.4 to 25.6°C) was less than half that of ambient air measured at the lodge sites (-41.4 to 32.4°C). Over the duration of the entire study, the mean daily T_L of lodge Nos. 8 and 14 varied between 4.8°C and 24.9°C, which is well within the thermoneutral zone reported by MacArthur (1989a) for beavers > 1 year old (0-28°C).

My findings generally agree with previous research on the temperature dynamics of beaver lodges. Coles (1967) reported an annual variation in the T_L of beaver lodges in New Hampshire of -4.5°C to 23.75°C, which was

similar to the T_L range recorded by Buech et al. (1989) for beaver lodges in northeastern Minnesota (-3.0-28.6°C). Stephenson (1969) recorded winter temperatures from a beaver lodge in Algonquin Park, Ontario, which varied from 0.8 to 1.6°C when T_a ranged from -21.0 to -6.8°C.

The significance of thermally buffered shelters to small mammals that are regularly active in cold regions has been well established (Hayward 1965; Glaser and Lustick 1975; Wolff and Durr 1986). The availability of such shelters would seem especially critical to semi-aquatic mammals that actively forage under the ice throughout the winter (MacArthur 1979; MacArthur and Dyck 1990). Recent evidence (MacArthur and Dyck 1990) suggests that beavers may mitigate abdominal cooling and thermoregulatory costs incurred during under-ice foraging excursions, by periodically returning to their lodge or burrow to rewarm. The year-round thermoneutral microenvironment provided by the lodge also ensures minimal energy expenditure during the resting phase of the diel activity cycle (MacArthur 1989a). Considering that winter activity of beavers may result in a deficit of energy (Novakowski 1967), any savings resulting from the utilization of a buffered microclimate may be critical to survival in northern regions.

Other studies (Coles 1967; Stephenson 1969; Buech et al. 1989) have shown that lodge temperature fluctuations may be influenced by ambient air and water temperatures, wall insulation (including snow cover) and the number of occupants. Recent investigations by Buech et al. (1989) revealed that shallow water temperature accounted for 93% of the variability in T_L during summer. Before freeze-up, I also found that T_w accounted for 90% of the variability in T_L of occupied lodges. Since the mean T_L of occupied and abandoned lodges did not differ prior to freeze-up, it appears that lodge temperature is controlled mainly by external environmental factors during

this season. During a period of hot weather, Buech et al. (1989) noted that beavers avoided a large open-water lodge in favor of cooler bank dens when temperatures in the lodge approached the upper limit of the thermoneutral zone (28°C). This observation emphasizes the importance of secondary shelters to beavers exposed to extended periods of high temperatures.

Results of this study suggest that external factors effect the T_L dynamics of active lodges minimally following freeze-up. None of the five variables measured was a significant predictor of T_L in occupied lodges during winter. In contrast, Buech et al. (1989) formulated a winter model of lodge temperature, in which the variables total wall thickness (including snow depth), lodge site, and relative mass of beavers explained 83% of the variation in mean T_L during winter. A potentially important predictor of T_L not estimated in the present study, was an index of the number of occupants in active lodges. Nonetheless, the influence of beaver presence on T_L dynamics was strongly suggested in Figs. 1-3 through 1-5. Abrupt diurnal changes in the T_L of lodge Nos. 8 and 14 coinciding with the presence or absence of at least one of the two telemetered beavers, suggests that the presence of animals in the lodge significantly altered the thermal conditions in the nest chamber during winter. A comparison of minimum T_L measurements in occupied and abandoned lodges (-0.4°C versus -6.0°C) supports this argument further. Daily fluctuations in T_L that reflect movements of beavers to and from the lodge may also be useful indicators of seasonal changes in the activity pattern of resident animals. Stephenson (1969) measured small daily fluctuations in T_L in winter, which suggested a diurnal activity rhythm. Data from the present study indicated a shift from the typical 24-h rhythm of nocturnal activity in fall (Fig 1-3), to a much more irregular pattern of activity in winter (Fig 1-4). This trend is

consistent with earlier studies indicating that activity rhythms of beavers in winter are often free-running, with a periodicity > 24 h (Bovet and Oertli 1974; Potvin and Bovet 1975; Lancia et al. 1982).

In conclusion, the construction and occupation of lodges by groups of beavers is an important behavioral adaptation which provides them with access to a year-round thermoneutral microclimate, even at north temperate latitudes. These thermal benefits are achieved at the expense of only limited disturbance in the respiratory gas concentrations inside the lodge, despite the large metabolic mass of the resident animals.

Part II

**Seasonal patterns of body temperature and activity
in free-ranging beavers**

Introduction

Homeothermy in small mammals inhabiting cold environments is achieved largely through a combination of behavioral avoidance of extreme cold and physiological mechanisms that retard heat loss (Pauls 1979; Randall and Thiessen 1980; Feist and White 1989). It is well known that many cold-climate species may also adopt seasonal torpor in order to reduce the energetic costs of temperature regulation, as well as enhance survival during periods of resource scarcity (Lyman et al. 1982; French 1986). Recent studies of the American badger, *Taxidea taxus*, and European badger, *Meles meles*, for example, have shown that periodic bouts of shallow torpor may result in considerable energy savings during winter (Harlow 1981; Fowler and Racey 1988). Earlier bioenergetic studies of the beaver suggested that this large semiaquatic rodent may also enter shallow torpor during periods of environmental stress. For example, Aleksiuik and Cowan (1969b) inferred a winter metabolic depression from the lack of growth, aphagia, low thyroid activity and apparent lethargy in captive northern beaver kits subjected to total darkness. Furthermore, Novakowski (1967) concluded that the winter food cache of northern beaver colonies was often insufficient to meet the energy requirements of the resident animals, assuming that beavers remain euthermic throughout the winter.

Thermoregulatory studies of beaver have also suggested the possible occurrence of shallow torpor in this species. For example, Smith et al. (in press) reported a significant, 1.0-°C reduction in the mean daily abdominal body temperature (T_b) of three free-living adult beavers during winter, but noted that the T_b of a single kit did not undergo a similar decline. These authors proposed that the maintenance of an elevated T_b in the kit facilitated continued growth during winter. Most previous investigations of

the thermoregulatory capabilities of these animals have focused on laboratory studies of captive beavers (Steen and Steen 1965; Aleksiuik and Cowan 1969b; Coles 1967; MacArthur 1989a; MacArthur and Dyck 1990). MacArthur and Dyck (1990) found that, despite a large body size, beavers were sensitive to immersion hypothermia. This finding suggests that behavioral strategies for T_b regulation may be critical to these animals, as reported for other semiaquatic species (MacArthur 1979; Fanning and Dawson 1980; Williams 1986). MacArthur (1989a) also found that the rectal temperature of a single kit (< 6 months old) was generally lower and less stable than the abdominal T_b of beavers > one year of age. He hypothesized that facultative heterothermy should be most critical to kits, since these animals have less time than adults to accrue fat reserves prior to the onset of winter and may be more sensitive to cooling during aquatic activity.

The primary objective of this study was to determine whether seasonal hypothermia exists in free-living beavers existing at a north temperate latitude. Also examined was the precision of T_b regulation and the role of behavior in T_b control of adult and juvenile beavers.

Methods

Animals

Hancock live traps baited with partially-skinned poplar saplings were used to capture nine beavers from four colonies near Pinawa, Manitoba (see study area description, Part I). These included three kits (sex unknown; 2.4 - 5.7 kg), one yearling (sex unknown; 7.7 kg) and four adults (two males, two

females; 13.2 - 18.1 kg) captured between 18 May and 5 October 1988. Kits were defined as beavers in their first year of life, yearlings were in their second year, and adults were \geq two years of age. Age-class designations were made at the time of capture on the basis of body size (Novak 1987). Captured beavers were transported to laboratory facilities provided by the Whiteshell Nuclear Research Establishment (WNRE), where each animal was implanted with a temperature-sensitive radio transmitter.

Surgical procedures

Prior to surgery, animals were weighed and anesthetized with an intramuscular injection of a drug mixture (0.45 ml/kg) consisting of ketamine hydrochloride (Rogar/STB Inc), Rompun (xylazine; Haver-Lockhart) and atropine sulfate. The drug mixture was prepared by combining 10 ml of ketamine stock solution (100 mg/ml) with 1 ml of Rompun (20 mg/ml), 3 ml of atropine sulfate (0.5 mg/ml), and 2 ml of sterile water. Animals were immobilized within 5 to 10 min of injection and remained anesthetized for 0.5 to 1.0 hours. Ophthalmic ointment (Vetropolycin, Pitman-Moore Inc.) was applied to the eyes of anesthetized beavers to prevent corneal dessication. A 5 X 6 cm area of abdominal skin was cleared of hair and disinfected with 70% alcohol. A 4-cm midline incision was made through the skin, followed by a 2-cm incision through the body wall along the linea alba. Transmitters were inserted into the body cavity, and the body wall and skin incisions were closed with 3-0 catgut and 000 silk sutures, respectively. At the completion of surgery, animals were given an intramuscular injection of a long-acting antibiotic (Derapen, Ayerst Laboratories) at a dosage of 0.22 ml/kg. Beavers were kept in the laboratory overnight and released at the capture site within 24 hours of the

operation. Implanted animals were not monitored for at least one week following surgery. Every effort was made at the end of the study to recapture implanted beavers to surgically remove and recalibrate radio transmitters. Examination of recaptured beavers revealed complete recovery from previous surgery.

Body temperature and lodge use measurements

Body temperatures of beavers were determined using 30-60 g model L-M radio-transmitters (Mini-mitters Inc., Sunriver, OR) accurate to within 0.2°C. Transmitter signals were received on a Realistic TRC-215 six-channel CB transceiver (Mini-mitters Inc.). Prior to implantation, each radio was calibrated at 1.0-°C increments from 25.0 to 34.0°C, and at 0.5-°C increments from 34.0 to 40.0°C, using a Haake A81 circulating water bath. The calibration was repeated one week later, and only those radios which showed no signs of drift were used in the study. Of the four operational radios recovered at the end of the study, two had not drifted at all, while the remaining two appeared to have drifted by only 0.002 and 0.003°C/day (assuming linear drift over the 6-10 mo. recording period). Body temperature recordings made with the latter two transmitters were corrected for drift prior to analysis. No correction was applied to the five unrecovered transmitters. However, T_b measurements taken from these animals were considered accurate, since seasonal means of corrected and uncorrected radios varied by only 0.5 - 1.2°C.

Two approaches were used to collect abdominal T_b and activity data from free-ranging beavers. The first involved an automated system that recorded the T_b and presence or absence of beavers in their lodges at 15-min intervals throughout the day. The second method involved the

manual recording of T_b and activity patterns of individual animals monitored during 10- to 300-min observation sessions (0500-2300 h).

The automated system consisted of two receivers (Realistic TRC-215, Mini-mitters Inc.), two tape recorders (Sony CF-400A) and a digital timer (RS Components Ltd.) housed in an insulated, weatherproof box situated 15-30 m from the lodge. The radio signal was detected with a folded dipole antenna mounted on top of the lodge and coupled to the receivers via coaxial cable. A 60-W light bulb powered by a 12-V car battery was used to heat the equipment box during winter. At 15-min intervals, the digital timer activated the receivers and tape recorders, providing a 42-s recording of the telemetered signal. At least 3-5 consecutive days of automated recordings were obtained from one or two animals at a given colony site before the system was dismantled and re-established at another site. Since transmitter signals were received only when instrumented beavers were in the lodge, the automated data series was used to derive both T_b and an hourly lodge use index. This index was defined as: (total recordings per h indicating presence of beaver in lodge / total recordings per h) x 100. The occurrence of a strong, stable radio signal over 7 h of consecutive recordings was taken as an indication that the resident animal was resting in the lodge. Measurements made in the final 2 h of such sequences were used to estimate mean resting T_b . To obtain a more precise estimate of daily lodge use in selected animals, the sampling interval of automated recordings was reduced from 15 min to either 2 or 5 min. The higher sampling frequencies reduced the likelihood that beavers might leave the lodge and return between successive recordings. The shortened recording interval was sufficient to determine the presence or absence of a radio-tagged beaver in the lodge, but could not be used to accurately

determine T_b .

Prior to freeze-up, an effort was made to correlate the T_b dynamics of active animals with the pattern of aquatic activity. Instrumented animals were monitored from a canoe, from concealed locations along the shoreline, or from a 3.4-m high observation tower erected about 20 m from the lodge. When a beaver moved beyond the transmitting range of the radio implant, continuous surveillance of the subject was maintained, and signal recordings were resumed when the animal was once again within reception range. During each observation session, T_b was usually determined at 5-10 min intervals. During winter, telemetered signals from beavers active under the ice were manually recorded at distances of 5-20 m from the animals. Ice cover made it possible for the observer to follow and maintain signal contact with animals engaged in under-ice excursions away from the resident lodge.

Statistical analyses

Mean T_b in summer (20 June - 31 August 1988), fall (1 September - 31 October 1988) and winter (1 November - 15 March 1989) was calculated for each animal. These data were also pooled by age-class and seasonal T_b means were calculated separately for kits and adults. Body temperature data collected from the single yearling were obtained mainly in summer and these data were pooled with the summer results for kits. Statistical comparisons were also made of pooled T_b data collected prior to freeze-up (20 June - 1 November), with that obtained following freeze-up (2 November - 15 March). Analysis of variance (ANOVA) was used to evaluate seasonal variations in T_b . Two-sample comparisons of means were made with Student's t -tests or paired t -tests. Significance was set at the 5% level

and means are presented with ± 1 SE.

Results

Seasonal patterns of body temperature and lodge use

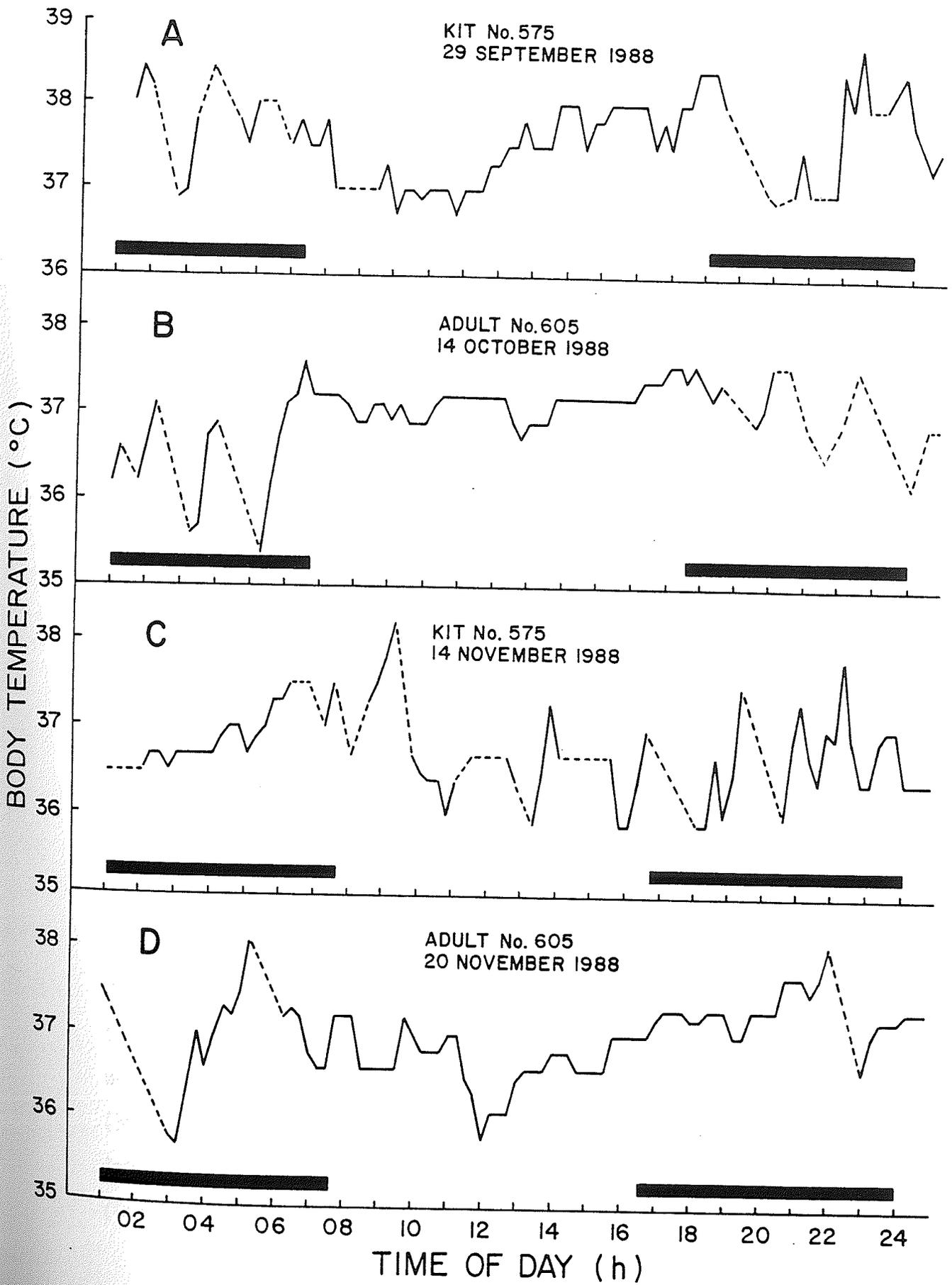
The mean abdominal T_b of all implanted animals remained remarkably stable throughout the year (Table 2-1). Kits demonstrated an overall mean T_b in summer of $36.9 \pm 0.02^\circ\text{C}$, which increased slightly in fall to $37.1 \pm 0.01^\circ\text{C}$, and declined again in winter to $36.7 \pm 0.02^\circ\text{C}$ (Table 2-1). Though statistically significant ($F_{2,122} = 10.43$, $P=0.0001$), this trend indicates a maximum seasonal reduction in mean T_b of only 0.4°C . The mean resting T_b of kits demonstrated a maximum seasonal reduction of 0.5°C ($36.8-36.3^\circ\text{C}$), which was also statistically significant ($F_{2,67} = 11.64$, $P=0.0001$). The overall, mean T_b of adult beavers exhibited a similar consistency, with summer, fall and winter means of $37.0 \pm 0.01^\circ\text{C}$, $36.8 \pm 0.01^\circ\text{C}$ and $37.0 \pm 0.01^\circ\text{C}$, respectively (Table 2-1). The maximum seasonal change in mean T_b of adult beavers was only 0.2°C , but again, this subtle difference proved statistically significant ($F_{2,100} = 3.14$, $P=0.048$). Maximum seasonal variation in the mean resting T_b of adults was also 0.2°C ($36.7 - 36.9^\circ\text{C}$), though in this case, the difference was not significant ($F_{2,64} = 2.34$, $P=0.104$).

There was considerable daily variation in the T_b of kits and adults monitored during autumn and early winter (Fig. 2-1). The most dramatic changes in T_b were associated with periods of aquatic activity. Abdominal T_b usually dropped by $1.0 - 1.5^\circ\text{C}$ during the period of absence from the lodge, then recovered (at least in part) when the animal returned to the lodge nest chamber, prior to the onset of the next excursion (e.g., Fig. 2-1B,

Table 2-1: Seasonal variation in mean body temperature of free-living beavers.

Age class	Animal no.	Mean summer Tb (°C)	Mean autumn Tb (°C)	Mean winter Tb (°C)
Kits	575	37.3±0.02 (15)	37.5±0.02 (18)	37.1±0.02 (17)
	615	36.8±0.02 (15)	36.8±0.01 (19)	36.5±0.03 (13)
	815	----	----	35.9±0.03 (6)
	835	36.7±0.03 (20)	37.2±0.12 (2)	----
	Pooled	36.9±0.02 (50)	37.1±0.01 (39)	36.7±0.02 (36)
Adults	555	----	----	36.5±0.04 (6)
	565	37.0±0.01 (20)	36.8±0.02 (16)	36.8±0.02 (8)
	605	----	37.0±0.02 (10)	36.9±0.01 (23)
	755	----	36.6±0.03 (6)	37.8±0.02 (14)
	Pooled	37.0±0.01 (20)	36.8±0.01 (32)	37.0±0.01 (51)

Note: Means are presented with ± 1 SE; values in parentheses indicate the number of days of data collection (52-96 observations per day).



0100 - 0800 h). Periods of inactivity were usually characterized by stable, or gradually increasing T_b values (e.g., Fig. 2-1A, 0800 - 1800 h). However, because the sampling interval was 15 min, beavers would have had ample time to leave the lodge and return between successive automated recordings. Undetected excursions (< 15 min duration) could account for sudden drops in T_b at times when the uninterrupted dataset suggested that the animal had remained in the house (e.g., Fig. 2-1D, 1115 - 1200 h).

Prior to freeze-up, hourly fluctuations in lodge use and mean T_b were similar in kits and adults (Figs. 2-2A and 2-3A). During this period, beavers were present in the lodge for only 35-50% of all nighttime recordings, compared to approximately 90% for all daytime measurements. Between 0600 and 1800 h, the mean hourly T_b of kits and adults increased at a rate of approximately $0.1^\circ\text{C}/\text{h}$ and peaked at, or just prior to, the onset of evening activity (Figs. 2-2A and 2-3A). In both groups, mean hourly T_b generally declined during the nocturnal active period, reaching a minimum shortly after sunrise. The maximum daily range in mean hourly T_b during the open water season was 0.8°C ($36.6 - 37.4^\circ\text{C}$) for adults, and 1.1°C ($36.5 - 37.6^\circ\text{C}$) for kits. Hourly variation in lodge use and mean T_b of the adults was much less pronounced following freeze-up (Fig. 2-3B). In this case, the hourly lodge use index varied from 65 to 97% (mean= $83.3 \pm 8.7\%$), and mean hourly T_b varied by only 0.2°C ($37.0 - 37.2^\circ\text{C}$). Interestingly, the kits demonstrated greater lability in lodge use and mean hourly T_b during the same period (Fig. 2-2B). Hourly lodge use of the kits fluctuated between 51 and 93% (mean= $75.1 \pm 10.9\%$), while their mean hourly T_b varied by 0.8°C ($36.3 - 37.1^\circ\text{C}$). Detailed 24-h lodge use measurements indicated that, in late summer, a single adult remained in the lodge for 39 - 68% of each day (Table 2-2). In contrast, during 12 days of intensive monitoring in late

Figure 2-2. Daily variation in lodge use and abdominal body temperature of beaver kits (Nos. 575, 615, 815, 835) before (A) and after (B) freeze-up. Histogram indicates hourly lodge use index (see text); closed circles, mean hourly body temperature. Each hourly mean is based on 46-258 observations; vertical lines denote ± 1 SE. Horizontal bars indicate the period of darkness, with variation in sunrise and sunset times represented by the cross-hatched areas.

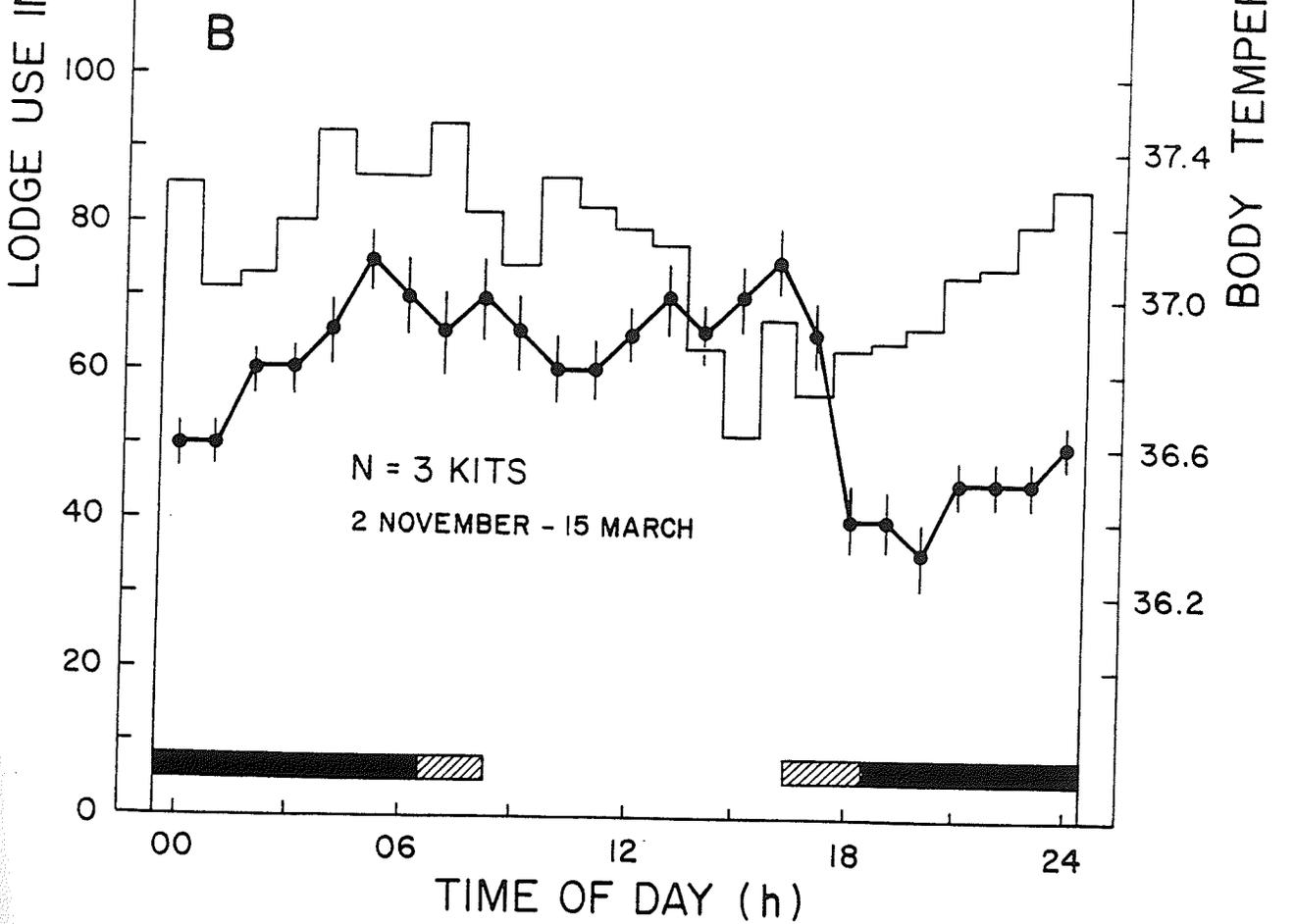
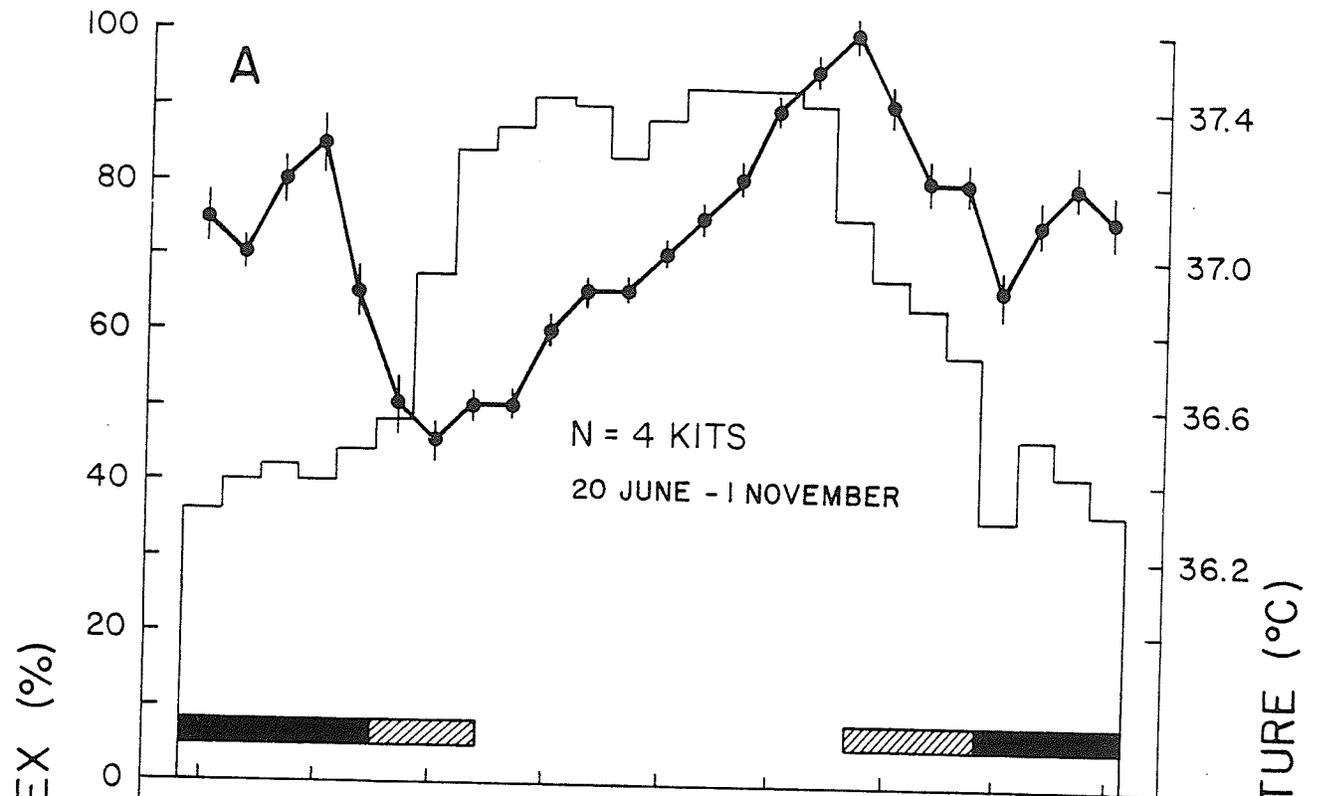


Figure 2-3. Daily variation in lodge use and abdominal body temperature of adult beaver (Nos. 565, 605, 755) before (A) and after (B) freeze-up. Histogram indicates hourly lodge use index (see text); closed circles, mean hourly body temperature. Each hourly mean is based on 37-158 observations; vertical lines denote ± 1 SE. Horizontal bars indicate the period of darkness, with variation in sunrise and sunset times represented by the cross-hatched areas.

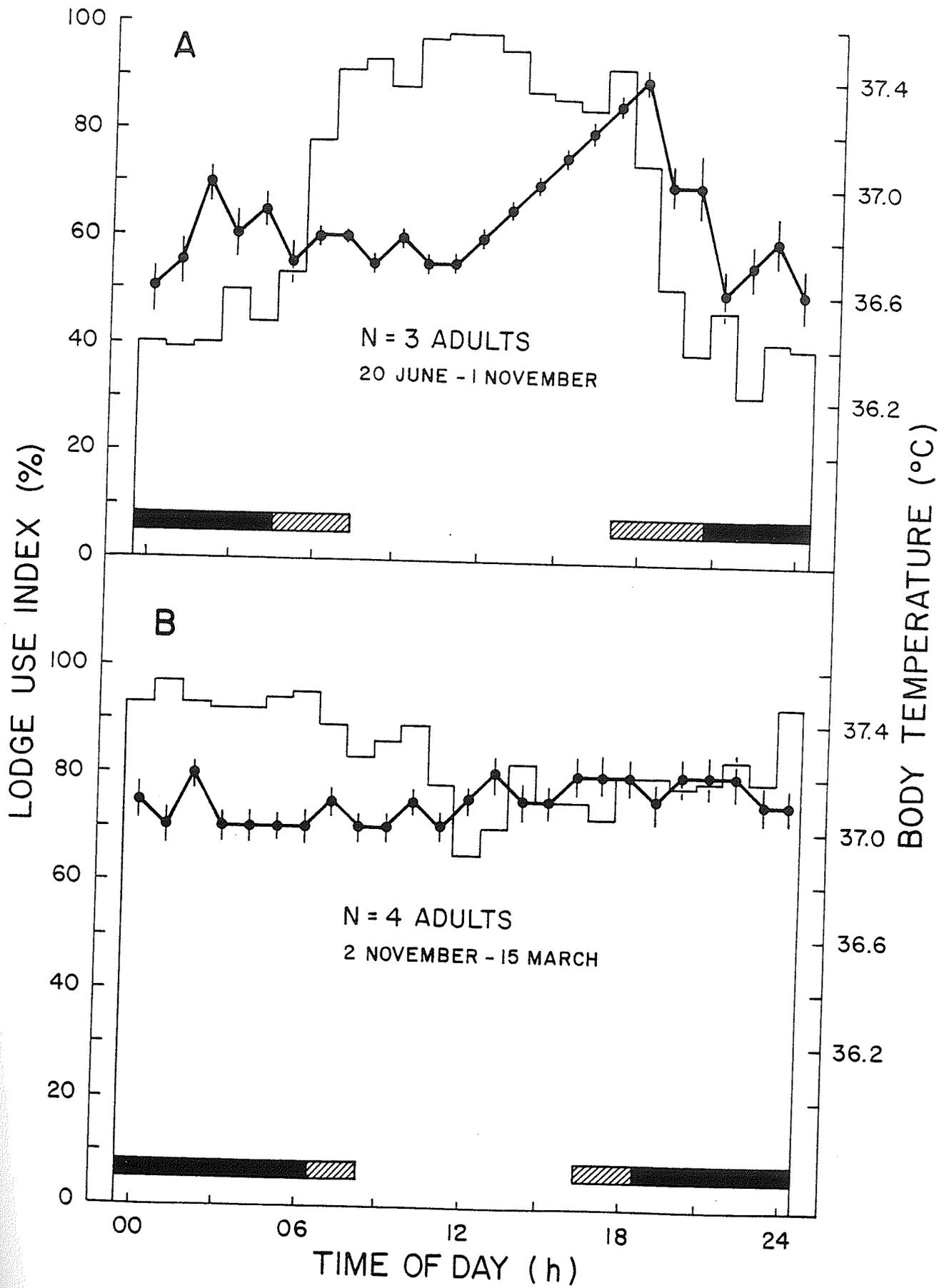


Table 2-2: Seasonal changes in daily lodge use by three adult beavers.

Animal no.	Sampling dates	Total period monitored (min)	Cumulative time in lodge (min)	% Time in lodge
*585	Aug 3-4	1440	935	65%
*585	Aug 5-7	2880	1970	68%
*585	Aug 11-12	1435	555	39%
605	Feb 16-20	6114	6056	99%
755	Feb 16-20	6114	5962	98%
605	Mar 10-14	5778	5490	95%
755	Mar 10-14	5778	5608	97%
605	Mar 17-21	5760	5572	97%
755	Mar 17-21	5760	5616	98%

* Animal monitored at 5-min intervals; all other beavers were monitored at 2-min intervals throughout the observation period.

winter, two adult beavers were present in the lodge for 95 - 99% of all recordings (Table 2-2).

Automated T_b recordings which indicated an animal had remained in the lodge for a minimum of five consecutive hours were used to analyze temporal changes in T_b prior to the onset of a major activity bout. Data from three kits (Nos. 575, 615 and 815) and four adults (Nos. 555, 565, 605 and 755) revealed a 0.22 - 0.64°C increase in mean T_b during the 3-h period immediately preceding the first excursion from the lodge (Fig. 2-4). For kits, the increase in T_b prior to leaving the lodge was significantly greater after freeze-up than during the open water season ($F_{1, 83} = 8.55, P = 0.004$). For adults, the mean maximum pre-activity rise in T_b was similar in both seasons ($F_{1, 62} = 2.33, P = 0.132$). The mean duration of the first of each sequence of excursions by kits away from the lodge was similar ($F_{1, 78} = 2.59, P = 0.112$) before and after freeze-up (42.2 ± 4.9 and 59.3 ± 11.4 min, respectively). Adults demonstrated a significant reduction in the mean duration of the initial excursion ($F_{1, 63} = 5.55, P = 0.022$), from 160.2 ± 40.7 min during the open water season, to 57.6 ± 9.2 min following freeze-up (Table 2-3). The first excursion usually signalled the beginning of a major bout of aquatic activity. All animals exhibited a mean drop in T_b during the first excursion, with no evidence of seasonal differences ($P > 0.05$) for either kits or adults (Table 2-3, Fig. 2-4). Within a major activity bout, the maximum rate of rewarming during intermittent periods in the lodge was calculated and compared to the maximum rate of pre-activity warming presented in Fig 2-4. It was found that, following aquatic activity, the maximum warming rates of kits (0.04°C/min, $n = 71$) and adults (0.02°C/min, $n = 38$) were 3-10 times higher than during the 3-h pre-activity period (0.003 - 0.01°C/min).

Figure 2-4. Pre-immersion changes in mean body temperature for (A) three kits before (open circles, n=57) and after (closed circles, n=25) freeze-up, and (B) four adults before (open circles, n=30) and after (closed circles, n=30) freeze-up. Means are presented with \pm 1SE. The dashed vertical line indicates the final body temperature recording made prior to the onset of aquatic activity. The asterisk (*) indicates the first body temperature measurement made subsequent to the animal's return to the lodge.

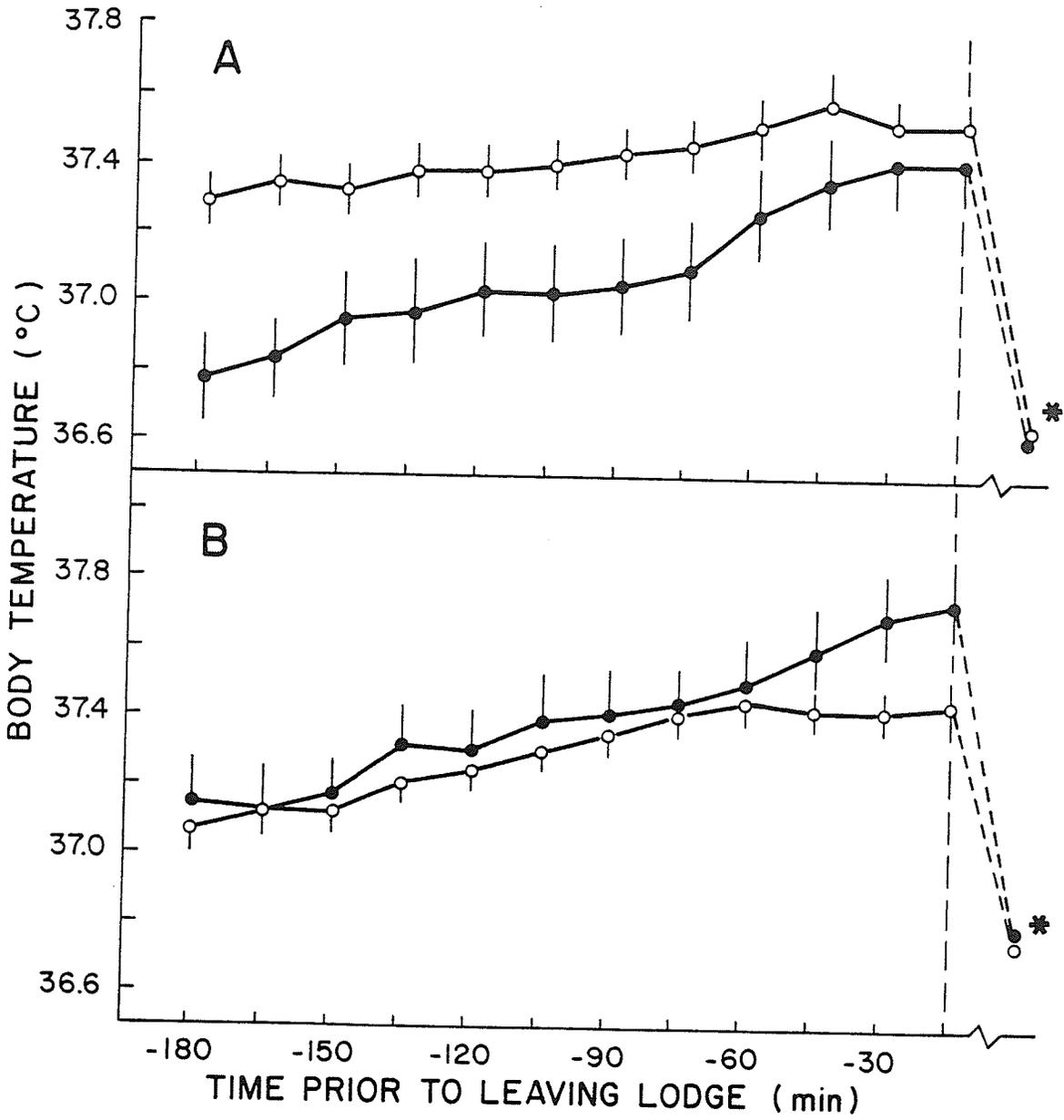


Table 2-3: Summary of excursion times and body temperature changes associated with activity in adult and juvenile beavers.

Age-class	Animal no.	Excursion time (min)	Preimmersion* ΔT_b ($^{\circ}C$)	Excursion** ΔT_b ($^{\circ}C$)	Season
Kits	575	38.6 \pm 7.9	0.1 \pm 0.1 (21)	-0.5 \pm 0.2	Before
	615	33.6 \pm 7.4	0.2 \pm 0.1 (25)	-0.5 \pm 0.1	
	835	64.6 \pm 9.7	0.6 \pm 0.2 (13)	-2.2 \pm 0.2	
Adults	565	195.6 \pm 55.4	0.5 \pm 0.1 (24)	-0.8 \pm 0.1	freeze-up
	605	96.4 \pm 33.4	0.1 \pm 0.2 (6)	-0.3 \pm 0.3	
	755	25.0 \pm 5.0	-0.02 \pm 0.3 (3)	-0.5 \pm 0.3	
Kits	575	49.6 \pm 13.2	0.4 \pm 0.2 (13)	-0.5 \pm 0.2	After
	615	75.0 \pm 20.1	1.1 \pm 0.2 (8)	-1.3 \pm 0.2	
	815	-----	0.4 \pm 0.1 (5)	-1.0 \pm 0.2	
Adults	555	116.3 \pm 34.3	0.8 \pm 0.3 (4)	-0.7 \pm 0.3	freeze-up
	565	72.0 \pm 40.9	0.6 \pm 0.4 (5)	-0.01 \pm 0.3	
	605	42.9 \pm 5.6	0.6 \pm 0.1 (14)	-1.1 \pm 0.2	
	755	45.0 \pm 11.0	0.5 \pm 0.3 (8)	-1.5 \pm 0.2	

Note: Data are presented only for the first of each sequence of excursions during major activity bouts. Means are presented with \pm 1 SE; values in parentheses indicate the number of observations.

* Preimmersion ΔT_b = Final T_b prior to leaving lodge - T_b 3 h prior to leaving lodge.

**Excursion ΔT_b = First T_b recorded after animal returned from initial excursion - final T_b recorded before animal left the lodge.

Body temperature dynamics during aquatic activity

Before freeze-up, detailed observations of the T_b changes that accompany aquatic activity were recorded from three kits and four adults during a total of 35 foraging excursions. Measurements usually began when the beaver was still inside the resident lodge or burrow, and continued after it emerged outside and remained active within viewing range. Activity typically consisted of extended periods of surface swimming interrupted by occasional short dives and brief trips onshore, or bouts of foraging in shallow water along the shoreline. In winter, ice cover precluded the direct observation of active beavers, though the transmitter implants permitted tracking of animals swimming under the ice. A total of nine under-ice excursions was recorded from one kit and two adults.

Aquatic activity almost invariably resulted in a decline in T_b , which usually continued to drop for 5-15 min after beavers returned to their lodge or burrow (Fig. 2-5). This was followed by a period of rewarming in the lodge prior to a subsequent excursion (Fig. 2-5). Kits appeared to be most sensitive to aquatic cooling (Table 2-4), with a mean rate of cooling in 1-9°C water ($0.11 \pm 0.02^\circ\text{C}/\text{min}$) which was 2.8 times greater than that of adults under similar conditions ($t = 2.84$, $df = 32$, $P = 0.001$). Kits spent less time in 1-9°C water (7.75 ± 1.83 min) than did adults (22.75 ± 2.78 min, $t = 4.0$, $df = 32$, $P = 0.001$). Interestingly, there was no difference between kits and adults in the mean net decline in T_b per excursion (Table 2-4, $P > 0.05$).

Figure 2-5. Body temperature dynamics associated with short-term changes in activity of free-living beavers. (A) 18.1 kg male, 28 November, 1988 (1215-1345 h). (B) 16.8 kg male, 6 October, 1988 (1727-1928 h). (C) 16.8 kg male, 22 September, 1988 (1638-1951 h). Symbols denote presence in the lodge or burrow (closed circles); swimming or floating in water (open triangles); and foraging in shallow water near shore (open squares). In (A) and (B), recordings at time 0 were made < 5 min after the animal had returned to the lodge or burrow.

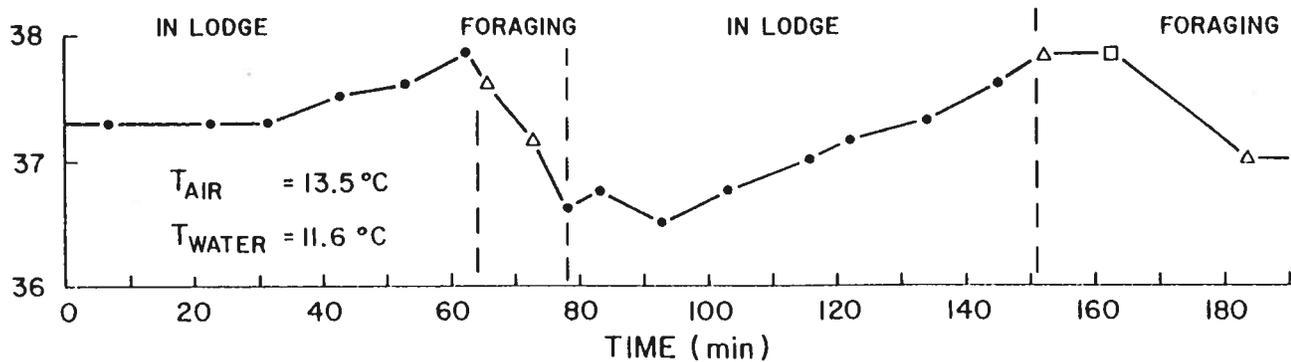
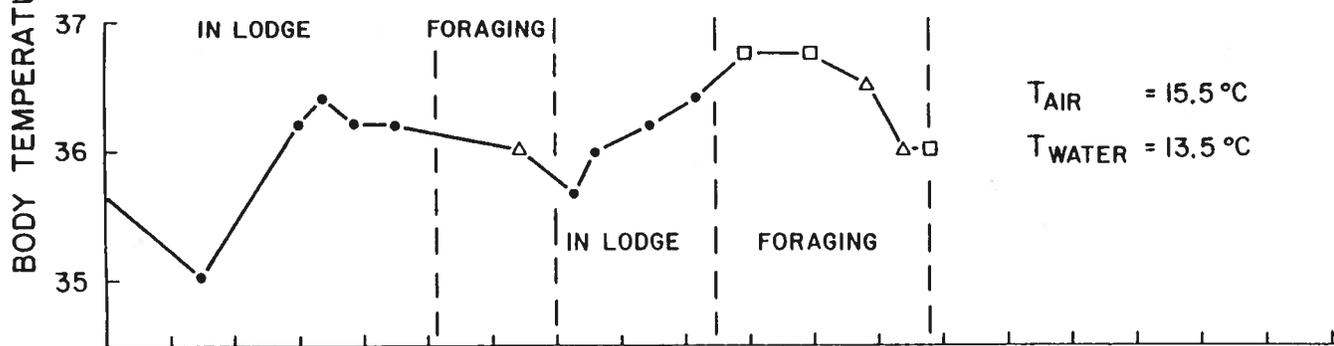
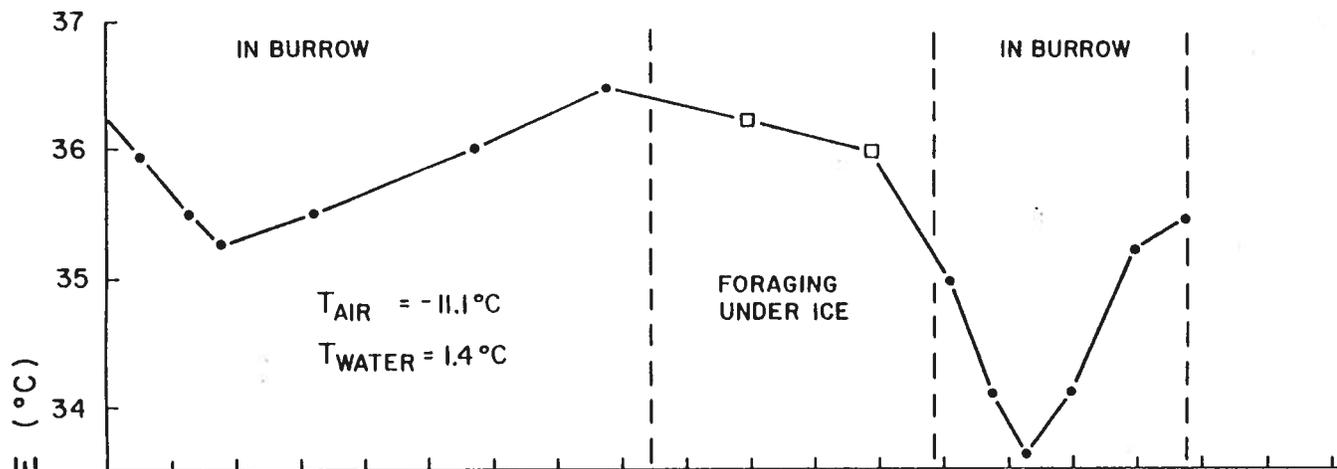


TABLE 2-4. Summary of voluntary immersion times and body temperature changes of free-ranging beavers.

Sampling period	T_w range (°C)	Period of immersion (min)		Maximum T_b decline per excursion (°C)		Cooling rate in water (°C.min ⁻¹)	
		Kits	Adults	Kits	Adults	Kits	Adults
September 14-30	10-12	----	14.0±3.65 (10)	----	0.45±0.13 (10)	----	0.04±0.01 (10)
October 5-21	6-9	8.8 ±2.32 (13)	23.4±3.08 (9)	0.57±0.10 (13)	0.91±0.11 (9)	0.10±0.03 (13)	0.04±0.004 (9)
October 26- February 11	1-2	5.10±2.61 (5)	21.9±5.27 (7)	0.51±0.18 (5)	0.87±0.40 (7)	0.14±0.05 (5)	0.04±0.17 (7)

NOTE: Data are included for three kits aged 4-7 months, and four adults ≥ 2 years old. Means are presented with ± 1 SEM; values in parentheses indicate number of aquatic excursions documented. Calculation of maximum T_b decline includes cases when abdominal cooling continued, following emergence of the animal from water.

Discussion

Results of this study revealed that the mean abdominal T_b of kits and adults remained close to 37.0°C throughout the year, with no evidence of shallow torpor in either age group. The T_b range of free-living beavers was comparable to that ($36.7 - 37.3^\circ\text{C}$) previously reported for captive animals (Coles 1967; MacArthur 1989a). On the other hand, Smith et al. (in press) reported a statistically significant, 1.0°C reduction in the mean daily T_b of three free-living adult beavers in northern Minnesota between autumn (36.3°C) and winter-early spring (35.3°C). Though the energetic saving associated with a 1.0°C reduction in mean daily T_b is questionable, it is conceivable that this may reflect an adaptive depression in resting metabolic rate in winter (Aleksiuk and Cowan 1969b; Smith et al. in press). However, the discrepancy between my findings and those reported by Smith et al. (in press) could also reflect differences in energy availability or thermal stress experienced by animals monitored in the two studies. For example, if the amount of vegetation stored in the food cache is inadequate to supply the entire colony (Novakowski 1967), or if winter ice conditions render the food pile inaccessible (Smith and Peterson 1988), then selection might favor a facultative reduction in metabolic rate and T_b during periods of inactivity in the lodge. However, it could also be argued that the frequency and duration of under-ice foraging excursions away from the cache should increase under these conditions. Since cold water immersion results in abdominal cooling (Table 2-4), an increase in foraging activity during winter could contribute to a reduction in mean daily T_b . In this context, it is relevant to note that the two adults that demonstrated a significant decline in T_b during winter in Smith et al.'s (in press) study, spent less time in the lodge (72 - 81% of total observations) than did the

two adults studied intensively in the present investigation (95 - 99%, Table 2-2). Furthermore, the mean daily range in T_b that I recorded for adults after freeze-up (0.2°C) was much lower than that (2.5°C) reported by Smith et al. (in press).

Daily fluctuations in T_b and lodge use prior to freeze-up followed a regular pattern of increasing T_b and near-continuous occupation of the lodge during the daylight hours, followed by a general decline in T_b and lodge use at night. Previous studies of captive animals (MacArthur 1989a) and free-living beavers monitored during the open-water season (Bovet and Oertli 1974; Potvin and Bovet 1975; Lancia et al. 1982; Smith et al. in press) have revealed similar diel T_b and activity rhythms. Data presented in Figs. 2-2A and 2-3A suggest the possibility of endogenous T_b changes independent of activity (Hart 1971; MacArthur 1979) during the open water season. The diurnal increase in T_b of beavers inside the lodge began abruptly, and proceeded at a relatively steady rate (Figs 2-2A and 2-3A). Furthermore, this rise in T_b began several hours before the animals initiated a major activity bout, as revealed by a reduction in lodge use (Figs. 2-2A and 2-3A). MacArthur (1979) postulated that separate endogenous oscillators governing T_b and motor activity patterns in muskrats may be closely synchronized in summer, but offset in winter, such that increases in T_b could precede the onset of activity (see below). The effects of different types and levels of motor activity would then be superimposed on these endogenous T_b changes.

After freeze-up, no obvious daily trends in T_b and lodge use were apparent for either kits or adults, though there appeared to be some evidence of a shallow diel cycle in each case (Figs. 2-2B and 2-3B). Daily variability in T_b and lodge use during winter appeared greatest in kits (Fig.

2-2B). This observation was at variance with Smith et al.'s (in press) finding that the mean daily T_b amplitude for adults increased during winter from 1.4 to 2.5°C, while that of a single kit declined from 2.2 to 1.4°C. Based on winter weight gains of juvenile beavers (Smith and Peterson 1988), Smith et al. (in press) proposed that a higher, more stable T_b , together with parental feeding and a reduction in activity outside the lodge, all contributed to the growth of kits during winter. However, without direct observation of parent-young interactions in the winter lodge, the question of parental feeding cannot be resolved. On the other hand, the variability in lodge use and T_b of kits observed in the present study suggests that these animals actively foraged away from the lodge during winter. Both kits and adults accrue significant fat reserves prior to the onset of winter, but as the season progresses, adults generally lose weight, whereas kits often gain it (Smith and Peterson 1988) and may even show signs of physical growth (D. Soprovich, personal communication). Larger size permits a greater dependence on body fat reserves (Young 1976; Lindstedt and Boyce 1985) and this in turn may reduce the need for adults to forage, thus minimizing the thermal stress associated with aquatic activity. Interestingly, adult beavers exhibited a significant reduction in excursion duration following freeze-up. Conversely, kits may have to increase their foraging activity in winter in order to sustain growth. The lack of seasonal variation in mean excursion time of kits (Table 2-3) suggests that these animals may not reduce their foraging activity during winter. Considering that kits are more sensitive to aquatic cooling than adults (Table 2-4), failure to reduce foraging activity could have contributed to the greater daily T_b fluctuations observed in these younger animals during winter (Fig. 2-2B).

A common T_b response of small semiaquatic mammals to extended

periods of immersion in water is usually one of continuous, or near-continuous cooling (MacArthur 1989b). Water shrews, *Sorex palustris* (Calder 1969), muskrats, *Ondatra zibethicus* (MacArthur 1979), water rats, *Hydromys chrysogaster* (Fanning and Dawson 1980) and mink, *Mustela vison* (Williams 1986), all demonstrate a steady decline in rectal or abdominal T_b during sustained immersion in cold water. In the laboratory, abdominal cooling was documented in adult and immature beavers at all water temperatures below 29°C (MacArthur and Dyck 1990), with the strongest cooling response recorded in a single 4-month-old kit. Therefore, it was not surprising that the T_b of free-ranging beavers generally declined when the animals engaged in aquatic activity (Fig. 2-5). My field data also indicated that kits were far more susceptible to abdominal cooling during aquatic foraging bouts than adults, and they appeared to compensate for this through a reduction in voluntary immersion time (Table 2-4). Despite dramatic differences in aquatic cooling rates, both age groups demonstrated the same net decline in T_b per excursion (Table 2-4). It is also noteworthy that T_b usually continued to drop for the first 5-15 minutes after the animal returned to the lodge from a foraging trip (Fig. 2-5). It is well documented that beavers are capable of pronounced regional heterothermy during cold water immersion (Cutwright and McKean 1979; Steen and Steen 1965; MacArthur and Dyck 1990). Therefore, it is possible that circulation of blood through cooled peripheral extremities may have contributed to this continued decline in deep T_b following the withdrawal of the animal from the water.

An ability to tolerate limited hypothermia and, thus presumably extend voluntary immersion time in cold water, has been reported in water shrews (Calder 1969), water rats (Fanning and Dawson 1980) and muskrats (Sherer

and Wunder 1979; MacArthur 1979). In addition, winter-acclimatized muskrats appear to delay the development of hypothermia by elevating T_b in the lodge prior to entry into near-freezing water (MacArthur 1979). A similar pre-activity rise in T_b during winter has been noted for the red squirrel, *Tamiasciurus hudsonicus* (Pauls 1979) and the Mongolian gerbil, *Meriones unguiculatus* (Randall and Thiessen 1980). Though a pre-activity elevation in T_b was noted in the current study (Fig. 2-4), the mean T_b increase was usually less than 1.0 °C (Table 2-3). Nevertheless, if it is assumed that deep body cooling ultimately limits voluntary immersion time in this species, then a pre-immersion rise in T_b of 0.6 °C could significantly increase available foraging time in cold water. For example, given that a swimming adult beaver cools at an average rate of 0.04 °C/min (Table 2-4) and, assuming an average T_b drop of 1.0 °C during a typical excursion, then a pre-immersion rise in T_b of 0.6 °C could extend available foraging time by about 15 min. It is also likely that rapid, intermittent rewarming during an activity bout enhances foraging efficiency in these amphibious mammals. The maximum rates of rewarming within a major block of activity were 3-10 times higher than the pre-activity warming rates, suggesting that the latter were well below the thermogenic capabilities of these animals. As suggested by MacArthur and Dyck (1990), a large portion of the thermoregulatory costs of aquatic activity may be met after the animals have left the water. Thus, beaver may postpone energetically costly increases in thermoregulatory heat production until after they have returned to the thermoneutral microclimate of the lodge (Part I).

Data presented in Fig. 2-5 suggest that behavioral mechanisms play a critical role in thermoregulation of beavers in nature. Like muskrats (MacArthur 1979) and water rats (Fanning and Dawson 1980), beavers seem

to mitigate body cooling and thermoregulatory costs incurred during aquatic excursions, by periodically returning to their lodge or burrow to rewarm. This response is probably most critical to kits, which appeared to compensate for their greater sensitivity to immersion hypothermia by spending less time in the water per individual trip than the adults. Older animals also appeared to reduce thermal stress and energy requirements during winter by remaining in the lodge for more than 80% of the day (Fig. 2-3B, Table 2-2), and by shortening the duration of under-ice excursions. Behavioral observations of beavers in their lodges are still required to clarify questions regarding age-related differences in foraging activity during winter. It appears that through a combination of physiological adaptations that retard heat loss and behavioral mechanisms for minimizing immersion hypothermia, beavers are able to regulate T_b economically and with a high degree of precision throughout the year.

Part III
Daily energy metabolism and thermoregulation of beavers
under simulated winter conditions

Introduction

Few mammals exhibit a greater capacity to alter the structure, dynamics and productivity of aquatic ecosystems than the North American beaver, *Castor canadensis*. Yet despite numerous investigations of foraging ecology and habitat manipulation (McDowell and Naiman 1986; Naiman et al. 1986; Novak 1987), few studies have addressed the energy and nutrient requirements of free-living beavers (e.g., Novakowski 1967). Estimates of the daily cost of free-existence are vital to the development of accurate seasonal energy budgets and for the testing and refinement of optimal foraging models (Jenkins 1980; Belovsky 1984; McGinley and Whitham 1985). A quantitative understanding of energy and nutrient requirements is also essential to the intelligent management of this prominent fur-bearer. Such information could, for example, contribute to the development of land capability models which attempt to predict beaver densities based on quantitative assessments of habitat quality (Slough and Sadleir 1977; Howard and Larson 1985).

Despite the growing interest in wildlife bioenergetics, few techniques are currently available for estimating energy costs in free-ranging animals. To date, one of the most ecologically meaningful approaches to this subject has involved calculation of the average daily metabolic rate (ADMR). The ADMR is defined as the mean rate of metabolic heat production measured over a 24-h period under a specified set of environmental conditions (Chappel 1980; Randolph 1980a, 1980b; Nagy 1989). Measurements of ADMR integrate the energetic costs associated with basal metabolism, locomotor activity, thermoregulation, heat increment of feeding and reproduction (Randolph 1980a; Karasov 1981). Calculations of ADMR are commonly used in energy budget calculations to predict long-term metabolic costs and to

estimate food requirements of free-living animals (e.g., Chappel 1980; Nagy 1989).

The purpose of the present study was to estimate the ADMR, as well as examine daily temporal patterns in metabolic heat production, body temperature (T_b) and aquatic activity of beaver living under simulated winter conditions. Previous studies (Part II; MacArthur and Dyck 1990) suggest that beavers are susceptible to immersion hypothermia and that the thermoregulatory costs of winter foraging may be high in this species. Therefore, a major objective was to examine the relationship between ADMR and daily immersion time in captive beavers. A second goal was to estimate the metabolic requirements of an entire beaver colony, and balance this cost against calculated estimates of the total energy reserves of the colony at the onset of winter. Though data are limited, there is some evidence (Novakowski 1967) that the energy reserves of the winter food caches of beaver colonies may be insufficient to sustain the animals through the winter, assuming maintenance of normal T_b and a basal rate of heat production. This apparent energy deficit may be met by foraging away from the food cache, subsisting on body fat reserves, or by depressing metabolic rate during winter (Aleksiuk and Cowan 1969a, b; Smith et al. in press).

Methods

Animals

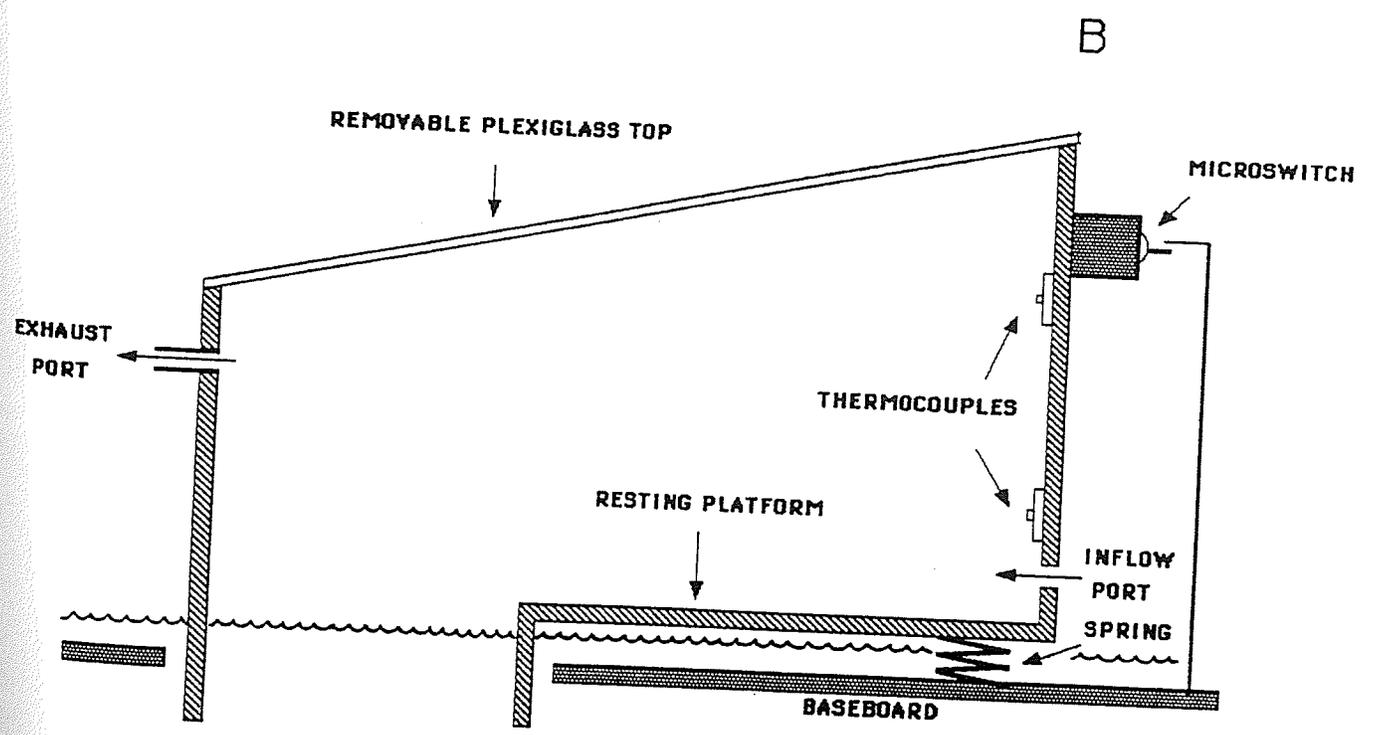
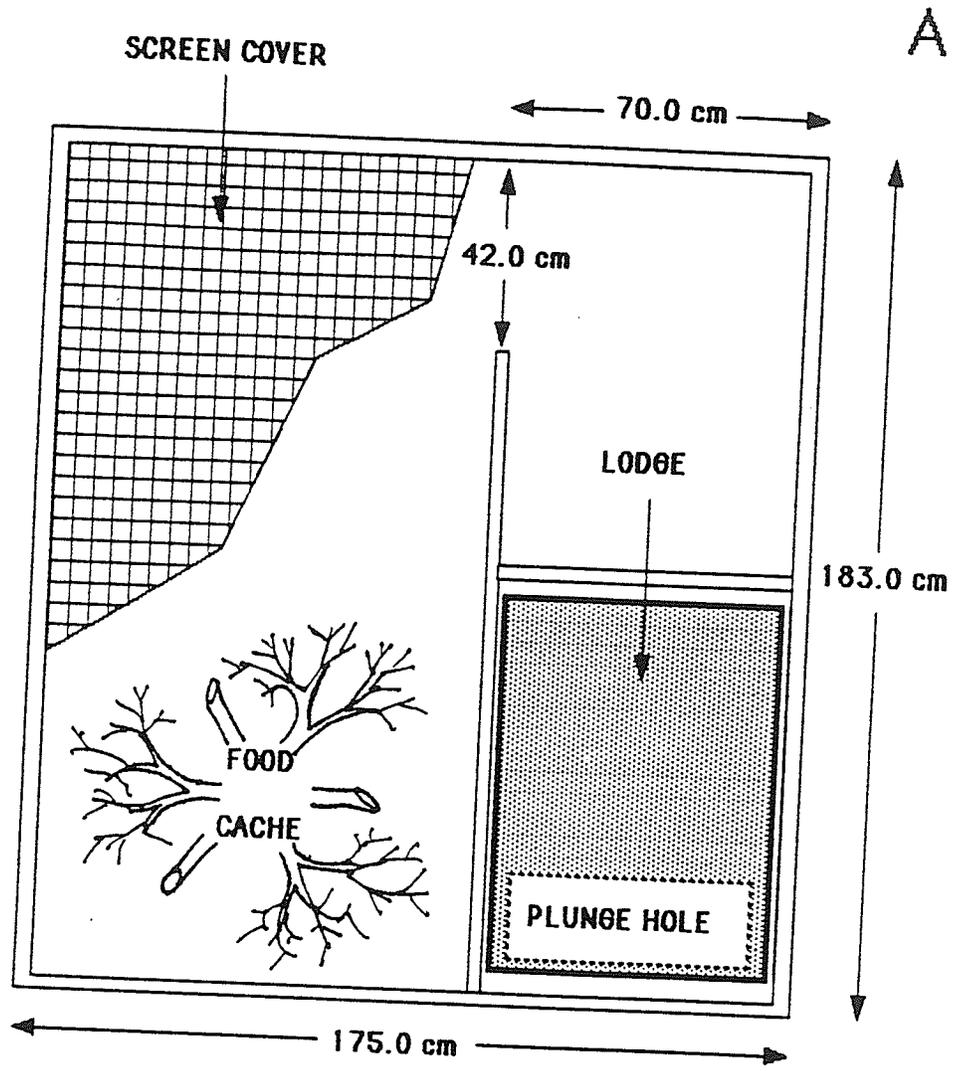
Beavers were livetrapped in late June, 1989, at two colony sites. Four animals were captured in boreal forest habitat near Pinawa, Manitoba (see Part I), and an additional pair was caught along the Assiniboine River within the City of Winnipeg, Manitoba (50°06' N, 98°20' W). These included four

yearlings (two males, two of unknown sex; 10.5-13.4 kg) and two adults (one male, one female; 17.3-18.6 kg). Animals were transported to the University of Manitoba agricultural research station located approximately 20 km south of Winnipeg, and housed in wire cages (240 X 114 X 86 cm) equipped with wooden, fiberglass-lined nest boxes (58 X 69 X 45 cm). Each cage held two animals. Cages were set at an incline on the bank of a small pond, such that the lower end of each cage was submerged to a maximum depth of approximately 40 cm. Diet consisted of commercial rodent chow (Wayne F-6 rodent Blox) provided *ad libitum*, supplemented with apples, carrots and fresh aspen saplings (*Populus tremuloides*). Beavers adapted well to captivity and, with the exception of one yearling, all animals gained weight on the diet provided. The aforementioned yearling appeared abnormally timid and lethargic during its stay in captivity and was not used in the study.

Metabolic rate determinations

Metabolic tests were performed on single animals in a set-up designed to simulate winter field conditions (Fig. 3-1). A fiberglass-lined, plywood tank filled to a depth of 68 cm with 4.0°C water was housed in a controlled-environment room kept at $5 \pm 1^\circ\text{C}$ with a photoperiod of 9L:15D. A single partition with a 42-cm opening at one end divided the tank into two compartments (Fig 3-1A). Removable wire screen covers secured to a frame 3 cm below the water level prevented diving beavers from surfacing at any point in the tank except in a respirometer designed to simulate a winter lodge. The latter consisted of a 141.7-L, fiberglass-lined, plywood chamber with a 45 X 50 cm resting platform and a clear Plexiglas top (Fig. 3-1B). A greased rubber gasket between the Plexiglas cover and the chamber walls

Fig 3-1 Schematic diagram of the microhabitat simulation for monitoring daily activity, oxygen consumption, and body temperature patterns of unrestrained beavers. **A**, plan view of simulation showing the position of the "lodge" (respirometer) relative to the food cache. **B**, detailed view of the "lodge".



ensured an airtight seal. To measure internal lodge temperature, two copper-constantan thermocouples were secured to the back wall of the chamber, 13 and 35 cm above the level of the resting platform. Additional thermocouples were used to monitor water temperature in the tank and ambient temperature in the controlled-environment room. Air, water and lodge temperatures were measured to the nearest 0.1°C with a Sensortec Model Bat-12 digital thermometer.

Room air was drawn into the lodge through an opening in the back wall just above the resting platform and exited via an exhaust port located near the top of the chamber, above the plunge hole (Fig. 3-1B). Flow rate downstream from the lodge was maintained at 30 L/min using a calibrated model 605 Matheson rotameter. A continuous record of the fractional O₂ content of the exhaust gas was obtained by routing a sample of chamber gas through water and CO₂ absorbents (drierite and soda lime, respectively), and then through an S3-A oxygen analyzer (Applied Electrochemistry Inc.) connected to a strip-chart recorder (SE-120, BBC Goerz Metrawatt). Based on a nitrogen dilution technique (Fedak et al. 1981), the time required for the respirometry system to achieve 95% equilibration was 12-15 min.

Strip-chart tracings were partitioned into 1-h blocks and the mean hourly fractional O₂ content of the exhaust gas was determined using a Jandel Digitizing Tablet and microprocessor to integrate the area beneath the O₂ tracing. Metabolic data collected during the first hour of each run were omitted from the analyses. The hourly rate of oxygen consumption was calculated according to equation 4b of Withers (1977), modified for measurements under non-steady state conditions (Pauls 1980). The wet flow rate of exhaust gas was converted to a dry gas value by calculating the moisture content, as described by Pauls (1980). The respiratory quotient

(RQ) determined by MacArthur (1989a) for non-fasted beavers (0.92) was used in oxygen consumption calculations and for converting these values to units of heat production (W/kg; Stanier et al. 1984). All metabolic measurements were corrected to standard temperature and pressure.

Metabolic runs were initiated between 0800h and 1200 h and continued uninterrupted for at least 25 h. Between 11 August 1989 and 25 October 1989, five complete trials were performed on each of five animals (total runs=25). Prior to, and following each run, animals were weighed to the nearest 0.1kg. To minimize potential stress and to familiarize individuals with the location of the lodge, animals were permitted to enter and exit the tank voluntarily for 5-30 min at the start of every trial. This was achieved by placing a beaver in an open holding cage on top of the screen cover (Fig. 3-1A) with free access to the tank and lodge. Once animals had explored the tank and settled in the lodge, the screen cover was secured in place and the lodge interior was darkened by placing black construction paper over the Plexiglas top.

Body temperature measurements

All beavers were instrumented with 60-g, temperature-sensitive, model L-M radio transmitters (Mini-mitters Inc., Sunriver, OR) 2 weeks prior to the commencement of metabolic tests. Surgical and transmitter calibration procedures are described in Part II. An automated data collection system (see Part II) was employed to record T_b at 5-min intervals. These recordings were then pooled to derive mean hourly T_b values. To enhance signal reception, a folded dipole antenna was suspended from the ceiling above the tank. After completion of the study, transmitters were surgically removed and recalibrated. None of these transmitters showed any evidence

of calibration drift during the 2-3 month duration of the study.

Aquatic activity and food consumption

To quantify the frequency and duration of underwater excursions, the lodge was mounted on a spring base and equipped with a weight-sensitive microswitch (Fig. 3-1B). Whenever the animal left the lodge, the upward displacement of the chamber closed the microswitch. When a beaver re-entered the lodge, the spring was depressed and the switch disengaged. Switch operations were recorded as real time events on a Model 1201 Grant Squirrel data logger. Cumulative time in the lodge and in the water were calculated on an hourly and on a daily basis for each run. Behavioral observations of beavers engaged in feeding activities inside the lodge were precluded by the formation of condensation on the inside of the Plexiglas top.

The simulated winter food cache consisted of a pre-weighed quantity of defoliated aspen saplings (maximum stem diameter= 5 cm) secured to a 62 X 92 cm metal grate located on the bottom of the tank (Fig. 3-1A). Beavers were required to swim a minimum underwater distance of 3 m in order to reach this submerged cache. Fresh aspen saplings were thoroughly wetted, blotted dry, and weighed prior to placement in the tank. Following the completion of a run, the tank was carefully drained and the remaining aspen collected, blotted dry, and re-weighed. The difference in the weight of aspen before and after each run was used to estimate food consumption. A representative sample of bark and terminal twigs was placed in a drying oven at 70°C and dried to constant mass in order to calculate % dry matter. The resulting estimate (58.7%) was used to determine the dry weight equivalents of the food consumed. Gross energy consumption was then

calculated using an energy equivalent of 20,494.44 kJ/kg dry matter for aspen bark and terminal twigs (Schwartz et al. 1988). Using the apparent dry matter digestibility of aspen bark (0.375) reported by Buech (1987), it was also possible to estimate the expected gross energy intake of each beaver, assuming that all of the animal's energy requirements were met from the submerged food cache. This expected value was derived by dividing ADMR by 0.375. The difference between the observed and expected daily energy intake provided an indication of the extent to which the animal depended on endogenous fuel reserves to meet its daily energy requirements.

Statistical analysis

ADMR, mean T_b , activity and food consumption were calculated for each individual and for all animals pooled together. Relationships between variables were determined using least-squares regression analysis (Statistical Analysis System, Raleigh, NC). Fisher's protected LSD test and analysis of variance were used to evaluate differences in the metabolic responses between runs and between individuals. Significance was set at the 5% level and means are presented with $\pm 1SE$.

Results

Aquatic activity and food consumption

Beavers engaged in an average of 117.0 ± 39.0 excursions per 24-h period, with a mean duration per trip of only 1.3 ± 1.4 min (Table 3-1). The mean cumulative immersion time was 140.5 ± 85.6 min, which represented only about 10% of each 24-h measurement period (Table 3-1). It appeared that beavers did not enter the water solely for the purpose of feeding, since

Table 3-1: Metabolic rate, Tb and aquatic activity of individual beavers under simulated winter conditions.

Animal*	Sex	Body weight (kg)	Average daily metabolic rate**		Daily energy expenditure kJ/day	Tb(°C)**	Aquatic activity		
			W/kg	W/kg ^{0.67}			No. excursions per day	Excursion duration (min)	Cumulative immersion time (min/day)
6Y	M	15.0±1.0 (13.8-16.6)	2.73±0.05 (1.64-4.00)	6.68±0.13 (4.02-10.09)	3547.87±394.21 (3191.00-4308.06)	36.6±0.03 (35.8-37.8)	113.0±30.0 (80.0-156.0)	0.9±0.9 (0.2-9.1)	99.4±29.4 (72.4-55.0)
555Y	M	14.8±0.5 (14.1-15.4)	2.86±0.08 (1.34-5.83)	6.95±0.19 (3.26-14.03)	3640.02±568.47 (3103.75-4734.89)	36.6±0.04 (35.2-37.6)	104.0±26.0 (79.0-152.0)	2.0 ±3.1 (0.2-20.6)	118.7±150.4 (48.8-474.2)
575A	M	18.1±0.7 (17.3-19.1)	2.73±0.06 (1.50-4.14)	7.11±0.16 (3.83-10.98)	4280.36±498.42 (3660.35-4776.00)	36.4±0.03 (35.7-37.2)	147.0±58.0 (96.0-236.0)	0.9±0.9 (0.2-19.0)	130.5±35.3 (81.4-178.1)
585A	F	19.7±0.7 (18.6-20.4)	2.64±0.06 (1.60-4.09)	7.05±0.16 (4.31-10.90)	4485.47±255.60 (4172.84-4781.02)	36.5±0.03 (35.8-37.2)	92.0±13.0 (83.0-115.0)	1.3±1.2 (0.2-10.5)	121.3±46.2 (82.5-206.5)
605Y	?	11.9±0.5 (11.2-12.5)	3.37±0.08 (1.73-4.94)	7.62±0.17 (3.97-11.16)	3449.23±212.65 (3090.47-3661.84)	36.7±0.04 (35.6-37.7)	133.0±24.0 (95.0-159.9)	1.3±1.2 (0.2-9.2)	168.2±63.1 (92.7-267.9)
Pooled		15.7±2.9 (13.8-20.4)	2.87±0.03 (1.34-5.83)	7.08±0.07 (3.26-14.03)	3880.59±586.15 (3090.47-4781.02)	36.5±0.02 (35.2-37.8)	117.0±39.0 (79.0-236.0)	1.3±1.4 (0.2-20.6)	140.5±85.6 (48.8-474.2)

Note: Values are presented as mean ± 1SEM (range).

* Y = yearling; A = adult

** Calculated from all hourly measurements

no relationship was observed between total immersion time and daily food consumption ($P > 0.05$). There was a definite 24-h rhythm in mean hourly immersion time, with maximum and minimum values occurring 2-3 h following "sunset" (lights off) and 1-2 h before "sunrise" (lights on), respectively (Fig. 3-2). The overall mean hourly immersion time was 5.9 ± 3.2 min. Conversely, mean hourly lodge use peaked 1-2 h before "sunrise", gradually declined during the daylight hours, and then reached a minimum 2-3 h after "sunset" (Fig. 3-2). On average, beavers spent 54.1 ± 3.2 min, or 90.2% (range= 81.9-99.7%) of each hour in the lodge.

During the course of each run, beavers usually dismantled the entire food cache, although some branches with uneaten bark were always left at the end of the trial. Branches stripped of bark were distributed throughout the tank at the end of every run, but most were usually recovered from directly beneath the lodge plunge hole. Animals often constructed nests in the lodge, consisting of shredded aspen and small de-barked branches.

Beavers generally lost weight on the aspen diet provided. This loss averaged nearly 3.0% ($2.93 \pm 3.41\%$) of the body weight measured at the start of each trial (Table 3-2). The mean gross energy intake of aspen was estimated at 6270.2 ± 3178.7 kJ/day, and animals demonstrated an average daily energy shortfall of 4078.1 ± 3000.1 kJ (Table 3-2).

Body temperature

The T_b of beavers in the winter simulation averaged $36.5 \pm 0.02^\circ\text{C}$ (Table 3-1), with a mean daily amplitude of $1.2 \pm 0.4^\circ\text{C}$ (range= 35.2 - 37.5°C). The mean hourly T_b of beavers exhibited a maximum range of only 0.2°C (36.4 - 36.6°C ; Fig 3-2) and was independent of hourly variation in mean metabolic rate, and mean immersion time ($P > 0.05$). There was no evidence

Fig 3-2 Mean hourly variation in the metabolic rate, abdominal body temperature, and activity of beavers living in the winter microhabitat simulation. Times spent in lodge and water are indicated by bar graphs. Each hourly mean is based on 25 observations. Vertical lines denote 1 SE; horizontal bars indicate the period of darkness.

METABOLIC RATE ($W \cdot kg^{-1}$)

3

37

36

36.

36.4

36.2

BODY TEMPERATURE ($^{\circ}C$)

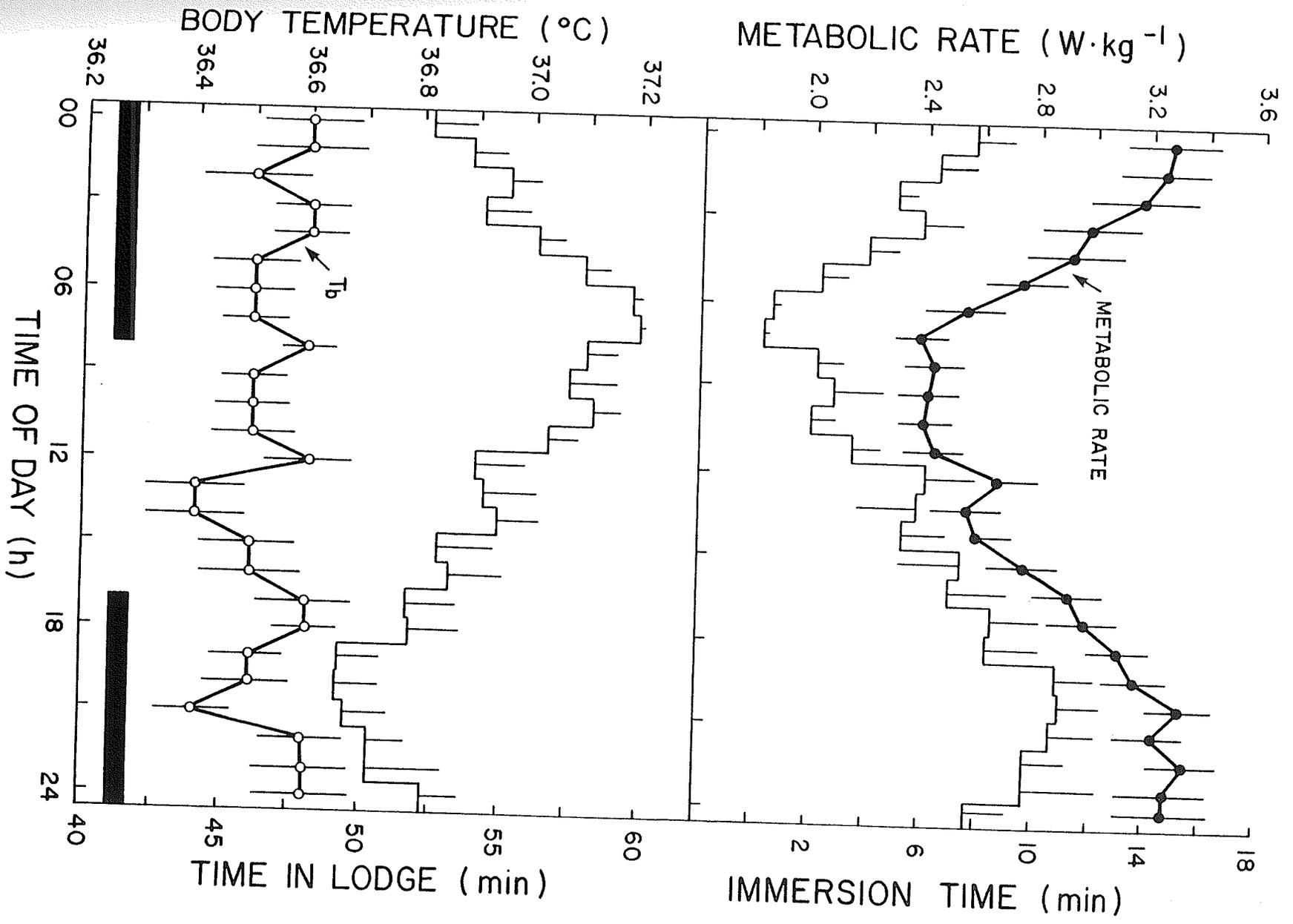


Table 3-2: Mean daily weight changes and gross energy consumption of individual beavers foraging on aspen.

Animal	Daily change in body weight (%)	Daily forage consumed		
		Dry weight (kg)	Gross energy (kJ)	Energy deficit* (kJ)
6Y	-3.05±1.36 (-4.36 to -0.66)	0.238±0.09 (0.159-0.424)	4877.06±1943.67 (3258.62-8689.28)	-4583.93±971.17 (-5134.95 to -2802.33)
555Y	-4.57±3.18 (-7.49-1.18)	0.210±0.09 (0.045-0.310)	4304.42±1960.65 (1922.25-6353.28)	-5402.30±2406.99 (-8788.73 to -2700.94)
575A	-1.13±5.14 (6.94-6.20)	0.464±0.19 (0.150-0.659)	9518.32±3884.83 (3074.17-13505.84)	-1895.97±4958.06 (-9481.99-3666.09)
585A	-1.58±2.41 (-4.04-2.47)	0.394±0.09 (0.233-0.519)	8086.72±1906.42 (4775.20-10636.61)	-3874.53±2353.92 (-7433.41 to -480.81)
605Y	-4.34±2.07 (-6.89 to -1.71)	0.222±0.06 (0.154-0.308)	4564.27±1267.50 (3156.14-6312.29)	-4633.69±1010.93 (-6233.71 to -3461.06)
Pooled	-2.93±3.41 (-7.49-6.20)	0.306±0.15 (0.045-0.659)	6270.16±3178.69 (922.25-1305.84)	-4078.09±3000.11 (-9481.99-3666.09)

Note: Means are presented with \pm 1 SEM; values in parentheses indicate ranges.
Y = yearling; A = adult.

*Energy deficit = observed minus expected gross energy intake, assuming an apparent dry matter digestibility for aspen of 0.375 (Buech 1987).

that beavers elevated either T_b or metabolic rate prior to initiating a major bout of aquatic activity.

Metabolic rate

The overall mean ADMR for all beavers was 2.87 ± 0.03 W/kg, or 7.08 ± 0.07 W/kg^{0.67} (Table 3-1). After correcting for intraspecific size variation (Heusner 1982), no differences between individuals were evident ($P > 0.05$). Within animals, ADMR was also consistent from run to run ($F_{4,20} = 0.83$; $P = 0.52$). The ADMR averaged 1.8 (1.7-2.2) times the minimum hourly metabolic rate measured when animals were least active. Beavers exhibited a distinct 24-h rhythm in metabolic heat production (Fig. 3-2), with a mean daily amplitude of 2.08 ± 0.50 W/kg. Mean hourly metabolic rate was strongly correlated with mean hourly immersion time (Fig. 3-2) ($F_{1,22} = 46.4$; $P = 0.0001$). Total daily energy expenditure varied from 3090.47 to 4781.02 kJ/day, and averaged 3880.59 ± 586.15 kJ/day (Table 3-1). Surprisingly, daily energy expenditure was independent of both the cumulative immersion time, and the frequency of aquatic excursions per day ($P > 0.05$).

Discussion

An important question that must be considered when interpreting the results of the present study is the extent to which beavers behaved normally in the simulated winter microhabitat. It is doubtful, for example, that free-ranging beavers engage in as many aquatic excursions per day as did the captive animals in this study (Table 3-1). Conceivably, the high frequency of exploratory excursions by captive beavers may have been a response to a novel environment. This suggestion is supported by the

apparent lack of correlation between total daily immersion time and daily food consumption. However, despite the seemingly high frequency of trips in the tank, it is relevant to note that the daily variation in hourly lodge use by captive animals (82-100%) was similar to that observed in free-ranging adult beavers during winter (Part II). Furthermore, all animals utilized the submerged food cache provided and usually constructed nests inside the artificial lodge.

Beavers tested under simulated winter conditions demonstrated mean abdominal temperatures comparable to those (36.3-37.3°C) previously reported for free-living (Part II; Smith et al. in press) and captive animals (Coles 1967; MacArthur 1989a; MacArthur and Dyck 1990). The apparent lack of a diel T_b rhythm is consistent with results of winter field studies (Part II), but differs from the circadian T_b rhythm reported for free-ranging animals prior to freeze-up (Part II; Smith et al. in press), and for laboratory-acclimated beavers tested in summer (MacArthur 1989a). Considering the beaver's propensity for aquatic cooling (MacArthur and Dyck 1990), my finding that mean hourly T_b was independent of mean hourly immersion time was unexpected. However, since animals in the tank set-up usually restricted their aquatic activity to excursions less than 2 min in duration (Table 3-1), they were probably not immersed long enough to experience any substantive deep-body cooling. In previous laboratory tests with similar-aged beaver, immersion in 1-4°C water resulted in an average rate of abdominal cooling of only 0.06 °C/min (MacArthur and Dyck 1990). Contrary to field investigations (Part II), there was no indication in this study that animals elevated T_b prior to entering the water. The reason for this apparent discrepancy between laboratory and field results is not known, but could relate to the short duration of the laboratory trials (25 h).

Previous investigations of beaver metabolism have been restricted to determinations of the thermoneutral zone (TNZ), basal metabolic rate (BMR) and resting metabolic rate (RMR) of animals in air and water (Coles 1967; MacArthur 1989a; MacArthur and Dyck 1990). MacArthur (1989a) reported a mean RMR of $4.78 \text{ W/kg}^{0.67}$ for non-fasted beavers ≥ 2 years of age, which is approximately 19% lower than my minimum estimate of mean hourly metabolic rate (Fig. 3-2). This was not surprising, since in the present study there was likely some effect of activity on mean hourly metabolic rate during all hours of the 24-h test period.

The ratio of ADMR to RMR is often used for interspecific comparisons of daily energy expenditure in mammals (Melcher et al. 1989). For 23 species of rodents that have been examined, this ratio varies from 1.4 to 5.7 (King 1974; Karasov 1981; Kenagy and Vleck 1982; Kenagy et al. 1989; Melcher et al. 1989). Applying MacArthur's (1989a) estimate of RMR, this ratio calculated for beavers (1.5), falls near the lower end of the aforementioned range. In contrast, Chappel (1980) reported that average daily metabolic costs for small arctic mammals, calculated over the entire year, varied from 2.9 to 4.0 times BMR.

Estimates of the daily energy expenditure of beavers living in the simulated winter microhabitat can also be compared to field metabolic rates (FMR) predicted from allometry (Nagy 1987). For example, my calculation of the daily cost of free-existence for a 15-kg beaver falls within the 95% confidence limits predicted for a similar-sized eutherian mammal, based on the equation, $\text{FMR} = 3.35W^{0.813}$, where W = weight in g (Nagy 1987). However, it exceeds the 95% confidence limits of the values predicted by this same author for both a similar-sized rodent ($\text{FMR} = 10.5W^{0.507}$) and a comparable-sized herbivore ($5.95W^{0.727}$). It should

be stressed that the 95% confidence limits of all of these equations encompass a very broad range, hence more meaningful comparisons are not possible until additional data on more species become available.

Unlike T_b , hourly metabolic rate exhibited a distinct diel cycle that was positively correlated with hourly immersion time (Fig. 3-2). Despite this strong relationship, total daily energy expenditure was independent of cumulative immersion time. It might be argued that seasonally induced shifts in daily metabolism could have masked the relationship between daily variation in ADMR and aquatic activity. However, ADMR was consistent from run to run within individuals, and comparisons of the 24-h metabolic rhythms of the most- and least-active beavers failed to reveal any obvious baseline shifts in metabolism. Therefore, the reasons underlying the lack of correlation between ADMR and total daily immersion time remain unclear. This may be due, at least in part, to the fact that the total time engaged in aquatic activity represented only a small proportion (about 10%) of the beaver's daily time budget (Table 3-1). My findings imply that aquatic activity during winter is an important determinant of energy expenditure on a short-term (hourly) basis, but is much less significant in the context of the beaver's daily or seasonal energy budget.

Previous estimates of the amount of woody forage consumed by beavers range from 0.5 to 2.5 kg wet weight/day (see Novak 1987). My estimates of daily aspen consumption varied from 0.08-1.12 kg, but averaged only 0.52 kg (wet weight). Despite the beaver's well-known preference for this forage (Novak 1987), aspen alone is apparently a deficient food resource in this species (Buech 1987). My results confirm Buech's (1987) observation that beavers are unable to sustain body weight on a diet consisting exclusively of aspen bark. In retrospect, more meaningful estimates of forage

consumption might have been possible if the simulated food cache had contained a mixture of forage species, as typically occurs in nature (Novakowski 1967; Slough 1978; Novak 1987).

In an investigation of the winter bioenergetics of beaver colonies in northern Alberta, Novakowski (1967) calculated colony energy requirements during the ice-bound season, using weight-predicted estimates of basal energy expenditure (Kleiber 1961). Since my findings suggest that the ADMR of beaver in winter may be 1.5 times greater than BMR (MacArthur 1989a), Novakowski (1967) probably underestimated the colony's metabolic costs during winter. For example, using my estimate of ADMR for animals ≥ 2 years of age (4382.92 kJ/day) and applying this to Novakowski's (1967) colony No. 26, the energy requirement for the 150-day ice-bound season would be approximately 657,438 kJ per animal, or 3,287,190 kJ for a colony of 5 beavers. If the total digestible energy available in the food cache of this colony was 1,956,132 kJ (Novakowski 1967), then my data suggest that the colony would experience an energy deficit of approximately 1,331,058 kJ, or 266,212 kJ per animal. This deficit estimate is approximately twice that determined by Novakowski (1967).

Assuming that the energy value of stored fat is 39.3 kJ/g (Schmidt-Nielson 1979), then the aforementioned deficit would require about 6.8 kg of fat per animal. Recent studies of the proximate composition of beavers in southern Manitoba (D. Soprovich, personal communication) have revealed that, in early winter, fat may account for as much as 24% of the body weight of animals ≥ 1.5 years of age (12–31 kg). Therefore, if the beavers studied by Novakowski (1967) had comparable fat levels, and assuming that fat was the only available body fuel reserve, then a 20-kg beaver in colony No. 26 would have insufficient fat stores (4.8 kg) to meet

the calculated energy deficit. These calculations would strongly suggest that beavers can balance their energy budget in winter only by supplementing food resources in the cache with aquatic vegetation acquired away from the food pile. Though infrequent, death by starvation has been documented in this species when the food cache was rendered inaccessible by drastic reductions in water level during early winter (D. Smith, personal communication).

Finally, it should be recognized that the current estimates of the ADMR in winter may be high, since they were derived for fall-acclimatized beavers tested in a simulated winter microhabitat. The true ADMR of free-living beavers would be lower if beavers are able to reduce T_b and depress metabolism during winter (Aleksiuk and Cowan 1969b; Smith et al. in press). Also, present estimates of gross energy intake during winter do not account for the potential energy acquired by animals that actively forage away from the cache. Thus, several aspects of this species' winter energy budget require further investigation. Additional metabolic testing of winter-acclimatized beavers, perhaps including application of the doubly-labeled water technique (Nagy 1987) to determine field metabolic rates during winter, may be required to clarify questions raised by this study.

Summary and Conclusions

Results of this study suggest that the construction and group occupation of lodges by *C. canadensis* is an important behavioral adaptation that provides this species with year-round access to a thermoneutral microclimate. These thermal benefits are achieved at the expense of only limited disturbance to the respiratory gas concentrations inside the lodge, despite the large metabolic mass of the resident animals. Factors that may potentially influence the composition of respiratory gases in beaver lodges include the presence or absence of a vent, the thickness and composition of lodge walls, and the respiratory demands of the resident animals. It appears that internal T_L is governed mainly by external environmental factors during the open-water season, whereas the number of lodge occupants may significantly affect T_L during winter. The utilization of a buffered microclimate in winter ensures minimal energy expenditure during protracted resting periods in the lodge, which may be critical to this species' survival in northern regions.

Free-living beavers did not demonstrate any evidence of seasonal hypothermia. Animals appeared to mitigate abdominal cooling by periodically returning to the thermoneutral microclimate of the lodge in order to rewarm. Kits compensated for their greater sensitivity to immersion hypothermia by spending less time in the water than adults. Adults also appeared to reduce thermal stress and energy requirements during winter by remaining in the lodge for more than 80% of each day, and by shortening the duration of under-ice foraging trips. If it is assumed that deep body cooling ultimately limits aquatic endurance in this species, then the observed pre-immersion rise in T_b could significantly increase available foraging time in cold water. For example, a pre-immersion rise in

T_b of 0.6°C should theoretically permit an adult beaver to extend available feeding time by about 15 min. Through a combination of physiological adaptations which retard heat loss and behavioral mechanisms for minimizing immersion hypothermia, free-ranging beavers are able to regulate T_b economically and with a high degree of precision.

Captive beavers tested under simulated winter field conditions demonstrated levels of T_b and activity that were similar to those recorded for free-living animals during winter. It appeared that aquatic activity was an important determinant of energy expenditure on a short-term (hourly) basis, but was much less significant in the context of the beaver's daily or seasonal energy budget. The inability of beavers to sustain body weight on a diet consisting exclusively of aspen bark suggested that this was a deficient food resource. Based on previous estimates of the energy content and digestibility of forage cached prior to freeze-up, it is unlikely that the winter energy requirements of this species can be met solely from the winter food cache. Winter energy deficits in this species may be met by subsisting on body fat reserves, or by foraging on submerged vegetation away from the food cache. Further metabolic testing on winter-acclimatized beavers and determinations of the field metabolic rate of these animals are required to refine estimates of this species' winter energy budget.

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