

THE UNIVERSITY OF MANITOBA

ASPECTS OF WINTER DORMANCY IN THE STRIPED SKUNK

(Mephitis mephitis)

by

GRAHAM RICHARD PERCY MUTCH

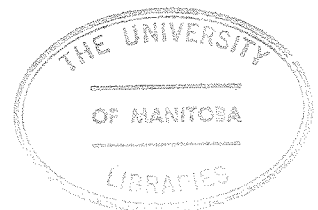
A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

WINNIPEG, MANITOBA

MARCH, 1976



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A dissertation submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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ABSTRACT

Selected aspects of winter dormancy in male striped skunks were studied in Delta Marsh, Manitoba, Canada. Diel activity patterns of skunks held in individual outdoor enclosures were determined for one year using radio telemetry and visual observations, while free-ranging skunks were monitored between May and October by telemetry. No significant differences were observed in diel activity indices of free-ranging and captive skunks. In summer, skunks were active on 90 to 100% of nocturnal observations, but were rarely active during daylight. Above-ground activity decreased greatly between September and mid-December, and was virtually nil between December and early April. However, movement was frequently noted within the nest chambers during winter. Surface activity resumed in March and increased in April.

Seasonal changes in abdominal body temperature (T_b) were studied using radio telemetry. The mean of 264 T_b recordings on 2 skunks in August was 37.7°C. Corresponding T_b means on 3 individuals in November, December, March, and April were 36.4°C, 34.4°C, and 37.7°C, respectively. Diel T_b variations and depressions were greatest in winter, with diel fluctuations

of up to 7.2°C and a minimum T_b of 28.4°C recorded. Maximum diel T_b ranges and minimum T_b 's in individual skunks in other seasons were, respectively, 2.2°C and 36.2°C (August), 3.4°C and 34.0°C (November) and 2.0°C and 35.0°C (April).

Mean body fat content of adult males in October was 32% of live weight, while in late April and early May it was 10% of live weight ($11,236 \pm 902$ (\pm S.E.) and $2,370 \pm 436$ kcal per skunk, respectively). Using theoretical calculations, the skunks would experience an apparent energy deficit of 44% if they existed at basal metabolic levels, calculated on fat-free body weights, for a winter period of 140 days. The winter reduction in surface activity, the retreat to a relatively warm den and the winter depression in body temperature apparently reduce energy expenditure sufficiently to enable the skunk to survive the winter in Manitoba by utilizing only fat reserves as an energy source.

ACKNOWLEDGEMENTS

I wish first of all to thank my supervisor, Dr. M. Aleksasuk, for all the patience and support he has shown for the entire duration of this study. The University of Manitoba Field Station (Delta Marsh) provided superb research facilities and accommodation, and the Director (Dr. J. M. Shay) and entire staff were always helpful in every way possible during the seventeen months that I spent there. Dr. H. Spencer assisted greatly with the design and construction of the radio transmitter system used for tracking purposes and the modification of the receiver to my purposes. The research was funded by the Manitoba Department of Mines, Resources and Environmental Management (through the University Field Station), National Research Council of Canada (through grants to Dr. M. Aleksasuk) and Gulf Oil Canada Limited. Support for my personal maintenance was received in the form of scholarships from these same bodies.

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INTRODUCTION

Within boreal regions a distinct group of carnivores undergoes a prolonged winter period of inactivity. The animals generally spend this period, which may last several months, in underground dens (Verts, 1967; Craighead and Craighead, 1970, 1972; Sunquist, 1974; many others). Long intervals of inactivity may be infrequently interrupted by brief forays to the outside by individuals of some species, especially during periods of warm weather (Allen, 1939; Verts, 1967; Cowan, 1973). The species commonly included in this group of carnivores are the black bear (Ursus americanus) (Hock, 1960; Folk, et al. 1970), grizzly bear (U. arctos) (Folk, et al. 1970; Craighead and Craighead, 1970, 1972), polar bear (U. maritimus) (Harrington, 1968; Folk, et al. 1970), raccoon (Procyon lotor) (Stuewer, 1943; Sharp and Sharp, 1956; Cowan, 1973), European badger (Meles meles) (Johansson, 1957), Asian raccoon dog (Nyctereutes procyonoides) (Novikov, 1956) and striped skunk (Mephitis mephitis) (Selko, 1938; Sunquist, 1974).

Little is known of the physiology, ecology and behaviour of these species during their winter denning period. The black bear has received most of the

attention in this respect (Hock, 1951, 1957, 1960; Folk, 1967; Folk, et al. 1970; Nelson, et al. 1973, 1975). Lesser amounts of data exist for the grizzly bear (Folk, 1967; Folk, et al. 1970; Craighead and Craighead, 1970, 1972), raccoon (Cowan, 1973; Thorkelson and Maxwell, 1974), European badger (Johansson, 1957) and striped skunk (Houseknecht, 1969, 1971; Sunquist, 1974; Aleksiuik and Stewart, in prep.). Several of the reports on bears have described limited body temperature depressions and large metabolic rate decreases during the winter denning period (Hock, 1951, 1957, 1960; Folk, 1967; Folk, et al. 1970). Observations on bears and raccoons in their winter dens indicate that the animals are much less alert than during summer sleep, although an individual can rapidly awaken and readily defend itself if sufficiently disturbed (Stuewer, 1943; Brown and Bellrose, 1943; Matson, 1954; Craighead and Craighead, 1970, 1972). The behavioural and physiological changes manifested by these species in winter have been summarized under the terms "dormancy" (Matson, 1946), "winterruhe" (Eisentraut, 1956 cited by Kayser, 1961), "carnivorean lethargy" (Hock, 1957, 1960), and "winter sleep" (Nelson, 1973).

Recent studies have provided quantitative descriptions of certain changes in the striped skunk's daily and seasonal activity and denning patterns (Verts, 1967; Houseknecht, 1969, 1971; Sunquist, 1974; Aleksasuk and Stewart, in prep.). Captive skunks held in outdoor enclosures with an artificial food supply showed greater outdoor activity during winter (Aleksasuk and Stewart, in prep.) than free-ranging skunks without an artificial food supply (Sunquist, 1974). Although Folk (1957) concluded that the skunk's body temperature is not labile, other authors have speculated that carnivorean lethargy, including body temperature depression, could possibly be expected in the striped skunk in the northern part of its range (Selko, 1938; Hock, 1951; Eisentraut, op cit; Morrison, 1960; Kayser, 1961, 1965; Nelson, 1973).

The striped skunk feeds opportunistically on insects, small mammals, birds' eggs, fish, amphibians and carrion (Hamilton, 1936, 1937; Selko, 1937; Kelker, 1937; Verts, 1967; Appendix 5). In boreal regions these food materials are very scarce or not available between approximately early November and mid-April. Concomitantly, the low ambient temperatures,

wind, and soft, deep snow greatly increase the energy requirements for thermoregulation and locomotion of skunks active above-ground. Such increased energy requirements would necessarily exacerbate the unfavourable energy balance which the essentially aphagic skunks experience at this time. The purpose of this study was to document in detail seasonal changes in activity patterns and abdominal body temperature of the striped skunk, with specific reference to environmental energy conditions which obtain during the winter in southern Manitoba.

MATERIALS AND METHODS

Study Area

This study was conducted in Delta Marsh, Manitoba, Canada ($50^{\circ} 11' N$, $98^{\circ} 23' W$), 5 to 6° latitude south of the northern limits of distribution of the striped skunk at this longitude (Hall and Kelson, 1959). Walker (1959) has described the area's vegetation in detail. A generally bare, intermittently inundated sandy beach along the south shore of Lake Manitoba slopes to a sandy, wooded ridge about 50 to 100 m wide and generally less than 2 m high. Tree species on the ridge include poplars (Populus spp.), willows (Salix spp.), Manitoba maple (Acer negundo), redberried elder (Sambucus pubens) and other, less abundant species. Herbs form a dense understory over most of the ridge. In the adjacent marsh south of the ridge, margins of open water are covered with dense stands of cat-tail (Typha latifolia) and bulrush (Scirpus spp.). Seasonally flooded sites have dense stands of common reed (Phragmites communis) or sprangle-top (Scholochloa festucacea). Sites subjected to little or no flooding support a mixture of grasses, such as couch grass (Agropyron repens)

and squirrel-tail grass (Hordeum jubatum), and herbs such as Canada thistle (Cirsium arvense), sweet clover (Melilotus alba) and asters (Aster spp.). Roadsides and dikes are covered predominantly with a mixture of brome-grass (Bromus sp.), alfalfa (Medicago sativa) and sweet clover.

Holding Facilities For Captive Skunks

Captive skunks were held in five adjacent wire mesh enclosures each measuring 5 m x 1.5 m x 1.5 m high (Appendix 1). The enclosures were constructed in the sandy ridge area of Delta Marsh. They afforded no protection from ambient weather conditions. Nearby trees, shrubs and tall forbs provided shade and a partial windbreak, and isolated the animals from the University Field Station buildings located 50 to 150 m away. A blind along one side of the holding facility allowed observations to be made without any disturbance to the animals. Each enclosure contained a simulated, hand-dug den (Appendix 1). The den consisted of a straight wooden and wire mesh tunnel (16 cm x 19 cm x 180 cm long) sloping from the ground surface to a subterranean wooden and wire mesh nest chamber (44 cm x

43 cm x 33 cm high). A small cover at each tunnel entrance reduced the opening to a triangle about 15 cm to a side and oriented it away from the direction of the prevailing winter winds. The nest chamber was covered with 75 cm of earth and 15 cm loose leaf and straw litter, while the tunnel was covered with correspondingly smaller amounts of the same materials. Two control dens, constructed for microclimate studies, were identical to the above dens in all respects, except that they did not hold skunks. The specifications of these artificial dens conform to the range of dimensions for natural skunk dens provided by Seton (1926), Allen (1939), Allen and Shapton (1942) and Storm (1972), within the limits imposed by the water table.

Nesting material in the form of dry grass was provided in excess within each enclosure. The skunks were fed a diet of "Tuffy's", a dry commercial dog chow (Star-Kist Foods, Inc., Perham, Minnesota), ad libitum except during the period November 17 to April 13. Between November 17 and 27 the amount of food provided was gradually reduced to zero and maintained at that level until feeding resumed ad libitum on April 13. Pipazine (piperazine dihydrochloride;

Gardo Products, Waterloo, Quebec) was administered orally to control ascarid parasites. Water was provided when snow was not present on the ground.

Between May and October above-ground shelters were provided in each enclosure, as skunks frequently utilize such retreats (Verts, 1967; Houseknecht, 1969, 1971). The shelters consisted of inverted wooden boxes (about 60 cm x 40 cm x 40 cm high) with a small opening cut in one side. Each skunk was free to enter either the box or the underground den in its enclosure.

Activity

Captive Skunks: Two methods were used to study activity of captive skunks: radio telemetry and visual observations. Between mid-April and October 1975, the activity of between two and four adult males per month was monitored by direct visual observation (Appendix 2). In this and all other phases of the study only males were used as subjects. This was done in an attempt to reduce variability, and also because of the greater numbers and/or ease of trapping

male animals in the study area. The skunks were held individually in the outdoor enclosures described above. Over a period of about six consecutive days each month between mid-April and October, 72 to 96 hourly observations were made on each captive animal. On each occasion the observer quietly approached the enclosure from behind the blind. A quick determination was made of whether or not each animal was "active" (i.e., digging, feeding, moving about, climbing or grooming) above-ground, or "inactive" (i.e., lying immobile above-ground or out of sight in one of the retreats provided). Nocturnal observations were made by very quickly shining a flashlight across the enclosures. Each individual was recorded as being either "active" or "inactive" in accordance with the above definitions, at the time of each observation. The observations at each hour for all captive animals were pooled on a monthly basis. This provided an hourly activity index, defined as the percentage of all observations made on which the skunks were observed active on the surface. This index, which is directly related to the animals' above-ground activity, is comparable to the activity indices utilized by Verts (1967), Houseknecht (1971) and Sunquist (1974) in their studies on the skunk.

Radio telemetry was used to study the activity patterns of four captive male skunks (three adults and one juvenile) held in the outdoor enclosures from early November 1974 to mid-April 1975. Three of these animals were denned individually while one was held with a juvenile female. The "click" radio signals of abdominally implanted radio transmitters (see following section, "Body Temperature") were used to provide an index of activity. Each subterranean nest chamber was provided with an auxiliary antenna system consisting of eight loops of No. 18 copper wire wound about the outside of the chamber. This was connected via 75 m TV antenna lead wire to a standard AM radio in a heated building. Due to the short range of the transmitters (about 0.5 m) the "click" radio signal could be picked up by the antenna system and subsequently monitored on the AM radio in the laboratory only when the skunk in question was in its nest chamber. Thus, on those occasions when the click signal was received on the AM radio receiver the animal was known to be in its nest chamber, and hence was defined as "inactive" insofar as surface activity was concerned. The lack of a click signal for one minute accurately predicted above-ground activity and the animal was

defined as being "active" on those occasions. During the period when this method was used the animals were never found inactive on the surface. These activity data were gathered on an approximately hourly basis for at least eight, 24-hour periods per month. An hourly activity index - the percentage of all observations made on which the animal was observed to be active - was derived for each individual in each month. Because monthly comparisons of these hourly figures revealed that the mean activity levels of the individual animals were generally very similar (Table 1) data were pooled to give hour-by-hour activity indices in each month. Due to a transmitter malfunction the activity patterns of a fifth, juvenile male skunk could not be monitored in the above manner. Instead, hourly observations were made visually (as described above for the April to October period) for four, 24-hour periods each month. As these data did not differ from those obtained by telemetry, they were incorporated into the hour-by-hour monthly indices of surface activity.

Movements of captive skunks within their nest chambers were detectable using the implanted radio transmitters. Short-term variations in the intensity of the click signal received indicated movements of

the transmitters, and hence the animals, relative to the receiving antennae. On this basis the skunks were described as being either "active" or "inactive" within the nest chamber on all occasions when surface activity was not found. Hourly indices of within-den activity (percentage of all observations when within-den movement was recorded) were derived for each of the four individuals in each month. Because the data from different animals were similar (Table 1), the hourly within-den movement indices of individual animals were pooled to give combined hourly indices of within-den activity in each month. The collection of all activity data on captive skunks by radio telemetry was terminated in mid-April due to the flooding of the nest chambers. After mid-April the skunks often rested above-ground, rendering the absence of a transmitter signal a poor indicator of surface activity.

Additional information on activity was obtained by checking the enclosures for evidence of surface activity each morning and evening between October 1974 and April 1975. Signs of feeding, digging, defecation or movement of excess nesting materials, and later the presence of tracks in the snow, all served as indicators of activity. The percentage of dens at which activity occurred each day and night was then calculated.

Free-ranging Skunks: The activity patterns of free-ranging male skunks were examined by radio telemetry. A total of 11 adult males were live-trapped in the study area between June and October 1974 and in May 1975. Each animal was immobilized with an intramuscular injection of Sernylan (phencyclidine hydrochloride; Bio-Ceutic Laboratories, St. Joseph, Missouri) at a dosage of 2 - 3 mg/kg body weight. The skunk was then fitted with a hand-constructed, collar-mounted radio transmitter similar to that described by Seidensticker, et al. (1970) (Appendix 3). Each transmitter weighed approximately 70 g and emitted a continuous-tone signal at a carrier frequency of between 27.005 and 27.255 MHz for a period of about one week. Subsequent to being fitted with the transmitter, the skunk was released at or near the capture site and allowed a recovery and re-orientation time of at least 12 hours prior to the onset of data collection.

Radio signals were received using a modified Fanon Model T606 Portable Transceiver (Fanon Electronics, Toronto, Ontario) equipped with a direction-finding loop antenna. Each observation consisted of monitoring the transmitter-emitted signal for a period of one minute. Rapid, irregular variations in the intensity of the continuous-tone signal indicated that the animal was

moving or "active" (Cochran and Lord, 1963; Verts, 1963). An unvarying tone for one minute indicated that the skunk was not moving, and the animal was defined as being "inactive". Activity observations were made at approximately hourly intervals between 1700 and 0700 h in all months when activity was monitored by this method (Appendix 2). Observations were made at regular intervals between 0800 and 1600 h in September and May, and less regularly in June, July, August and October. An hourly activity index (percentage of hourly observations in which the animals were active) was calculated for each month. These hourly indices were compared with the hourly indices for captive animals (data pooled) for those months when data on both captive and free-ranging skunks were available (Table 1). Data were combined to give hour-by-hour activity indices.

Searches were made for evidence of activity of free-ranging skunks from late December to mid-April, when snow was present on the ground. A regular route was followed over the study area at approximately weekly intervals in December, January and February. For the period 1 March to 10 April a total of 11 dens known to be regularly utilized by skunks were checked on four or

more days per week for evidence of skunk activity during the preceding night. A den was considered to have been recently utilized by skunks if fresh skunk tracks were present at the den mouth and if a grass plug previously placed loosely in the entrance by the investigator was dislodged.

Body Temperature

Abdominal body temperatures of skunks were determined by radio telemetry. Two adult male skunks (mean weight: 4.35 kg) were live-trapped in Delta Marsh in late July 1975. In early August 1975 they were implanted intraperitoneally (under a combination of Nembutal (about 30 mg/kg), Sernylan (about 3mg/kg) and ether anaesthesia) with previously calibrated, miniature radio transmitters (Mini-Mitter Co., Inc., Indianapolis, Indiana), and placed separately in the enclosures. The implanted transmitters emit "click" radio signals at temperature-dependent rates (Osgood, 1970). An auxilliary antenna system, which consisted of a grid of No. 18 copper wire on the enclosure floor joined to 75 m TV antenna lead wire, transmitted the signals from each transmitter to the

laboratory. In the laboratory, standard AM radio receiver - tape recorder systems automatically recorded the signals for one minute per hour for each animal, for five and six days respectively between 10 and 17 August. Each hourly body temperature (T_b) was later derived by determining the click rate for each transmitter and comparing this rate to that transmitter's calibration curve.

In October 1974 three male skunks (mean weight: 3.24 kg) were implanted with transmitters as described above. The auxilliary antenna system as described earlier (under "Activity", "Captive Skunks") carried the "click" radio signals from the subterranean nest chambers to an AM radio in the laboratory. The diel body temperature dynamics of the skunks were derived by tallying the number of transmitter-emitted "clicks" for one, 3-minute interval per hour per skunk for 24 consecutive hours. This procedure was performed for 24 consecutive hours at approximately weekly intervals rather than for longer, but much less frequent, intervals in order to follow seasonal trends in detail. Meltwaters flooded the nest chambers in mid-April, rendering the receiving system inoperative. In late April the skunks were placed in individual, covered cages with food and water ad libitum and allowed 24

to 36 hours to become accustomed to confinement. Body temperatures were determined hourly for one 24-hour period by placing the radio receiver near the cages and monitoring the click signals manually, with a minimum of disturbance to the animals. The transmitters were removed from the skunks on May 2 and immediately re-calibrated. Correction factors were applied to the data to compensate for drift in the calibration curves.

Determination of Body Fat Content

Five adult male striped skunks were captured in Delta Marsh in October 1974. The animals were killed with ether, weighed and immediately frozen. Each animal was later thawed and dissected into small pieces. The scent sacs and contents of the digestive tracts were removed, weighed and discarded. The remains were brought to a constant weight in a drying oven at $30 \pm 5^{\circ}\text{C}$ and then passed through five sequential changes of ethyl ether (fat extraction quality) over a period of two to three months at $25 \pm 10^{\circ}\text{C}$. The residue was subsequently dried to a constant, fat-free weight at $30 \pm 5^{\circ}\text{C}$. The quantity of fat was derived

by subtracting the dry, fat-free weight from the weight of the individual after initial drying to a constant weight. The percentage of fat in relation to the live weight was calculated. This procedure is a reliable method of determining total fat content in animal carcasses (Mackenzie, 1964).

This procedure was repeated for five adult male skunks killed in late April and early May 1975. Two of these animals were captured in the wild while three had been held in captivity since October 1974, as described above.

Macro- and Micro-environmental Temperatures

The metal-encased tip of a telethermometer thermistor probe was inserted 2.5 cm through the roof and into the nest chamber of each simulated den. Hourly temperature readings of occupied dens were taken with a YSI telethermometer (YSI Co., Inc., Yellow Springs, Ohio) on those occasions when body temperatures were recorded. The temperatures of the two empty control dens, soil at the same depth as the probes within the nest chambers (90 cm) and shaded ambient air temperatures 0.5 m above the soil or snow surface were recorded at the same time. Daily ambient maximum and minimum temperatures were available from the University Field Station meteorological station.

RESULTS AND DISCUSSION

Diel and Seasonal Activity Patterns

Marked seasonal changes occurred in the activity of male striped skunks (Figs. 1, 2; Appendix 2). Activity was highest in the period May to September inclusive. In these months above-ground activity occurred primarily during the hours of darkness (Fig. 2). During this period activity prior to the hour before sunset was uncommon. Activity indices increased greatly in the hour following sunset. Both free-ranging and captive animals tended to be active on almost all occasions when nocturnal observations were made. The skunks' activity decreased in the hour following first light, and at about sunrise they were active on 25% or less of occasions sampled. Individuals occasionally became active between sunrise and noon, but between mid-day and the evening resumption of activity, above-ground movement was virtually nonexistent. In September, the activity of captive skunks followed this basic pattern, but free-ranging individuals showed a post-sunrise bout of activity which lasted until nearly noon (Fig. 3). Activity

levels then declined, and were low until activity resumed at about 1600 h. The activity index subsequently decreased after midnight, and remained in the 20 to 50% range until sunrise.

Hourly activity indices during September nights were not as high as during May to August nights (Appendix 2). Whereas earlier in the summer a given individual would generally be found active at each hourly nocturnal observation, in September the activity of an individual was less predictable. The combined activity index of all animals studied (sum of hourly activity indices in any month divided by 24) in September showed very little decline from the August index (Fig. 1). As October, November and December progressed, combined monthly indices rapidly decreased (Fig. 1; Appendix 2). An individual was frequently found inactive on several consecutive hourly observations, apparently becoming active above-ground only once or twice in a night. Unusually mild fall weather and lack of snow may have resulted in activity later in the season than in more normal years. A small increase in activity levels occurred in late November and early December (Fig. 1). Aleksasuk and Stewart (in prep.) also observed an

Table 1. F-values obtained from comparisons of activity patterns among captive individuals, among free-ranging individuals, and between captive and free-ranging individuals for striped skunks in Delta Marsh, Manitoba. Variation among individuals was tested against diel variation within individuals. Numbers of skunks studied are found in Appendix 2.

Months	F Values			
	% Activity, among captive individuals	% Activity, among free-ranging individuals	% Activity, captive vs. free-ranging individuals	In-Den movements, among captive individuals
January	0.870	-	-	0.493
February	0.000	-	-	1.195
March	3.117*	-	-	3.712*
April	1.544	-	-	0.852
May	0.418	-	1.096	-
June	0.896	-	0.176	-
July	0.254	0.000	1.494	-
August	2.185	0.003	1.795	-
September	0.109	0.755	5.402*	-
October	1.023	-	-	-
November	1.568	-	-	2.512
December	6.619**	-	-	1.960

* $p < 0.05$

** $p < 0.01$

Fig. 1. The annual pattern of surface activity of male striped skunks at Delta Marsh, Manitoba. The activity index represents the combined number of observations of captive and free-ranging active skunks made in each weekly or monthly period, expressed as a percentage of all observations made in that period. The solid bar represents the interval during which snow was present on the ground. Sample sizes and numbers of observations and 95% confidence intervals on the activity indices are presented in Table 3 of Appendix 2.

A = food supply reduced; B = food supply terminated; C = food supply returned.

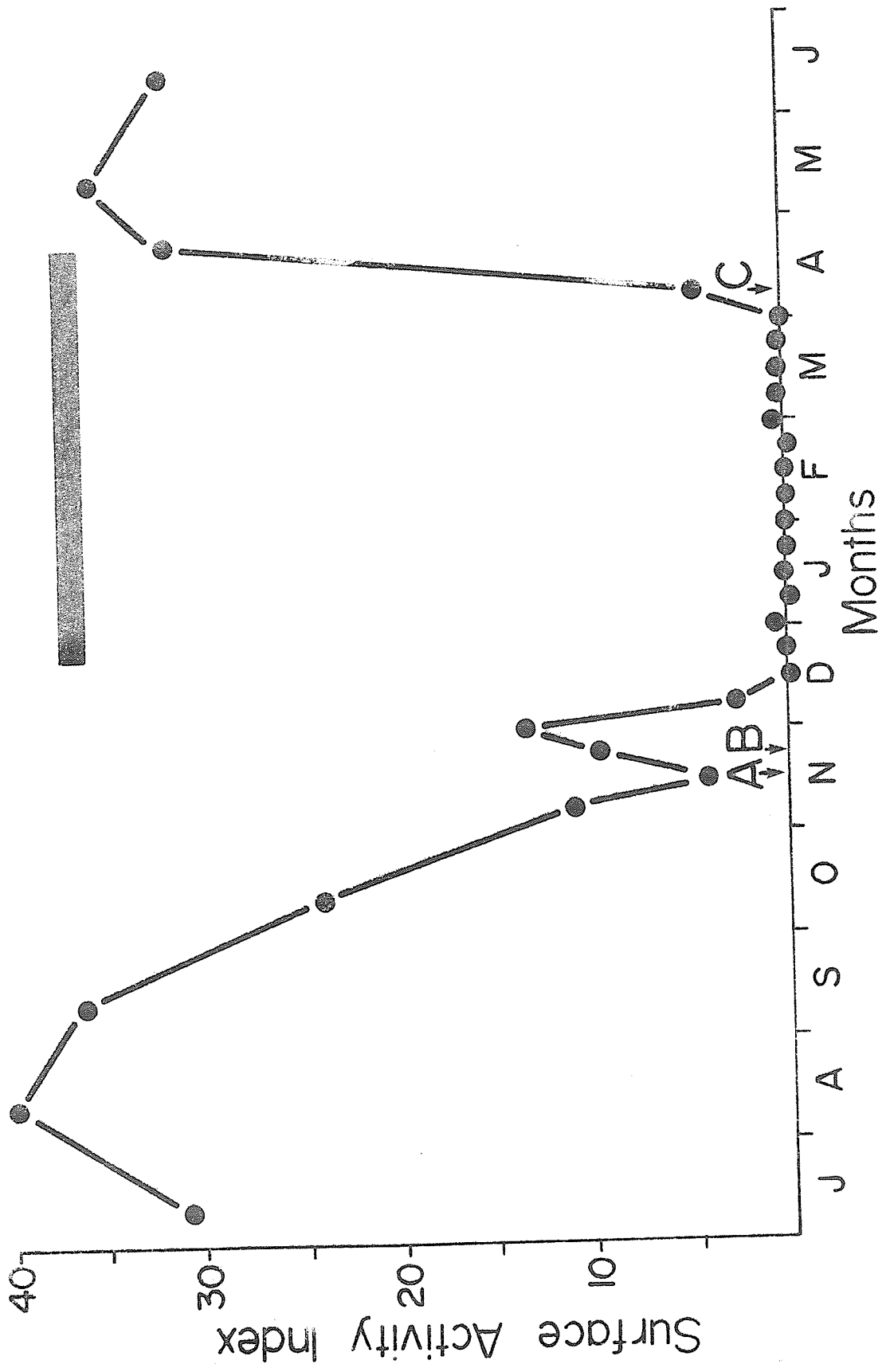


Fig. 2. Representative diel patterns of surface activity in male striped skunks at Delta Marsh, Manitoba during summer, autumn, winter and spring. Each graph represents data collected over a period of one month. The activity index represents the number of observations of active skunks in each period, expressed as a percentage of all observations made in that period. Data from captive and free-ranging skunks were pooled. Arrows indicate sunrise and sunset time at mid-month. N values are the total number of animals studied per month, while n values are the total number of observations per month. See Appendix 2 for further details.

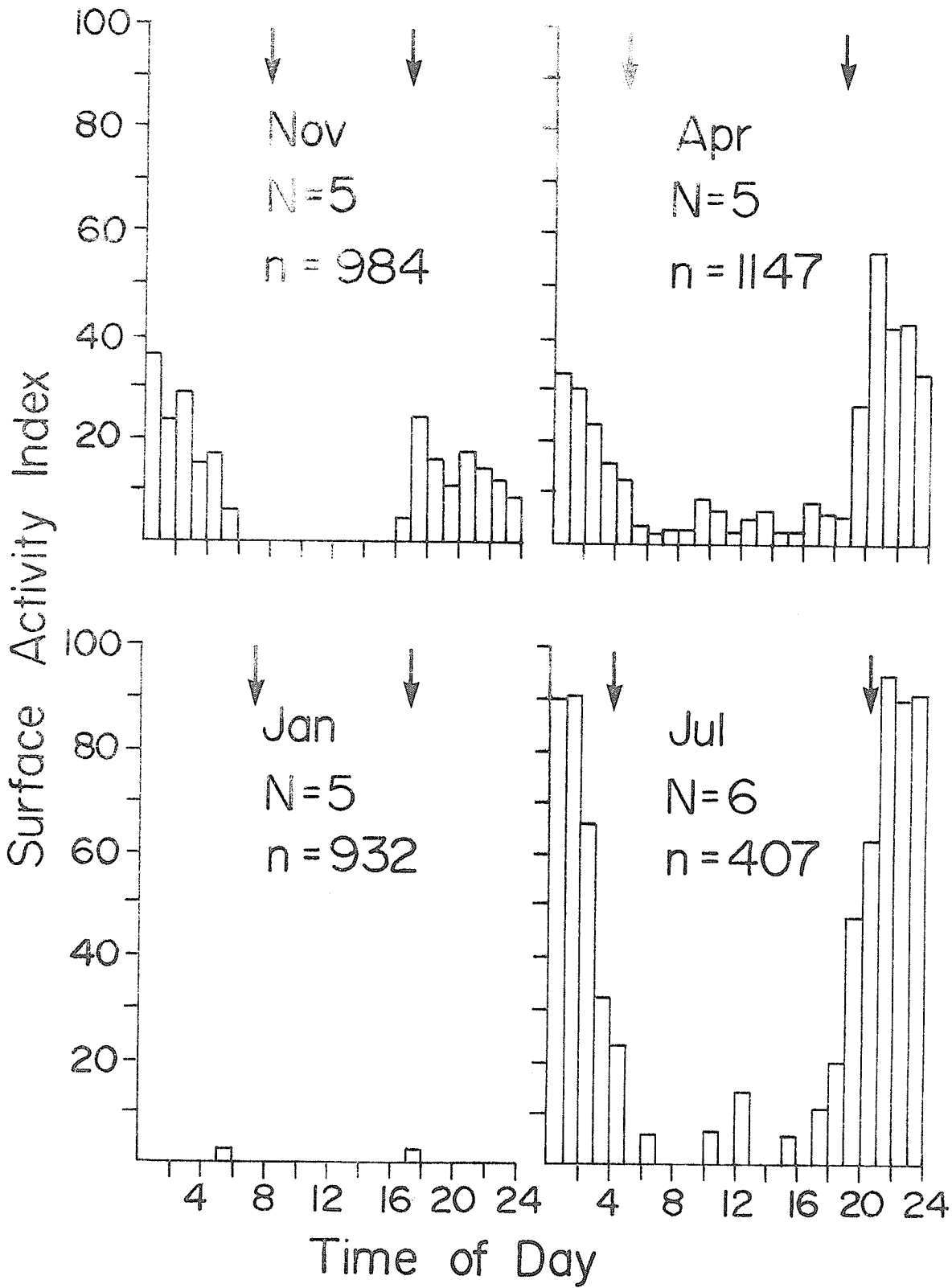
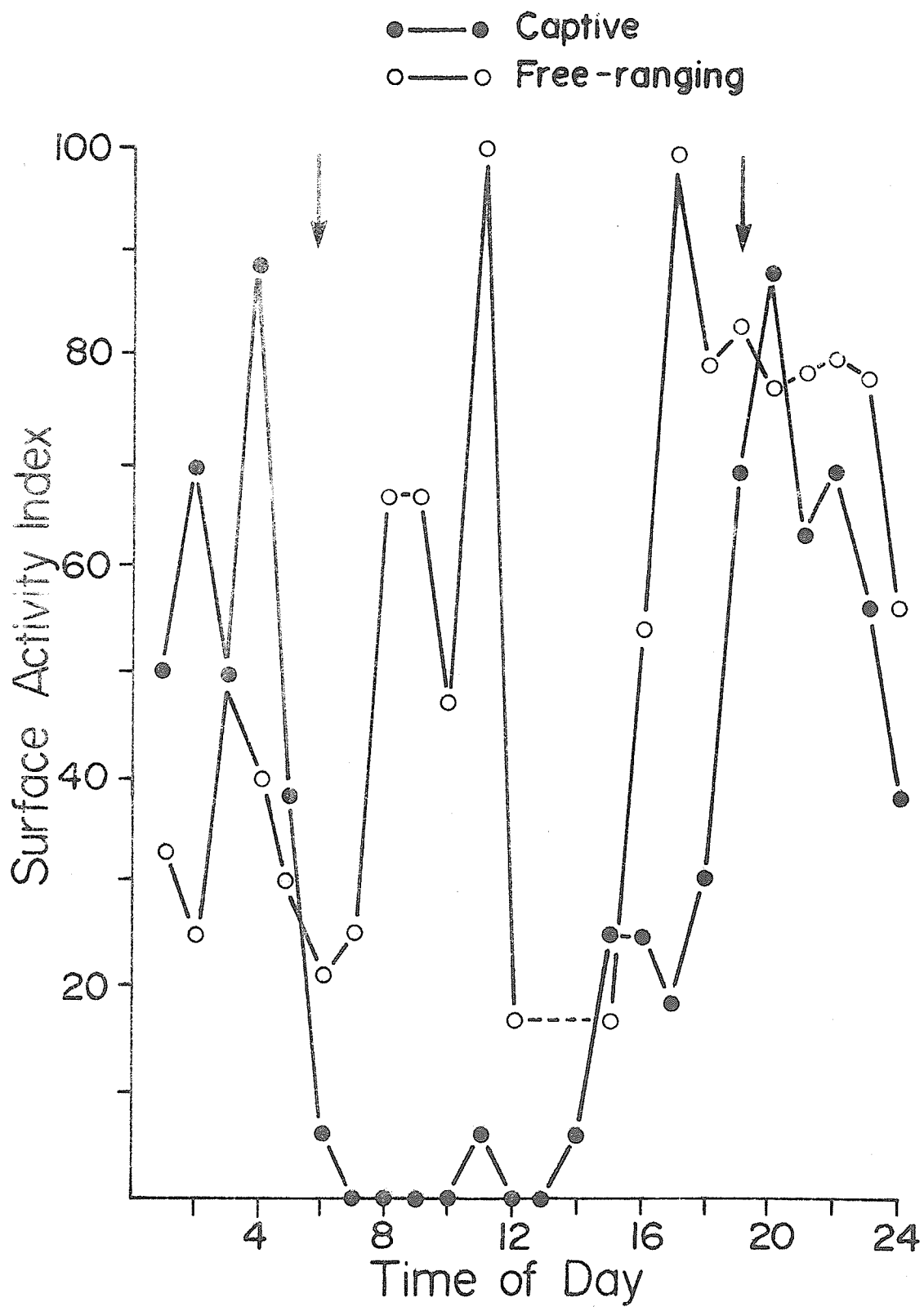


Fig. 3. Diel patterns of surface activity of captive and free-ranging male striped skunks at Delta Marsh, Manitoba in September. The activity index represents the number of observations of active skunks made in each monthly or weekly period, expressed as a percentage of all observations made. Sample sizes and numbers of hourly observations made are presented in Appendix 2. The arrows represent sunrise and sunset times at mid-month.



increase in the activity of captive skunks at this time. The adaptive significance of increased activity in late autumn is unclear. Following this temporary increase, activity indices fell to near zero in the third week of December. A snowfall of 14 cm on 22 December drifted to a depth of 35 cm in the enclosures. After this snowfall the captive animals' surface activity fell to virtually nil. Except for very brief (5 m or less) nocturnal excursions by three animals in early January, above-ground activity was not observed until 28 February (Fig. 1). Three brief bouts of activity were noted in the first 10 days of March. In late March and early April, following a 30 cm snowfall and drop in ambient temperatures, above-ground activity again ceased (Fig. 1). In the second week of April all animals resumed surface activity. Individuals were generally active for only brief periods at this time: bouts of surface activity, generally of only a few minutes duration, were usually followed by a retreat to the den for several hours. Activity was primarily nocturnal, although some diurnal activity occurred as well (Appendix 2). This daytime activity increased as April progressed until by the end of the month

most individuals were active at least once during each diurnal period. Diurnal activity decreased in May as nocturnal activity indices increased (Appendix 2).

On the basis of these indices of above-ground activity, four seasonal activity patterns are apparent. In summer - May to September inclusive - activity indices were at or approaching 100% during the hours of darkness and near 0% during daylight, except for free-ranging skunks in September. In autumn - October, November and early December - hourly activity indices progressively decreased to zero. In winter - late December to early March - skunks were almost totally restricted to their subterranean dens. The animals emerged from these retreats in spring (late March and April), and both nocturnal and diurnal activity indices increased as the season progressed.

Although significant differences were not present in the diel activity indices (the sum of hourly indices divided by 24) of captive and free-ranging skunks (Table 1), values were slightly lower for the captive individuals in all months when both forms of data were available (Appendix 2). This difference was greatest in September.

Kavanau and Ramos (1975) propose that the activity phasing of captive animals is the best index of true light-level preferences. The higher diel activity indices of free-ranging skunks possibly reflects the fact that such animals required longer to fulfill their feeding needs than the captive animals did. Free-ranging skunks often travel considerable distances between resting sites and foraging areas (Verts, 1967). September is the last month when the skunk's foods are readily available, and rapid increases in body weight occur during this period (Verts, 1967). While captive animals fed ad libitum can easily fulfill their high food-intake requirements during darkness, free-ranging skunks may often be unable to do so, thus necessitating the high level of diurnal activity in September.

The results of field studies on the striped skunk are in agreement with observations of activity patterns made in the present study. Verts (1967) found a high (88.8%) activity level in juvenile skunks between sunset and sunrise during summer and fall. Storm (1972) observed skunks leaving their underground retreats shortly after sunset in summer. He found movement in 86.8% of nighttime records of skunks, but

only in 0.6% of diurnal observations. Houseknecht (1971) made similar observations on skunk activity patterns. The male striped skunk may therefore be considered a typical nocturnal mammal in summer. The activity patterns of many mammalian species have also been observed to follow the changing light intensities of natural and artificial twilights (deCoursey, 1960; Berner and Gysel, 1967; Kavanau and Ramos, 1972, 1975; many others).

A reduction in activity and decreased regularity in the times of initiation and cessation of activity were found in the autumnal activity patterns of individual skunks. Skunks became almost strictly nocturnal at that time, although times of sunset and sunrise no longer appeared to have a controlling influence on times of starting and stopping activity. Similar changes in autumnal activity have been noted for free-ranging skunks by Verts (1967), Houseknecht (1971) and Sunquist (1974), and by Aleksasuk and Stewart (in prep.) for captive animals. These authors all noted some diurnal activity, however.

In September and October three of the four captive animals studied often did not seek refuge in their dens when inactive. These individuals

were frequently observed sleeping at the entrances to their dens or in the above-ground resting sites (inverted boxes), regardless of weather conditions at this time. Unusually mild weather may have extended this period past the time when dens would normally be used in colder autumns. It was not until November that the captive skunks were observed to use their nest chambers regularly and to carry quantities of shredded grass into their dens. After mid-November the nest chambers were well-insulated with nesting materials and tunnel entrances were kept plugged on most occasions when the animals were in their dens.

Several authors have speculated that ambient temperatures are an important factor controlling autumnal activity in skunks (Hamilton, 1937; Selko, 1938; Storm, 1972), but apparently this was not the case in the present study. Between 27 November (when food was no longer available) and 22 December (when the first major snowstorm occurred) the number of captive animals active each night did not correlate with ambient temperatures ($p < 0.05$, Table 2). Activity indices decreased in October and November despite the availability of food. Aleksasuk and Stewart (in prep.) found that captive skunks fed

Table 2. Relationships between activity of striped skunks and ambient temperatures (T_a), expressed as correlation coefficients (r).

Variables:	n	r
(1) Daily percentage of artificial dens showing activity, and daily T_a minima, 27 November to 22 December 1974.	5 dens, 16 days	0.17
(2) Daily percentage of artificial dens showing activity, and daily T_a maxima, 27 November to 22 December 1974.	5 dens, 16 days	0.24
(3) Daily percentage of natural dens showing evidence of activity, and T_a minima from 1 March to 10 April 1975.	11 dens, 29 days	0.50*
(4) Daily percentage of artificial dens showing evidence of activity, and T_a minima from 1 March to 10 April 1975.	5 dens, 29 days	0.72*
(5) Mean weekly percentages of artificial dens showing surface activity, with mean weekly T_a minima from third week of October 1974 to 30 April 1975.	5 dens, 26 weeks	0.87*
(6) Mean weekly percentages of artificial dens showing surface activity, and mean weekly T_a minima from third week of October 1974 to 30 April 1975.	11 dens, 26 weeks	0.84*
(7) Percentage of natural dens showing evidence of activity, and percentage of artificial dens showing evidence of activity, 1 March 10 April.	29 days	0.67*

* $p < 0.01$

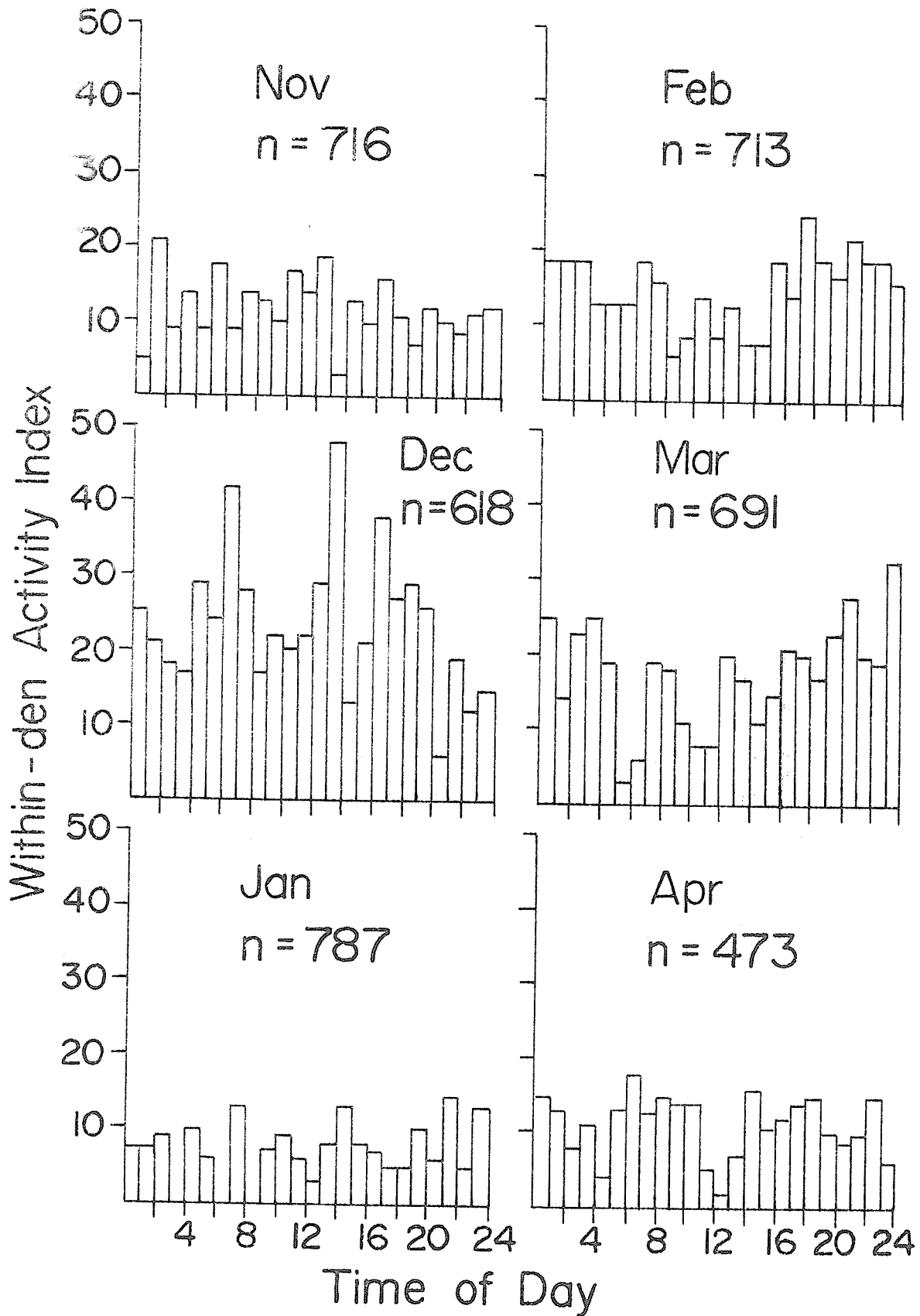
ad libitum gradually became hypophagic between October and mid-December. These apparently endogenously controlled decreases in activity and food consumption indicate that skunks are probably physiologically prepared for winter dormancy prior to the onset of lethargy. Possibly, upon attaining a specific weight or state of obesity the individual may require only the stimulus of cold, snow and/or some other factor(s) to initiate its winter inactivity. Similar decreases in activity and food consumption under favourable conditions in autumn have been described for other species, including the Richardson's ground squirrel (Spermophilus richardsonii) (Pengelley and Fisher, 1963; Mrosovsky and Barnes, 1973), the black bear (Matson, 1946) and the beaver (Castor canadensis) (Aleksiuk and Cowan, 1969). Craighead and Craighead (1970, 1972) describe a great reduction in activity and awareness, which they term "prehibernation lethargy", which may occur in the grizzly bear in late autumn. A heavy snowfall has been suggested as the stimulus that causes both grizzly bears (Craighead and Craighead, 1970, 1972) and raccoons (Mech, et al. 1966) to enter their dens. In the present study, surface activity ceased for 14 days following the first heavy snowfall.

Captive skunks provided with food ad libitum continue to show some activity outside their nest boxes for the entire winter, although activity is greatly decreased during the coldest months (Aleksiuk and Stewart, in prep.). In the present study, unfed captive skunks were totally inactive for extended periods in winter. Intensive and systematic searches failed to reveal any indications of activity by free-ranging skunks between late December and early March. Other investigators found free-ranging skunks to be primarily inactive in winter (Hamilton, 1937; Selko, 1938; Verts, 1967; Houseknecht, 1971; Sunquist, 1974). In contrast to the hiemal inactivity of unfed, northern skunks, free-ranging skunks in the southern portions of the species' range remain active for the entire year (Cuyler, 1924; Stout and Sonenshine, 1974). The sporadic resumption of surface activity between 1 March and 10 April was positively correlated with ambient temperature. The daily percentage of both 11 natural and five artificial dens showing evidence of skunk activity was significantly correlated with diel temperature minima ($p < 0.01$, Table 2). An example of this apparent relationship between weather and surface activity at that time of year occurred in

late March 1975. A 30 cm snowfall followed by a period of exceptionally low ambient temperatures coincided with an almost total cessation of surface activity by both captive and free-ranging skunks for a period of about one week. Activity resumed in the second week of April (Fig. 1). The mating season occurs at the same time as this spring resumption of above-ground activity (Wight, 1931; Hamilton, 1963; Verts, 1967). Free-ranging skunks in the present study often visited several dens in the course of a night's wanderings in March and April.

Activity patterns within the nest chambers followed no readily discernible diel pattern (Fig. 4). The skunks had the lowest indices of within-den activity in January and the highest in December. A one-way analysis of variance indicated no significant differences among the mean levels of within-den activity of the individual skunks except in March (Table 1). Comparisons among the combined within-den activity levels of the four individuals showed that these levels did not differ significantly between March and December, March and February, and April and November. Only rarely did a 24-hour period pass without movement being recorded for each individual.

Fig. 4. Activity of four male striped skunks within subterranean nest chambers, plotted on an hourly basis. The activity index represents the percentage of all observations during which activity in the nest chamber was detected, calculated on a monthly basis. The n values represent the total number of observations made in each month.



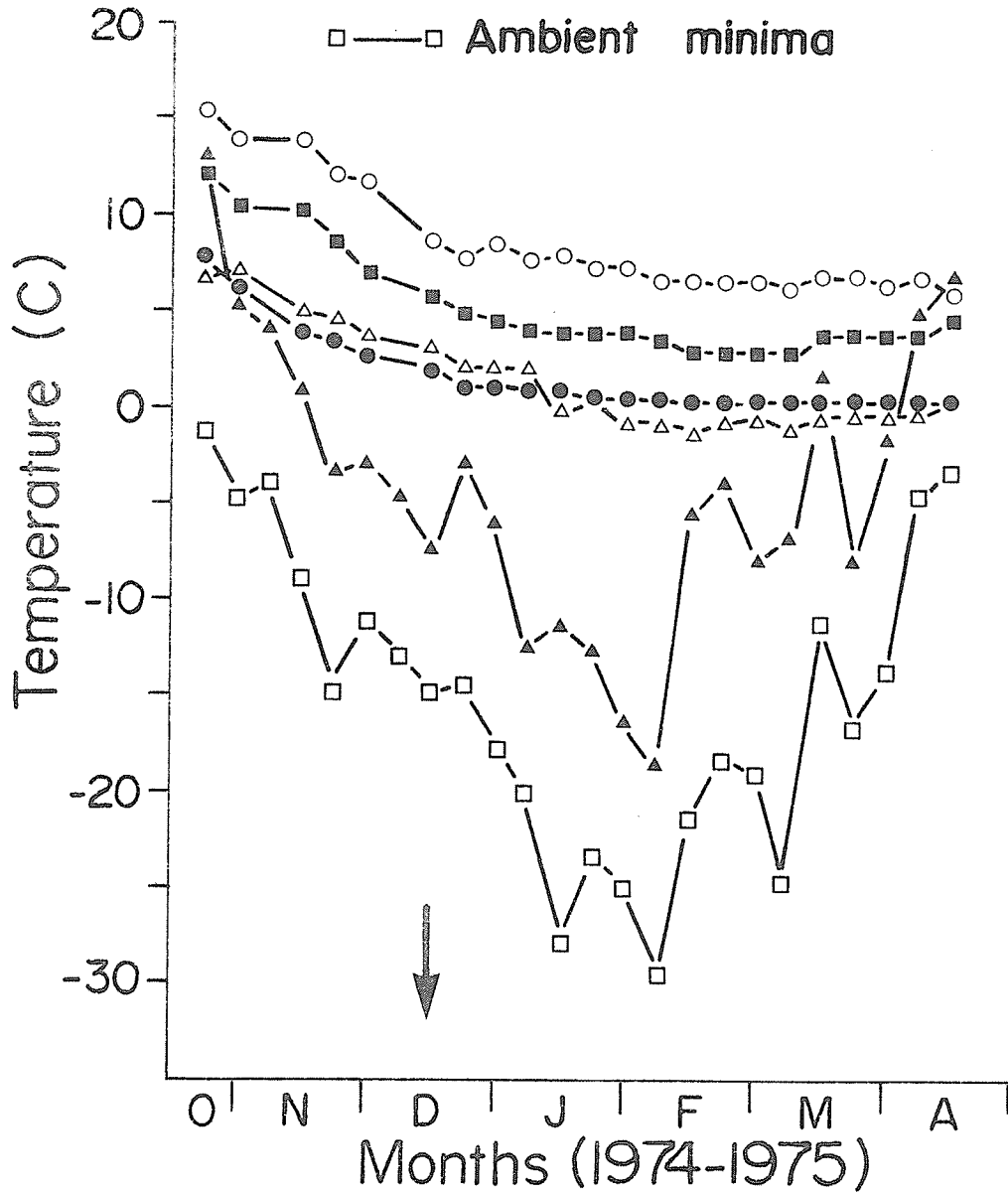
These data are in apparent contrast to those of Sunquist (1974). He utilized continuous tone, collar-mounted transmitters and automatically recorded the signals at 45 sec intervals. His data indicated that movements of skunks within natural winter dens followed a pattern similar in diel periodicity to above-ground activity during summer. While confined to winter dens, 70 and 77% of the in-den activity of adults and juveniles respectively occurred at night, with peaks in apparent association with the time of sunset. A general lack of synchronization of within-den activity between individuals was evident (Sunquist, 1974). It is not known why the data from the two studies are so dissimilar.

Temperatures of Simulated Dens

The simulated dens provided the captive skunks with a relatively warm micro-environment (Fig. 5). The temperatures of the dens were very constant during the period when the dens were covered with snow. Soil temperatures at a depth of 90 cm reached a winter minimum of -1.0°C . The lowest temperature

Fig. 5. Temperatures of artificial nest chambers, soil temperatures at 90 cm depth near the nest chambers, and maximum and minimum ambient temperatures, for the period October 1974 to April 1975. Each den and soil temperature is the mean of 24 consecutive hourly readings; all ambient maxima and minima are weekly means of daily values. The arrow indicates the start of the period of permanent snow cover.

- Den with two skunks
- Den with one skunk
- △—△ Soil at 90 cm depth
- Empty (control) dens
- ▲—▲ Ambient maxima
- Ambient minima



recorded in an unoccupied control den was -0.3°C . The minimum temperature in a den occupied by one skunk was 2.1°C , and the lowest weekly mean for such a den was 2.7°C . A one-way analysis of variance indicated that temperatures of dens occupied by single skunks were not significantly different ($p > 0.01$). The weekly mean temperatures of these dens were considerably higher than those of the two control dens and lower than those of the den occupied by two skunks (Fig. 5). Before permanent snow cover was present, weekly mean temperatures of the soil at 90 cm depth, control dens and dens occupied by one skunk all were positively correlated ($p < 0.01$) with weekly mean ambient temperature minima. While snow cover was present there was no significant correlation ($p > 0.05$) between ambient temperatures and the temperatures of the soil and dens listed above. Soil temperatures at a depth of 90 cm at the enclosure site and in the preferred denning area of free-ranging skunks were similar (Appendix 4).

Body Temperature Dynamics

Significant seasonal changes were found in the body temperature (T_b) dynamics of confined male striped skunks (Figs. 6, 7). Abdominal body temperatures had similar diel patterns in both individuals studied in August (Fig. 6). T_b began to rise from its constant daytime levels in late afternoon, prior to the resumption of outside activity. A peak in T_b occurred at about midnight after which T_b declined to a minimum between 0900 and 1200 h. Diel ranges in T_b varied between 1.0 and 2.2°C, with a mean range of 1.6°C. The maximum T_b recorded was 39.0°C while the minimum was 36.2°C. The mean of 264 readings was 37.7°C. A similar diel pattern was observed in free-ranging beavers by Aleksjuk (in press).

Although T_b values were lower in November, diel patterns were similar to those of August. T_b generally rose from about 35.5°C to about 36.5°C between 1500 and 2000 h, and then usually remained constant until about midnight. After midnight an irregular decline took place until 0700 to 1100 h, with T_b declining to as low as 34.0°C. A slight increase was followed by relatively stable temperatures until T_b again began to increase in late afternoon. In November, T_b ranged between 34.0 and 38.0°C. The mean of 192 readings on three animals was 36.4°C.

Fig. 6. Selected diel patterns of abdominal body temperatures in male striped skunks held in confinement under outdoor conditions at Delta Marsh, Manitoba. (A) illustrates the patterns for two individuals in August 1975, while (B) illustrates the patterns for three individuals in January 1975. Details of variation are given in the text and in Fig. 7.

Abdominal Body Temp. (C)

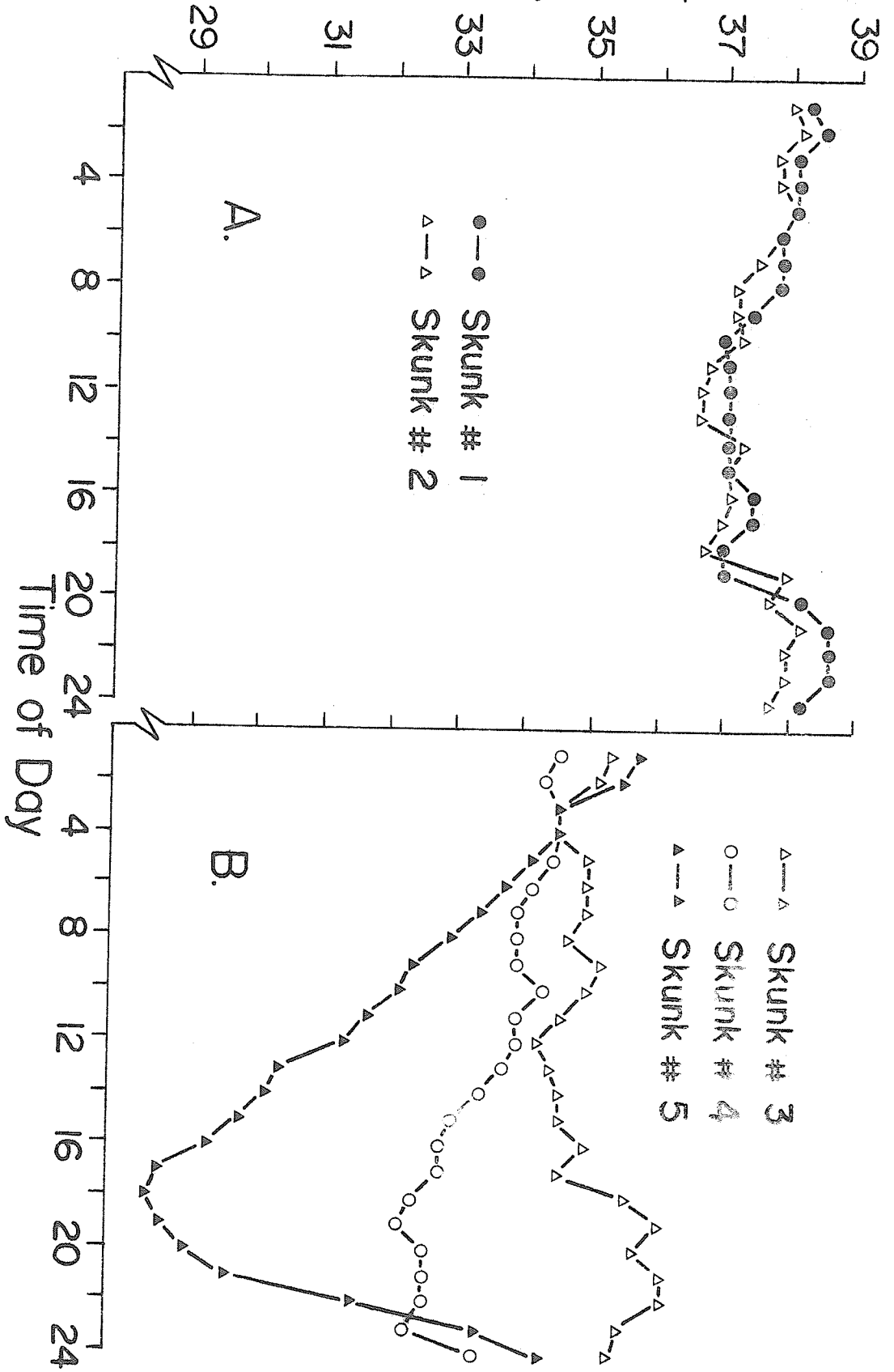
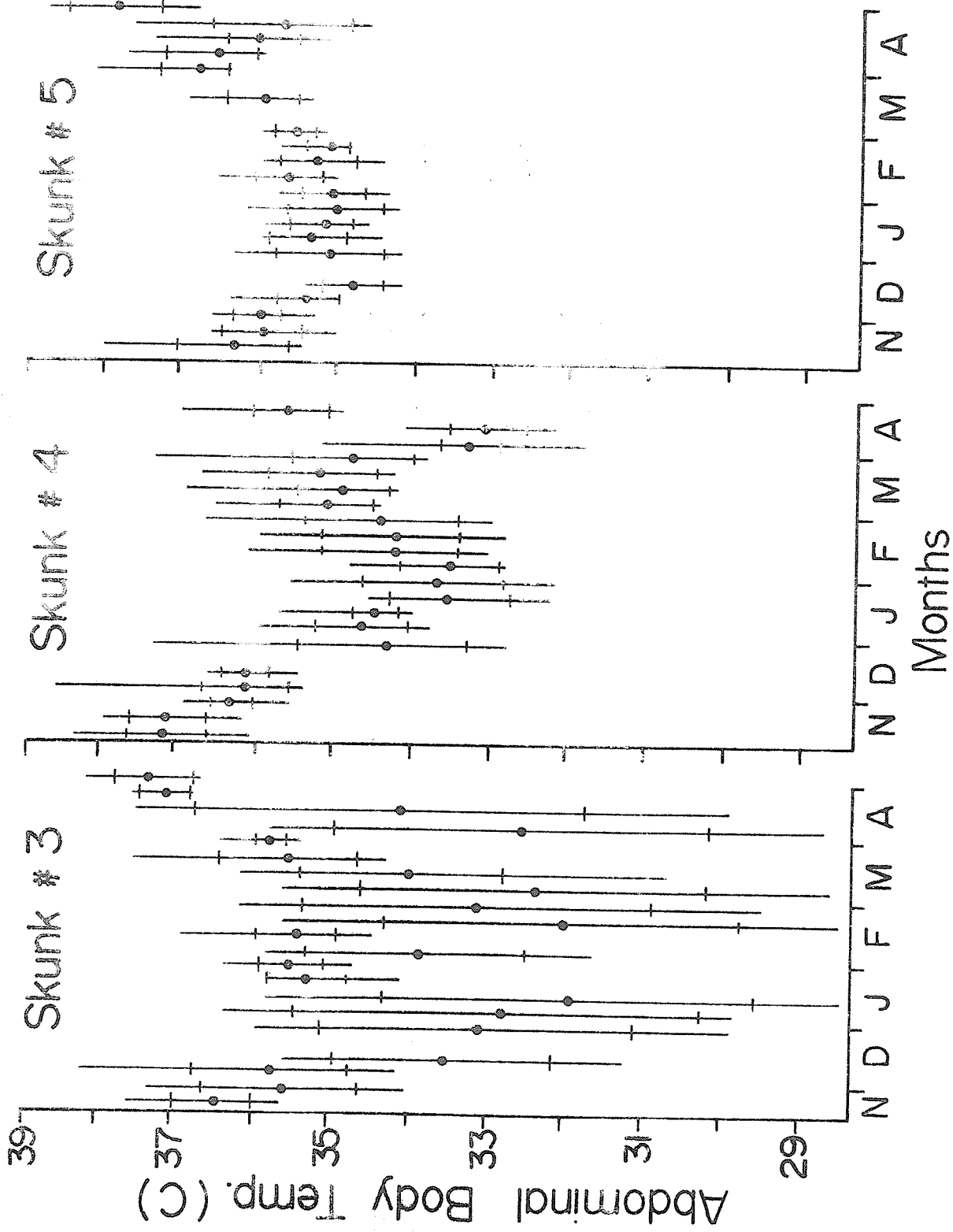


Fig. 7. Diel ranges (vertical lines) and means (closed circles) \pm one S.D. of the mean (brackets) of abdominal body temperature in three male striped skunks held in confinement under outdoor conditions during the period of natural dormancy at Delta Marsh, Manitoba. The means are of 24 consecutive hourly readings and are plotted at approximately weekly intervals.



Body temperatures were most variable in winter (Figs. 6, 7). In almost all cases studied a distinct diel T_b cycle was present in each of the three individuals monitored, although the timing of diel maxima and minima varied widely both between individual animals on the same day and for the same animal on different days. An example of the diel T_b pattern of each of the three captive skunks in January, illustrating the lowest T_b reached by each animal in that month, is presented in Fig. 6. T_b maxima in winter generally occurred in hours of outside darkness. Skunk No. 3 showed the greatest variability in T_b , with a daily amplitude of up to 7.2°C . That individual's T_b began to increase from the diel minimum at about 1800 to 2000 h on most days, rising at a rate of up to 2.2°C per hour. After a diel T_b maximum was reached, generally at about 0300 h, a two or three hour period of constant T_b often occurred. This was followed by a steady decrease in T_b until the evening increase began. Even though the other individual skunks underwent smaller diel variations in T_b , the pattern was frequently quite similar (Fig. 6). The data strongly suggest an endogenous circadian rhythm in body temperature may exist in skunks confined to their underground dens during winter. Further research is necessary to ascertain whether or not this is the case.

Diel T_b ranges were often highly variable on a week-to-week basis (Fig. 7). Skunk No. 3, an adult, showed the greatest variability. Although diel minima varied between 28.4 and 34.6°C in the mid-December to mid-March period, diel maxima remained relatively constant between 35.6 and 37.0°C during this same time. Increases in T_b accompanied the sporadic surface activity in the latter half of March. In early April the diel T_b minimum dropped to 28.6°C. With the resumption of regular surface activity in mid-April, T_b increased and remained within the 36.6 to 38.2°C range.

Appreciable, but less dramatic, diel fluctuations in T_b occurred in the other transmitter-implanted skunks (Fig. 7). The daily T_b minima of Skunk No. 4, a juvenile, progressively decreased to 32.2°C during December and January, and then gradually rose to 34.2°C during February and early March. Although this animal had not shown surface activity prior to the end of March, the inclement weather at that time coincided with a sharp drop in the individual's T_b minimum, to 31.8°C. Animal No. 5, an adult, had the smallest winter depression in T_b as well as the least diel variation. Following initial small declines, its T_b remained

stable before rising through late February and March. A small decline in early and mid-April was followed in late April by an increase to the T_b levels found in skunks in August. Body temperature readings ranged between 28.4 and 37.4°C for the three captive individuals between mid-December and mid-March. The mean of 840 readings on the three individuals during this period was 34.4°C.

By late April T_b values were similar to those of August (Figs. 6, 7), although the diel patterns tended to be less predictable. The range of T_b values for three skunks on 30 April was 2.2°C (between 36.6 and 38.8°C). The mean of 72 readings on three individuals was 37.7°C.

The minimum T_b recorded in this study, 28.4°C, is lower than has been reported for other species that undergo carnivorean lethargy. The lowest T_b previously noted for a member of this group under natural conditions was 31.2°C in the black bear (Hock, 1957, 1960).

Numerous other reports on both black and grizzly bears place their T_b 's at 34 to 37°C during winter dormancy (Erickson and Youatt, 1961; Folk, 1967; Folk, et al. 1970; Brown, et al. 1971; Nelson, et al. 1973).

Raccoons have been recorded at 35°C (Thorkelson and

and Maxwell, 1974) and European badgers at 35.5°C (Johansson, 1957). The skunk T_b 's recorded in winter during the present study were frequently lower than the values from these other species. Because of surface/volume ratios and pelage thickness differences, Fourier's Law of Animal Cooling (Kleiber, 1972) predicts that heavier, better-furred animals in "hibernation" could be expected to have a larger body temperature - ambient temperature gradient than smaller animals. Species such as the skunk might thus be expected to cool to a lower point than the raccoon, the badger and especially the bears (Morrison, 1960; South and House, 1967).

Energy Reserves for the Winter Period

Like true hibernators and many other mammalian species inactive for the winter (Kayser, 1961), skunks become obese by October (Table 3). Skunks are not known to store food for the winter and apparently subsist on internal stores of energy during the entire winter period when feeding either occurs very rarely or not at all. Studies on other mammalian species that pass the winter with little or no food intake indicate that depot fat reserves provide almost the entire winter energy supply (Kayser, 1961; Nelson, et al. 1973, 1975).

Table 3. Fat content of adult male striped skunks at Delta Marsh, Manitoba in autumn and spring, with a comparison of the energy contained in the available fat and the theoretical basal metabolic energy requirements during the dormant period (140 days). All figures are means \pm standard errors of the means.

n	Autumn 1974	Spring 1975
	5 adults	5 adults
Collection dates	3-27 October	24 April-4 May
Live weights (g)	3769 \pm 191	2584 \pm 209
Dry weights (g)	1903 \pm 111	884 \pm 59
Water (% live weight)	46.7 \pm 1.4	64.3 \pm 2.0
Dry, fat-free weight (g)	694 \pm 16.2	629 \pm 49.1
Weight of fat (g)	1208 \pm 97	258 \pm 47
Fat (% live weight)	31.9 \pm 1.3	10.1 \pm 2.1
Kcal available in stored fat	11236 \pm 902	2370 \pm 436
Calculated daily basal metabolic requirements (kcal) at fat-free weight	142 \pm 4.6	-----
Energy available as fat expressed as a percentage of energy required for existence at BMR for 140 days	56.5 \pm 1.5	-----

The fat content of skunks killed in fall and spring differed markedly (Table 3). In autumn, skunks had a much higher percentage of live body weight as fat and a lower percentage as water than in spring. Mean dry, fat-free body weights and weights of body water did not differ significantly between specimens killed in October and in April and May (Student's t-test, $p > 0.05$; Table 3). Mammalian white fat has a caloric content of 9.3 kcal per gram (Dargol'ts, 1974). The skunks analysed in October had a mean of 11,236 kcal as fat, while animals killed in spring had 2,370 kcal as fat (Table 3). Assuming that the skunk's basal metabolic rate (BMR) can be accurately predicted by standard formulae (Kleiber, 1961), then the theoretical BMR's of skunks killed in October may be calculated, based on their fat-free weights. A comparison of the energy available in the fat reserves with these predicted BMR requirements for an aphagic period of 140 days reveals a shortage of 44% (Table 3). Therefore, some mechanism(s) for energy conservation must be employed during the winter period in order to reduce utilization to a rate well below the theoretical basal metabolic rate.

CONCLUDING REMARKS: A Strategy of Winter Survival

The energy reserves of the striped skunk in October are not adequate to allow it to subsist through the winter at a level of energy utilization equivalent to its predicted basal metabolic rate. Morrison (1960) has suggested that it would be impossible for an animal of the skunk's size to store enough fat to enable it to survive an aphagic period such as is experienced during the winter in southern Manitoba, without some decrease in its metabolic rate. The results of the present study suggest that the skunk has several adaptations which significantly reduce the rate of energy utilization between late autumn and early spring.

The skunk undergoes profound behavioural modifications during fall, winter and early spring. By greatly reducing surface activity, the skunk conserves energy that it would otherwise expend on locomotion. In laboratory rats, 24% of energy usage is for locomotion (Morrison, 1968). Corresponding figures for steers are 15 to 25% (Benedict and Ritzman, 1923) and for Peromyscus, 20% (McNab, 1963). Apparently the skunk may reduce energy expenditure by up to 25% by greatly reducing surface activity. In addition to the

energy which the skunk would have used for locomotion per se, activity in the cold supranivean environment would undoubtedly necessitate an increase in metabolic rate for thermoregulation. The skunk is poorly adapted for activity in the extreme cold. Its appendages and belly are very thinly furred. The back fur is coarse and easily blown by the wind, resulting in a great potential for heat loss (Tregear, 1965; Moen and Jacobsen, 1974). Even in calm weather, exercise may have deleterious effects on temperature regulation due to decreases in the effectiveness of the pelage as insulation. Furthermore, heat produced for thermoregulation tends to be independent of that produced by work (Hart and Heroux, 1955). Such heat losses, and consequent energy expenditures, are avoided by the skunk's retreat to a subterranean den. Thus, the den conveys the advantage of a relatively warm microhabitat, even if occupied by only one skunk. Free-ranging skunks frequently den communally. Seton (1926) recorded up to 20 individuals in one large den, and smaller aggregations are very common (Hamilton, 1937; Allen, 1939; Allen and Shapton, 1942; Dean, 1965; Shirer and Fitch, 1970; Houseknecht, 1971; Sunquist, 1974). The very significant energy savings

from the use of a nest as well as from the decrease in effective surface area by huddling have been well-documented for various species of rodents by Kinder (1927), Prychodko (1958), Pearson (1960), Hayward (1965), Tertilt (1972) and others. Such benefits may also be expected to accrue to the denning skunk.

A second major aspect of winter dormancy in the skunk is the depression in body temperature. If the mean of 312 April and August body temperature measurements, 37.7°C , is taken as the "normal" body temperature of male striped skunks, then the mean of 840 mid-December to mid-March readings, 34.4°C , represents a mean winter T_b depression of 3.3°C . The mean T_b depressions of individual animals varied between 2.4 and 4.1°C . The range between highest summer and lowest winter T_b 's is 10.6°C . Hock (1960) found that the metabolic rate of a lethargic black bear with a probable T_b depression of 4 to 7°C was 50 to 60% of the normothermic rate. Folk, et al. (1970) recorded a 71 to 90% decrease in the resting heart rates of dormant black bears between September and December, accompanied by a 4°C drop in T_b . These data indicate that profound decreases in metabolic

rate accompany small decreases in T_b of lethargic bears. Skunks, which undergo similar decreases in body temperature, can similarly be expected to have significant reductions in metabolic rate and therefore energy expenditure.

The winter is a critical period in the skunk's annual cycle of life in northern regions. In order to survive the winter, the skunk has evolved a clearly defined strategy. In summary, the first aspect of this strategy is the accumulation and storage of energy in the form of fat during summer and early fall when food supplies are plentiful and weather conditions favourable. This is followed by a prolonged aphagic period during which energy expenditure is reduced by an almost total cessation of surface activity, a retreat to a relatively warm underground den and a depression in body temperature. This strategy enables the skunk to overwinter successfully at northern latitudes without resort to either winter feeding or true hibernation, and is an important element ensuring its survival over a very large boreal region.

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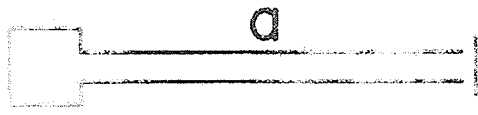
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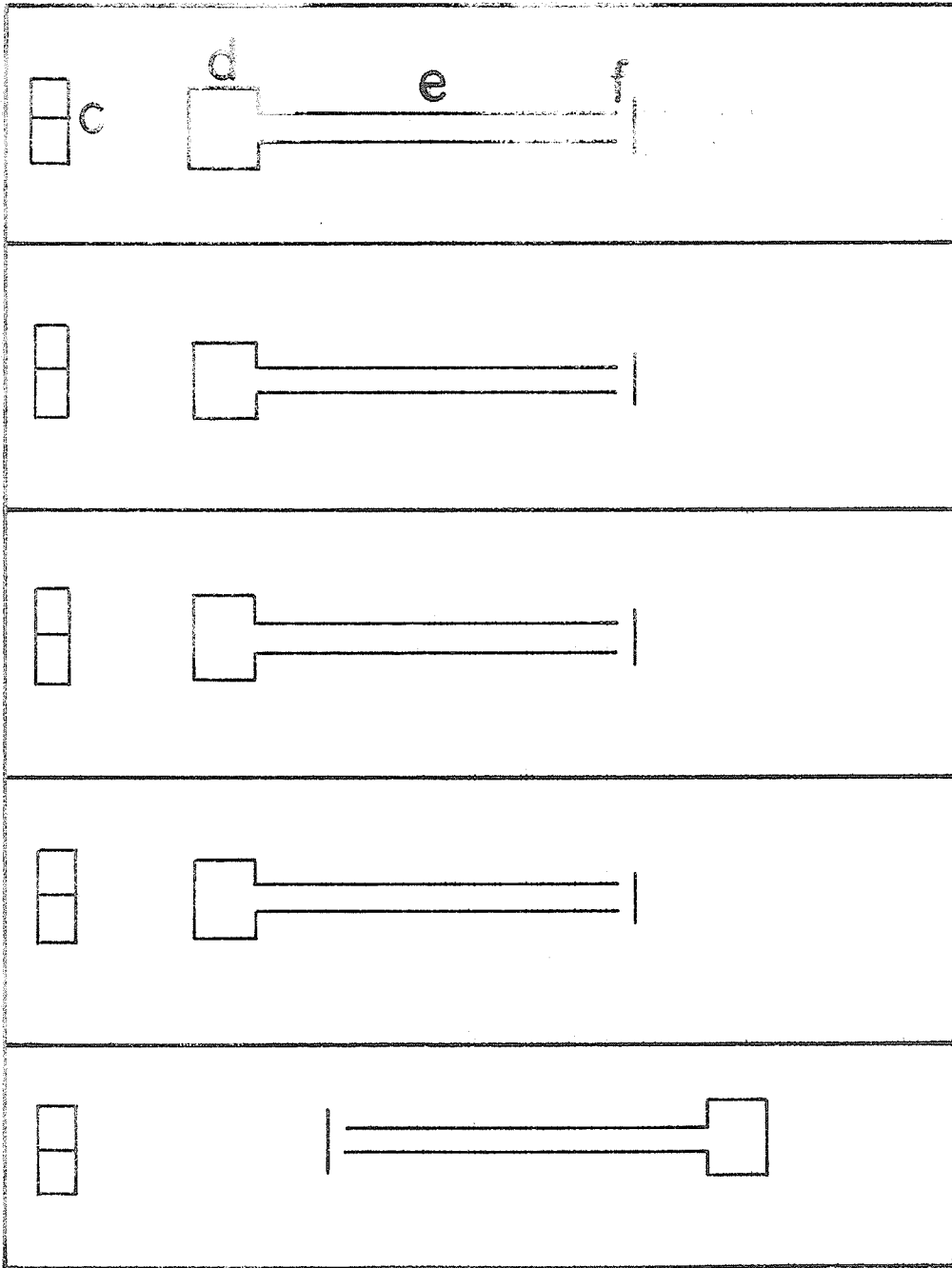
Appendix 1: Outline diagrams of artificial holding facility for striped skunks at the University Field Station, Delta Marsh, Manitoba.

Fig. 1. Digrammatic representation of artificial holding facility for captive striped skunks.

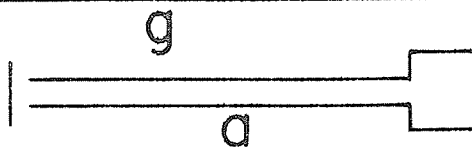
- Legend:
- a - control dens
 - b - walls of occupied enclosure constructed of 2.5 cm mesh poultry wire
 - c - food and water dishes
 - d - subterranean nest chamber
 - e - buried tunnel
 - f - cover over tunnel entrance
 - g - viewing blind
 - h - telethermometer probe, buried 90 cm deep in soil



b



● h



0.5m

Fig. 2. Diagrammatic representation of the subterranean nest chamber and tunnel system in the artificial holding facility for captive striped skunks.

Legend:

- a - soil surface
- b - cover over tunnel entrance
- c - buried tunnel
- d - subterranean nest chamber
- e - No. 18 copper wire
(auxilliary antenna)
- f - wire mesh side of nest chamber
- g - coaxial cable and TV antenna
lead wire running to AM radio
receiver in the laboratory
- h - telethermometer probe buried
90 cm in soil

Appendix 2: Numbers of captive and free-ranging male striped skunks studied each month in Delta Marsh, Manitoba, numbers of observations made per hour, and pooled percentage activity of captive and free-ranging skunks.

Table 1: Numbers of individual skunks (N) studied each month, total numbers of observations (n) in each hourly interval, percent hourly activity (activity index, %A) and 95% confidence intervals (95%CI) on each percent hourly activity index of male striped skunks held in outdoor enclosures at Delta Marsh, Manitoba.

Time CSR	January		February		March		April		May		June		July		August		September		October		November		December	
	N	%A (95%CI)	N	%A (95%CI)	N	%A (95%CI)	N	%A (95%CI)	N	%A (95%CI)	N	%A (95%CI)	N	%A (95%CI)	N	%A (95%CI)	N	%A (95%CI)	N	%A (95%CI)	N	%A (95%CI)	N	%A (95%CI)
01	33	0(0-11)	36	0(0-10)	36	0(0-10)	40	33(19-47)	10	70(35-93)	8	88(44-100)	12	100(83-100)	12	75(46-83)	16	50(25-74)	16	50(42-85)	39	36(22-51)	33	17(4-28)
02	36	0(0-10)	36	0(0-10)	36	3(2-23)	40	30(17-45)	9	56(21-90)	6	83(32-100)	14	86(62-100)	12	83(58-83)	16	69(42-86)	16	75(25-74)	31	23(10-42)	28	14(2-27)
03	36	0(0-10)	36	0(0-10)	40	3(2-20)	40	23(11-38)	8	75(29-98)	6	100(43-100)	14	50(25-66)	12	75(58-83)	16	50(25-74)	16	38(49-90)	35	29(15-45)	25	5(0-20)
04	32	0(0-11)	36	0(0-10)	36	3(2-23)	44	16(7-29)	7	43(10-93)	7	43(10-93)	14	50(25-66)	12	67(37-81)	16	88(64-94)	16	38(15-64)	32	15(6-33)	33	13(0-15)
05	34	0(0-11)	36	0(0-10)	36	0(0-10)	45	13(5-26)	11	22(3-51)	8	25(4-70)	14	7(0-32)	12	33(10-62)	16	38(15-64)	16	38(15-64)	35	17(7-33)	31	0(0-12)
06	36	0(0-10)	36	0(0-10)	36	3(2-23)	48	4(1-14)	6	33(5-93)	6	17(0-75)	14	0(0-22)	12	0(0-26)	16	6(0-30)	16	6(0-30)	31	6(1-21)	33	12(2-25)
07	36	0(0-10)	36	0(0-10)	36	0(0-10)	45	2(0-11)	7	17(0-67)	6	0(0-52)	14	7(0-32)	12	0(0-26)	16	0(0-21)	16	0(0-21)	34	0(0-11)	31	0(0-15)
08	36	0(0-10)	36	0(0-10)	36	0(0-10)	40	3(0-13)	8	0(0-39)	6	0(0-52)	14	0(0-22)	12	0(0-26)	16	0(0-21)	16	0(0-21)	39	0(0-9)	27	0(0-13)
09	44	0(0-8)	36	0(0-10)	40	0(0-9)	40	3(0-13)	7	14(0-67)	6	17(0-75)	13	0(0-24)	12	0(0-26)	16	0(0-21)	16	0(0-21)	35	0(0-11)	31	0(0-12)
10	32	0(0-11)	36	0(0-10)	44	0(0-8)	44	9(3-21)	5	0(0-62)	6	0(0-52)	12	0(0-26)	12	8(0-38)	16	0(0-21)	16	0(0-21)	42	0(0-9)	33	0(0-11)

Table 1 cont'd

Time	January	February	March	April	May	June	July	August	September	October	November	December
11 36	0(0-10)	40 0(0-9)	40 0(0-9)	44 7(1-18)	7 14(0-67)	8 0(0-39)	10 0(0-31)	12 0(0-26)	16 6(0-30)	16 0(0-21)	33 0(0-11)	29 0(0-12)
12 40	0(0-9)	36 0(0-10)	36 0(0-10)	43 2(0-12)	7 0(0-44)	8 0(0-39)	11 0(0-28)	12 0(0-26)	16 0(0-21)	16 0(0-21)	39 0(0-9)	32 0(0-11)
13 36	0(0-10)	36 0(0-10)	40 0(0-9)	41 5(1-16)	10 0(0-31)	8 0(0-39)	14 14(3-40)	12 0(0-26)	16 0(0-21)	16 0(0-21)	40 0(0-9)	32 0(0-11)
14 40	0(0-9)	40 0(0-9)	36 0(0-10)	46 7(1-18)	7 0(0-44)	8 0(0-39)	14 0(0-22)	12 0(0-26)	16 6(0-30)	16 0(0-21)	32 0(0-11)	36 0(0-10)
15 43	0(0-8)	40 0(0-9)	44 0(0-8)	58 2(0-9)	7 0(0-44)	8 0(0-39)	14 0(0-22)	12 0(0-26)	16 25(8-52)	16 0(0-21)	34 0(0-11)	41 0(0-9)
16 40	0(0-9)	40 0(0-9)	40 0(0-9)	46 2(0-11)	7 0(0-44)	10 0(0-31)	14 7(0-32)	12 0(0-26)	16 25(8-52)	16 13(2-38)	43 0(0-8)	53 0(0-7)
17 48	0(0-8)	48 0(0-8)	52 0(0-7)	60 8(3-18)	10 0(0-31)	8 0(0-39)	12 0(0-26)	12 8(0-38)	16 19(4-45)	16 0(0-21)	58 5(1-15)	56 2(0-10)
18 44	2(1-15)	44 0(0-8)	44 0(0-8)	64 6(2-15)	6 0(0-52)	8 0(0-39)	12 8(0-38)	12 50(22-73)	16 31(11-58)	16 13(2-38)	59 25(15-37)	49 8(1-17)
19 48	0(0-8)	40 0(0-9)	52 0(0-7)	59 5(1-14)	12 0(0-26)	8 13(0-57)	12 0(0-26)	12 50(22-73)	16 69(42-86)	16 50(25-74)	57 16(8-27)	48 5(1-14)
20 45	0(0-15)	56 0(0-6)	44 0(0-8)	60 27(20-44)	16 13(3-43)	8 25(4-70)	12 8(0-38)	12 58(29-78)	16 88(64-94)	16 31(11-58)	54 11(5-22)	52 2(0-11)
21 36	0(0-10)	36 0(0-10)	36 0(0-10)	54 57(44-69)	13 77(53-90)	9 67(29-98)	12 50(22-73)	12 75(46-83)	16 63(36-83)	16 44(20-68)	51 18(9-30)	43 8(1-19)
22 43	0(0-8)	52 0(0-7)	44 0(0-7)	50 42(28-57)	10 100(69-100)	8 100(55-100)	12 92(76-100)	12 67(37-81)	16 69(42-86)	16 44(20-68)	47 15(6-27)	43 3(0-12)
23 42	0(0-9)	36 0(0-10)	48 0(0-8)	48 42(31-54)	8 100(55-100)	8 100(55-100)	12 100(83-100)	12 58(29-78)	16 56(30-79)	16 38(15-64)	49 12(5-24)	46 8(1-18)
24 36	0(0-10)	36 0(0-10)	36 0(0-10)	48 33(21-45)	8 100(55-100)	8 88(44-100)	12 88(76-100)	12 92(76-100)	16 38(15-64)	16 69(42-86)	35 9(2-23)	39 9(2-21)

Table 2. Numbers of individual skunks studied (N) in each month, total numbers of observations (n) in each hourly interval, percent hourly activity (activity index, %A) and 95% confidence intervals (95%CI) on %A for free-ranging male striped skunks monitored by radio telemetry in Delta Marsh, Manitoba.

Time CST	May		June		July		August		September		October	
	N	1	N	3	N	2	N	2	N	2	N	1
01	7	86:37-100	5	100:38-100	8	75:33-100	7	86:37-100	3	33:0-100	-	-
02	7	86:37-100	7	100:50-100	8	100:55-100	4	75:18-100	8	25:4-70	-	-
03	7	86:37-100	12	92:56-100	7	100:50-100	7	86:37-100	8	50:15-93	2	50:0-100
04	7	86:37-100	15	47:21-73	8	100:55-100	9	89:49-100	10	40:12-74	-	-
05	7	71:27-100	3	0:0-100	5	20:0-56	15	80:52-96	13	31:24-61	-	-
06	8	50:15-94	2	0:0-100	-	-	17	47:22-75	17	21:59-92	1	100:0-100
07	6	0:0-52	1	0:0-100	1	0:0-100	4	50:8-100	8	25:4-70	3	33:0-100
08	5	20:0-56	1	0:0-100	-	-	-	-	9	67:29-98	-	-
09	5	20:0-56	1	0:0-100	-	-	-	-	9	67:29-98	1	0:0-100
10	4	25:0-100	-	-	-	-	-	-	17	47:22-51	-	-
11	6	0:0-52	-	-	4	25:0-100	-	-	4	100:43-100	2	0:0-100
12	6	0:0-52	10	0:0-31	1	0:0-100	-	-	6	17:0-75	-	-
13	7	0:0-42	4	0:0-78	-	-	1	0:0-100	-	-	2	0:0-100

Table 2 continued on page 68

Table 2 cont'd

Time CST	May		June		July		August		September		October	
	n	%A:95%CI	n	%A:95%CI	n	%A:95%CI	n	%A:95%CI	n	%A:95%CI	n	%A:95%CI
			1	3	2	2	2	2	2	1		
14	7	0:0-42	-	-	-	-	1	0:0-100	-	-	1	0:0-100
15	9	11:0-50	10	0:0-31	-	-	3	0:0-100	6	17:0-75	2	0:0-100
16	8	0:0-39	1	0:0-100	2	0:0-100	4	0:0-78	13	54:18-78	1	0:0-100
17	8	0:0-39	-	-	1	0:0-100	3	0:0-100	4	100:43-100	1	0:0-100
18	8	0:0-39	2	0:0-100	7	14:0-64	12	33:10-66	14	79:48-99	2	0:0-100
19	13	15:0-37	11	9:0-41	8	50:15-94	13	77:44-100	12	83:47-100	4	75:18-100
20	8	63:24-100	10	50:19-81	9	100:49-100	11	100:61-100	13	77:44-100	2	100:0-100
21	8	100:55-100	8	63:24-100	4	100:18-100	6	100:43-100	9	78:39-100	3	100:0-100
22	7	100:50-100	16	100:73-100	7	100:50-100	8	88:44-100	10	80:44-97	-	-
23	7	100:50-100	9	89:49-100	9	78:39-100	8	100:55-100	9	78:39-100	-	-
24	7	100:50-100	6	100:43-100	10	90:35-100	7	86:37-100	9	56:21-100	2	100:0-100

Table 3. Summary of weekly and monthly surface activity indices of male striped skunks at Delta Marsh, Manitoba. N is the combined number of captive and free-ranging individuals studied in each period indicated, n is the total number of observations made during each period, %A is the diel activity index (the sum of all combined hourly indices divided by 24) and 95%CI is the 95% confidence interval on %A.

Months	N	n	%A	95%CI
January*	5	352	1	0-2
	5	120	0	0-.3
	5	340	0	0-.2
February*	5	120	0	0-.3
	5	348	0	0-.2
	5	352	0	0-.2
March*	5	120	0	0-.3
	5	360	1	0-2
	5	120	1	0-5
April*	5	364	1	0-2
	5	120	1	0-5
	5	120	0	0-.3
May**	5	360	5	3-8
	5	248	17	13-22
	3	417	31	25-37
June**	4	378	36	31-41
July**	6	314	32	27-38
August**	6	407	31	27-35
September**	5	428	40	36-44
October**	6	595	36	33-39
November*	5	413	24	20-28
	5	120	20	12-28
	5	624	10	8-12
December*	5	120	4	1-9
	5	120	8	4-13
	5	120	13	8-19
	5	548	2	1-4
	5	120	0	0-.3
	5	120	0	0-.3

* Captive animals only

** Captive and free-ranging animals combined

Appendix 3: Circuit diagram for radio transmitter used in monitoring the activity of free-ranging striped skunks in Delta Marsh, Manitoba.

Fig. 1: Circuit diagram for radio transmitter used to monitor activity of free-ranging striped skunks. The transmitter is similar to that described by Seidensticker, et al. (1970).

Legend:

Antenna loop - A - 16 mm diameter brass welding rod encased in polyvinyl chloride tubing.

Loop diameter is 7 to 8 cm.

Capacitors - C_1 - 180, 220 pf

- C_2 - 10, 22 pf

- C_3 - 5, 6 mf

- C_4 - 0.01 mf

Resistors - R_1 - 220, 270 kohms

- R_2 - 1 kohm

Crystal - X - Citizen's Band frequencies (27.005 to 27.255 MHz)

Transistor - Q - 2N3694, M9568

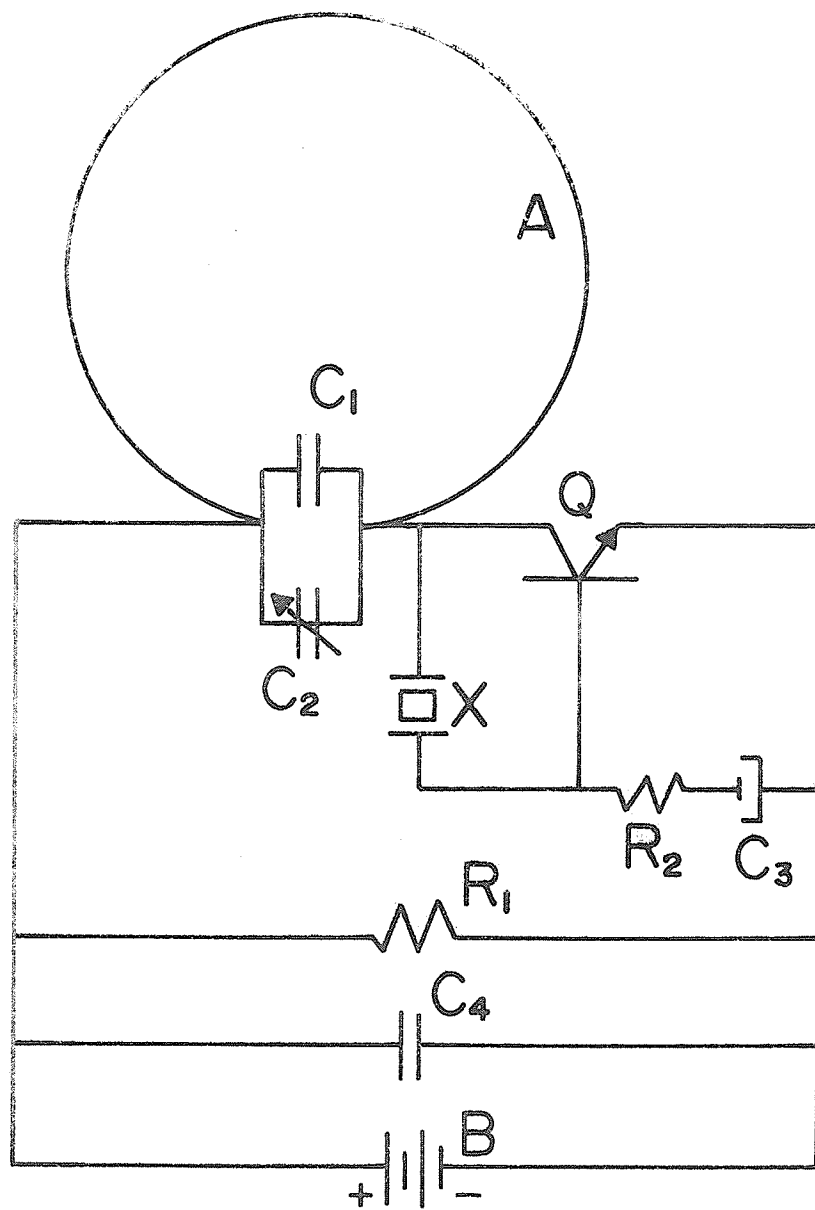
Battery - B - Mallory TR-133 (1.4 v, 1000 mah)

Literature cited: Seidensticker, J. C., IV, M. G.

Hornocker, R. R. Knight, and S. L. Judd.

1970. Equipment and techniques for radio-tracking mountain lions and elk.

Idaho Cooperative Wildl. Res. Unit, Forest, Wildl. and Range Exp. Station Bull. No. 6, 20 pp.



Appendix 4: Locations of winter dens utilized by
striped skunks in Delta Marsh, Manitoba.

Introduction

Burrowing mammals, both true hibernators and those which undergo carnivorean lethargy (Hock, 1960), must find and if necessary prepare a suitable den for occupancy during late fall, winter and early spring. A well-chosen den site under most conditions would theoretically be one which is in stable, well-drained soil in an area which does not flood in early spring and in which the nest chamber can be placed sufficiently deep to avoid freezing during winter. The present note describes the location of 19 dens used by striped skunks (Mephitis mephitis) in Delta Marsh, Manitoba, Canada during November and December 1973 and March and April 1975. Data on soil temperatures and snow conditions in the various areas utilized are also presented.

Methods

The study was conducted at the University Field Station, Delta Marsh, Manitoba on a strip of land extending about 2.5 km south from and paralleling the Lake Manitoba shore. Based on topography and vegetation, the area can be roughly subdivided into three sub-areas. The first, a 50 to 200 m wide sandy ridge parallel to the

lake shore, supports stands of Populus spp., Salix spp., Sambucus pubens, Acer negundo and other tree and shrub species, as well as an understory of dense herbs.

The second sub-area, marsh, has areas of open water (natural channels and man-made borrow pits) fringed with Typha latifolia and Scirpus spp. Sites subjected to prolonged seasonal flooding support Scholochloa festucacea and Phragmites communis, while drier meadows are covered with Agropyron repens, Hordeum jubatum, Sonchus arvensis, Cirsium arvense and Melilotus alba.

The third subdivision is a raised dike forming one side of the Assiniboine Floodway Diversion. The top of the dike is a gravelled road, while the sides are covered with a dense mixed stand of Bromus sp., Medicago sativa and Melilotus alba, which is sometimes mowed in summer.

Walker (1959) has described the vegetation of Delta Marsh in detail.

Soil temperatures were monitored weekly between late October and mid-May by means of telethermometer probes permanently buried to a depth of 90 cm into the soil at one site in each of the three sub-areas described above. The probes were at approximately the level of the October water table in the marsh, but somewhat above the water tables in the ridge and on the dike embankment. Snow depths were recorded weekly at each of 12 permanent snow stations in each habitat. Snow hardness was determined

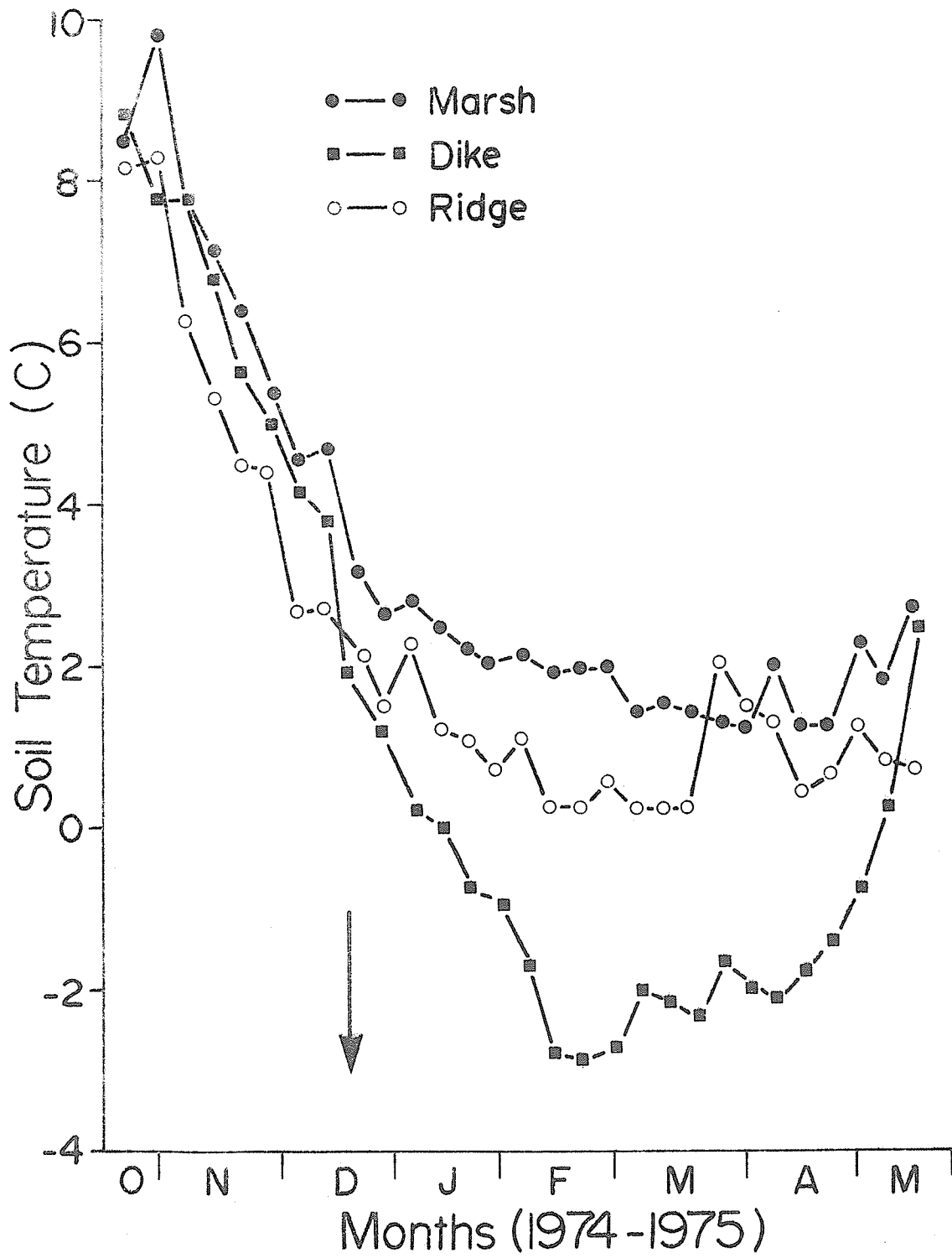
weekly at these same stations using a modified NRC snow kit apparatus to measure the pressure (in gm/cm²) required to compress the surface snow to a depth of 2 - 3 cm, or break the surface crust.

Occupied dens were found in November and December 1973 by tracking in the snow and looking for signs of fresh digging. Locations of occupied dens in March were determined by tracking the animals in the snow at the first signs of above-ground activity by skunks in early spring following the extended period of winter inactivity which individuals of the species undergo in this area.

Results

The changing temperatures of the soil at 90 cm depth in each of the three sub-areas are depicted in Fig. 1. All three locales experienced rapid declines in temperatures until the third week of December, when a heavy snowfall occurred. Following this snowfall, the rate of decline in the marsh soil temperature became very gradual. The soil temperature at 90 cm depth remained above 1°C for the remainder of the winter.

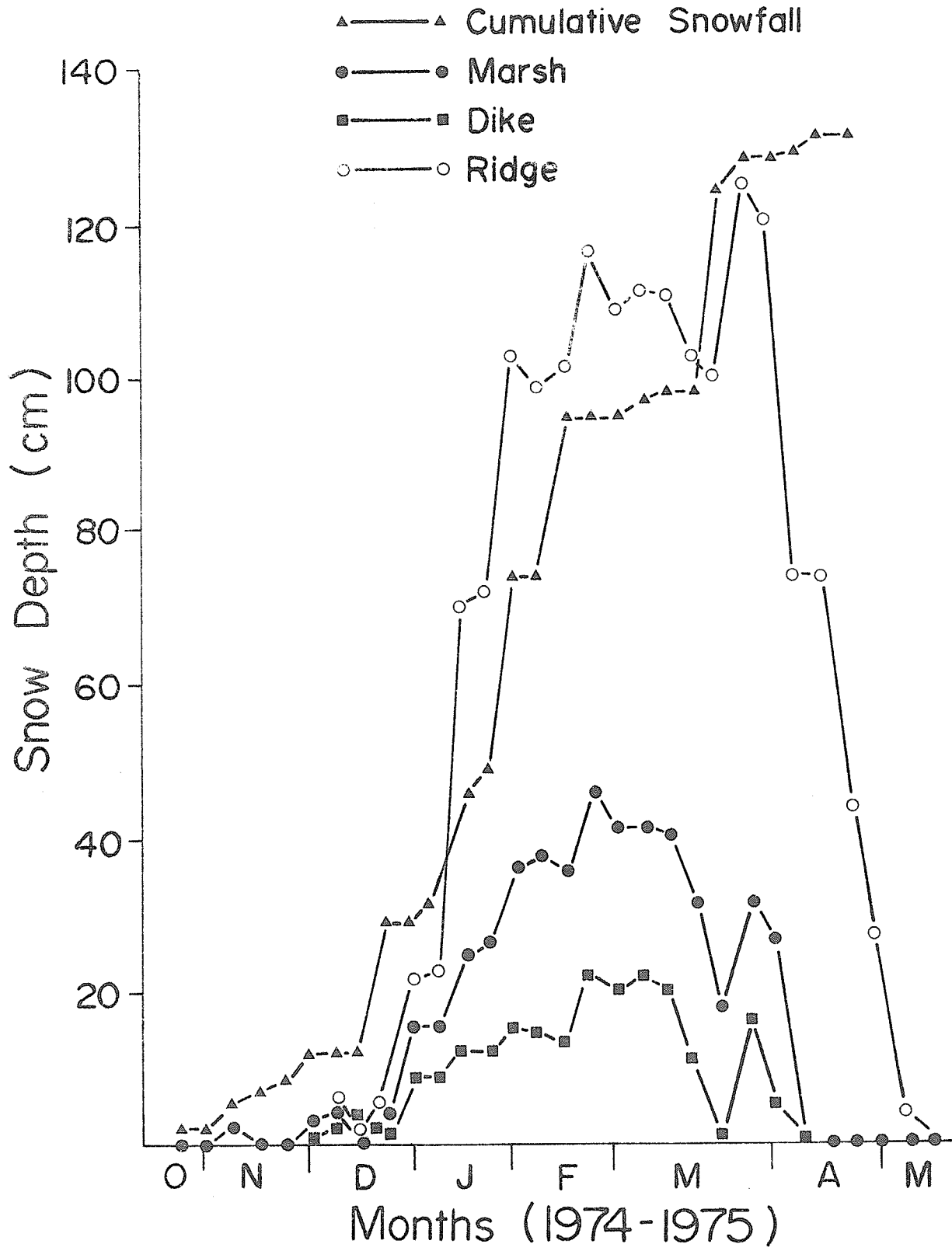
Fig. 1. Weekly soil temperature readings at 90 cm depth in the marsh, dike embankment and wooded ridge at Delta Marsh, Manitoba for the period October 1974 to May 1975. The arrow indicates the start of the period of permanent snow cover.



The warming of the soil at the site of the marsh probe in May was also very gradual. Soil temperatures in the sandy, wooded ridge followed a pattern similar to that in the marsh, although the soil at 90 cm depth was consistently about 1°C lower than in the marsh (Fig. 1). The lowest soil temperatures were found in the dike embankment, where declines to -3°C at 90 cm depth occurred in mid- to late February.

Snow depths varied considerably in the different areas (Fig. 2). The cumulative snowfall of 130 cm was subject to relatively little drifting in the marsh, where the vegetation tended to hold it in place. It was, however, subject to compaction due to its own weight, and to loss by melting and sublimation. The snow which accumulated in the marsh remained soft and loose, generally requiring a pressure of less than 6 gm/cm² to compact it to a depth of 2 to 3 cm. The dike, by contrast, was windswept and the road surface scoured free of snow. The mowed slopes of the embankment trapped only a small quantity of snow, which melted in March, especially on the east-facing side. The snow rarely became very hard in this area. The wooded ridge was subject to large accumulations of snow blown from the adjacent lake by the strong

Fig. 2. Weekly mean snow depths in the marsh, on the dike embankment and in the wooded ridge (12 stations in each sub-area) at Delta Marsh, Manitoba, for the period October 1974 to May 1975. The cumulative snowfall was measured at the University Field Station meteorological station.



north and northwest winds which prevailed during storms. Drifts were deepest in the centre of the ridge and adjacent to the lake. The snow in these drifts often became very hard, requiring up to 100 gm/cm^2 to compact it to a depth of 2 to 3 cm. The drifts were often absent or greatly reduced on the marsh side of the ridge, particularly where the ridge was more than 100 m wide.

Skunk tracks were occasionally found in November and December 1973. No skunk tracks were found in January and February 1975, but they were very commonly found in March and early April. Tracks on the ridge were very rare at all times, except in the area immediately adjacent to the marsh. The greatest concentration of tracks was found in the marsh during all of the above periods.

Nineteen dens repeatedly utilized by skunks were found. None of these were located in the ridge. Three were on the marsh - ridge boundary where the vegetation, snow depth and hardness, and soil conditions were more similar to those of the marsh than of the ridge. No active skunk dens were found on the dike embankment. Three were found on other, slightly raised road embankments and one beneath an old culvert.

All of these were in sites with snow accumulation and vegetation conditions more similar to the marsh than the dike. The remaining 12 dens were located in the marsh, frequently in stands of Phragmites communis. Of these, two were on the downwind side of a small water body and hence subject to localized heavy drifting. It was not possible to ascertain what species of animal had originally excavated most of the dens.

Discussion

The present survey indicates that striped skunks in Delta Marsh utilize winter dens located primarily in flat, low-lying areas, often in Phragmites communis stands. These sites tend to have heavy, poorly drained soils and a high water table. Furthermore, complete inundation invariably occurs when the snow melts, generally in late March or early April. These features would theoretically appear to be strong disadvantages to denning in such localities. The results of studies in other regions indicate that skunks and other burrowing, terrestrial mammals consistently choose winter den sites with well-drained soils. Selko (1938), Scott and Selko (1939), Allen and Shapton (1942) and Verts (1967) all

reported that skunks prefer well-drained areas, often sloping surfaces in hilly or rolling country, for their winter dens. Bailey (1971) found that skunks in a Lake Erie marsh denned exclusively in artificial dikes. Houseknecht (1969) reported that skunks denned almost entirely in upland habitats in winter, in contrast to the summer period when a significant proportion of rest sites, many of them above-ground, were in lowland areas.

Local conditions, peculiar to the marsh situation, may necessitate winter denning in sites that are avoided in other environments. True upland sites are lacking within the strip of marsh and wooded ridge paralleling the lake shore. The wooded ridge, despite drier soils, a lower water table and only very localized spring flooding, has limitations. The soil, essentially pure sand, is probably too unstable for den construction. The deep (2 m or more), very hard snow which blankets the ridge until May would probably impede or even prevent entrance to or emergence from the den in spring. The occurrence of the rut in March and April (Verts, 1967) makes easy access to the den essential. The dike embankments are well-drained and of firm soil. They are, however, blown clear of snow, with the result

that soil temperatures at 90 cm depth fell to -3.0°C . The lower temperatures of northern latitudes, in contrast to those of areas where the other studies cited were conducted, may necessitate that skunks den in the warmest areas available to them. The soft snow provides insulation to the soils in the marsh sub-area, and at the same time is not deep enough to trap skunks in their dens. The ground water in these wetter areas is a reservoir of heat, ensuring warmer soil temperatures (the recorded minimum temperature at 90 cm depth was 1.1°C , and at 45 cm depth was -0.5°C).

These factors are probably important in winter den site selection by striped skunks in Delta Marsh. Delta Marsh is in many respects excellent habitat for skunks, particularly in relation to abundance of food. The absence of, or low temperatures within, sites preferred for denning in other localities have not prevented the species from attaining a high population density in Delta Marsh (Lynch, 1972). An adequate winter retreat is essential for the skunk at these latitudes. It is therefore evident that the striped skunk has adapted to the local conditions, and that the marsh dens fulfill their requirements in this regard.

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Appendix 5: Food habits of striped skunks in Delta
Marsh, Manitoba.

Food habits of Delta Marsh striped skunks (Mephitis mephitis) were analysed by the examination of scats and stomach contents of autopsied animals. Fresh skunk scats were collected whenever found, primarily on the roads and trails in the study area. They were dried and stored for later analysis. Scats were softened in water and then washed in a sieve with a water spray. The resultant mass of solid material was examined macroscopically for identification and classification of contents. The washings were examined for rodents' teeth. Visual estimates (to the nearest 5%) of percentage volume composition of the scats were made. No attempt was made to estimate the percentage of each dietary item eaten, nor to correct the scat compositions for the different amounts of indigestible material in different foodstuffs. Table 1 summarizes the scat analysis data.

Qualitative notes on the different forms of food utilized by skunks in Delta Marsh follow. The most common food item, at least in terms of indigestible remains found in feces, is insects. Grasshoppers (Orthoptera) are utilized primarily in fall, when they are largest and most abundant. Other insects commonly

Table 1. Percentage composition (by volume) of striped skunk scats in Delta Marsh, Manitoba. The n value is the number of scats analysed in each month.

Month	n	Percentage composition of skunk scats								
		Frog	Fish	Eggs	Grass-hopper	Insects	Vegetation	Soil	Birds	Small Mammals
May	6	-	15	-	-	43	15	-	-	28
June	12	2	16	13	-	8	38	11	3	8
July	12	15	4	3	-	17	15	10	13	23
Aug.	8	14	-	-	-	42	26	14	-	5
Sept.	22	37	-	-	10	24	5	4	4	15
Oct.	25	20	5	-	32	18	3	1	11	11
NOV.	3	33	-	-	-	-	3	-	63	-
Means	88	17	6	2	6	22	15	6	13	13

eaten are beetles (Coleoptera) and bugs (Hemiptera), including aquatic forms. Frogs and toads are the next most utilized food item. Amphibians may be extremely common in Delta Marsh in late summer and fall. Utilization of this food resource decreases after the fall retreat of frogs and toads to their winter refuges, although dead frogs are commonly found washed up along the Lake Manitoba shoreline until freeze-up. Vegetation is common in many scats, although this is not digested and is apparently ingested incidentally in the course of eating other food materials. Soil and small stones are apparently ingested in a similar manner. Feathers were found in the scats, most often in fall. These are primarily from ducks and geese, and are probably a result of eating carrion, which is plentiful at this season because of locally intensive sport hunting. In spring, remains of young birds were occasionally found. Evidence of predation on eggs indicated that these comprised only a relatively small proportion of foodstuffs eaten, even in spring. Small mammals, which are abundant in the marsh, appear to be an important food item throughout the skunks' active season. Fish are also eaten, although this is apparently scavenged as carrion. Dead fish may frequently be

found on the lake shore, and carp (Cyprinus carpio) frequently die during summer in those ditches and channels of ~~the~~ marsh to which they have gained entry. These data confirm the skunks' omnivorous habits in the present study area. They also indicate the limited extent of conflict with man in terms of their feeding habits.