PHYSIOLOGICAL AND ECOLOGICAL ASPECTS
OF WINTER TORPOR
IN
CAPTIVE AND FREE-RANGING
STRIPED SKUNKS

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by

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ABSTRACT

The principle objective of this investigation was to develop an understanding of the physiological response and ecological aspects of winter torpor of small carnivores, specifically striped skunks (*Mephitis mephitis*) in the northern environment. An experiment was undertaken to investigate the physiological response of skunks to solitary and communal over-winter strategies. Solitary skunks were able to undergo daily torpor to conserve energy to survive the winter, whereas communal skunks were able to use social huddling to reduce energy expenditure and rarely entered torpor. Due to seasonal changes in life requirements, den selection criteria change throughout the year. I examined the landscape metrics and habitat characteristics surrounding dens to evaluate the hierarchical selection and use of dens during winter (i.e., for torpor) and summer (i.e., for parturition). Den structures commonly used for winter dens were buildings, whereas den structures used for maternity dens were rockpiles and underground burrows. Habitat surrounding den sites influenced den use; animals chose den sites closer to roads, water sources, habitat edges, and crop fields. Seasonal movements of skunks from winter dens to the following summer home ranges were examined with respect to winter grouping (i.e., solitary or communal) and winter den structure (i.e., underground burrow or building) to investigate factors that influence spatial distribution of skunks. Male and female skunks moved similar distances (~1.5 km) from winter dens to the center of home ranges established in summer, irrespective of winter grouping status and winter den structure use. Due to limited movement in spring, skunks from communal winter dens had higher spatial overlap of summer home ranges than did skunks from solitary dens, producing spatial aggregation of skunk activities surrounding winter communal den sites. Consequently, winter communal dens represent localized “hotspots” in the landscape. The effects of extrinsic variables (i.e., environment and diseases) and intrinsic characteristics (i.e., age, gender, and body condition) on cumulative winter survival rate were examined. Winter survival rates were driven mostly by winter condition (i.e., low ambient temperature and snow depth), rabies, and body condition. These results suggest that winter severity probably poses a limit on the northern distribution of the species.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 Resource seasonality

The seasonality of food resources in temperate environments poses physiological and ecological constraints on animals. Birds and mammals need to generate heat to maintain body temperature of about 35 to 40 ^{o}C to remain physiologically functional (Swan 1974). During food shortage, animals experience an energy deficit that is not sustainable over time. To meet normal energetic demands of daily activities during fasting, the body requires fat reserves. If fat reserves are depleted, structural protein and carbohydrates are used, eventually leading to emaciation and death. Consequently, some endotherms have evolved the physiological strategy of torpor to decrease metabolic rates during periods of food shortage.

1.2 Physiological and ecological aspects of carnivore wintering strategy

Torpor is an energy-conservation process where a torpid animal is able to decrease its metabolism and return to normothermy through endogenously generated heat (Lyman et al. 1982). There are two distinct patterns of torpor based on oxygen consumption rate and bout length: hibernation and daily torpor (Geiser and Ruf 1995). In the Order Carnivora, physiological processes linked with hibernation have been studied mostly in larger (>75 kg) animals such as bears (*Ursus* spp.). However, many constraints on hibernation and torpor are directly related to body size (Morrison 1960, Geiser and Ruf 1995), and studies of large carnivores have not yielded insights into physiological or behavioural processes that may exist in smaller carnivores (~ 3.5 to 12 kg) that are inactive during winter.

The annual cycle of carnivores that undergo winter inactivity can be divided into three critical periods: pre-winter, winter, and post-winter emergence. During each period, physiological and ecological factors interact, thereby influencing the dynamics of animal populations. The pre-winter period is critical for ensuring over-winter survival of individuals because the onset of hibernation is usually affected by body condition (i.e., body fat reserves) and not by temperature alone (Matson 1946, Schwartz et al. 1987). The primary role of fat reserves is to provide the energy source for winter and spring survival when food resources are minimal (Bailey and Davis, 1965, Mutch and Aleksiuk 1977, Kristiansson 1990). Environmental variables (i.e., food resource availability) and intrinsic characteristics (i.e., age and gender) can act independently or interactively to influence the ability of an animal to deposit body fat reserves.

During winter, torpid animals are especially vulnerable to winter severity (i.e., the duration of winter, snow depth, and low ambient temperature), the duration of the food shortage and, due to limited mobility, to predation risk or disturbance. Thus, animals that become inactive during the winter not only must store enough fat to survive the prolonged inactivity, but also must choose a suitable winter site. Good sites for winter inactivity may provide beneficial thermal conditions and protection from predators (Linnell et al. 2000, Rödel et al. 2004). Hibernating animals that use winter dens which offer good thermoregulatory properties and refuge from disturbance should have higher over-winter survival than animals that use winter dens that lack either quality (Webb et al. 1996). Therefore, selection of winter dens should be important for survival. Some mammals such as woodchucks (*Marmota monax* -- Armitage et al. 1976), deer mice (*Peromyscus maniculatus*) and bank voles (*Clethrionomys glareolus* -- Gebczynski 1969) use huddling behaviour to facilitate thermoregulation during winter. Communal denning appears to be a winter survival strategy in which the benefits for thermoregulation exceed the cost of social grouping. However, social thermoregulation can pose a disadvantage by facilitating disease transmission amongst group members (Kristiansson 1990). Over-wintering with diseased individuals could compromise survival.

The struggle for survival of animals that become inactive over-winter does not end when spring arrives. Animals that emerge from winter dens have usually experienced extensive mass loss from autumn to spring (Beer and Richards 1956, Douglas et al. 1976, Tietje and Ruff 1980, Farley and Robbins 1995). In spring, food resources are still limited and scarce. Animals that conserved more energy over-winter and emerge in spring with better condition likely have fitness advantages over animals that emerge from winter in poor condition. Animals that over-winter in groups have an advantage over animals that over-winter solitarily because group members represent potential mating partners and the time spent after spring emergence in finding potential mates is reduced (Douglas et al. 1976). Therefore, den sharing not only is an adaptive strategy for thermoregulation and survival, but it could potentially affect reproductive success. In species that share winter shelters with potential mates, successful mating may pose another evolutionary pressure (Douglas et al. 1976). Among mammals, for example, males of promiscuous species have disproportionate and highly variable mating success (i.e., a few males breed with most of the females in the population – Bronson 1989). Even if a winter shelter is valuable, the aggregation of kin in the shelter in the next winter may decrease its value to males due to decreased fitness from inbreeding (Bronson 1989). Consequently, movement or dispersal from winter dens would influence the spatial distribution and organization of animal populations across the landscape.

1.3 Winter strategy of striped skunks

The striped skunk (*Mephitis mephitis*; Order Carnivora, Family Mephitidae) is a small carnivore that is widely distributed in North America, ranging from northern Mexico and to the boreal forests of southern Canada (Rosatte and Larivière 2003). Skunks are resource generalists and feed opportunistically on insects, small mammals, carrion, amphibians and bird eggs (Hamilton 1936, Verts 1967, Greenwood et al 1999). Northern populations of striped skunks experience extreme seasonality in food availability and endure long periods of winter inactivity.

In northern regions, food resources are scarce or unavailable from early November to mid-April. To survive periods of food shortage and cold winters, striped skunks store body fat, reduce aboveground activity and retreat to warmer microenvironments in dens or den communally (Selko 1938), and undergo mild hypothermia (Mutch and Aleksiuk 1977). Unlike striped skunks in the southern part of their range that remain active all year (Davis 1951, Stout and Sonenshine 1974), skunks in the northern part of their range become inactive during winter (Hamilton 1937, Selko 1938, Sunquist 1974, Verts 1967, Mutch and Aleksiuk 1977). However, when winter food is available, captive striped skunks are active and do not enter torpor (Aleksiuk and Stewart 1976).

Although most carnivores are mainly solitary, there is evidence that striped skunks, which are solitary for most of the year, congregate during autumn and winter and undergo winter inactivity in communal dens in northern locales (Gunson and Bjorge 1979). In contrast, striped skunks in the southern part of their distribution are exclusively solitary animals throughout the year except during mating season in February and March (Wade-Smith and Verts 1982). A significant cost to social behaviour in skunks is that group denning likely facilitates transmission of infectious diseases such as rabies, a major mortality factor for prairie skunks (Hayles and Dryden 1970, Greenwood et al. 1997).

1.4 The thesis

The thesis is composed of four integrated parts that examine ecophysiological processes occurring at different life cycle of a population of striped skunks. The first part (Chapter 3) presents an experimental examination of the physiological and behavioural processes associated with winter inactivity in skunks. I evaluated the physiological responses of solitary and group skunks to elucidate the interaction between torpor and huddling and the plasticity of winter torpor expression. The second part (Chapter 4) considers selection criteria for winter and maternity den sites at multiple spatial scales. I consider choices made at local (i.e., den structure) and regional (i.e., surrounding habitat) scales because animals typically use hierarchical cues to select resting sites in accordance to their specific life requirements. The third part (Chapter 5) examines the effects of communal denning on movement patterns of skunks from winter dens to the center of their summer home ranges. In addition, I examine the spatial organization of skunks in summer in relation to winter denning strategy (i.e., communal or solitary). The fourth part (Chapter 6) considers the effects of environmental seasonality and individual characteristics (i.e., age, gender, and body condition) on cumulative winter survival and population dynamics of skunks living in the northern environment. The last part (Chapter 7) presents an integration of all the components of the thesis.

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CHAPTER 2. STUDY AREA AND GENERAL METHODS

2.1 Study area

Field work was conducted in the aspen parkland region of southeastern Saskatchewan, Canada. The 302-km^2 area is located approximately 24 km west from Yorkton (51^o 16’ N, 102^o 28’ W), near the village of Willowbrook (Fig. 2.1). Total annual precipitation of the area averages 420 mm, with an annual snowfall of 127 cm (Environment Canada Climate Data). Average autumn temperature from 1 October to 31 December is –5.7 ^{o}C (min = -10.9 ^{o}C; max = -0.6 ^{o}C). Average monthly temperature ranges from –7.6 ^{o}C to –18.1 ^{o}C from January to March (Environment Canada Climate Data). In prairie Canada, snow is generally present on the ground from end of October until early April (Environment Canada Climate Data). Mean July temperature is 18.0 ^{o}C. The landscape is gently undulating to rolling plain of glacial deposits, with well-drained black soil interspersed with numerous permanent and seasonal wetlands. The region has lost most of its native vegetation due to extensive cultivation for crop production. Small groves of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and willows (*Salix* spp.) can be found on moist and wet sites around wetlands and streams. The area is farmed intensively for cereal crops (wheat, oats and barley), and oil-seed crops (canola and flax); it also has livestock production. An extensive network of grid roads (every 1.6 km N/S and E/W) covers the area.

Figure 2.1 Location of the study site. Gray shaded area represents the current distribution range of striped skunks (*Mephitis mephitis*) in North America.

2.1 Location and capture of striped skunk

Striped skunks were captured in opaque plastic live traps (Dura-poly livetrap®, Bert "Ram" Trap Ltd., Birtle, MB) placed opportunistically in areas deemed most likely to capture animals throughout the study area from 1999 to 2003. Intensive trapping effort was conducted in autumn and summer trapping sessions. During autumn, I used three 7-day trapping sessions separated by 7-day intervals from late September to late October. During summer, there were three 7-day trapping sessions separated by 20-day intervals from late April to mid June. Traps were baited with canned cat food, and checked each morning. Captured skunks were anesthetized with halothane and Telazol® (Larivière and Messier 1996a, Larivière and Messier 1996b). Gender and age (young, adult) were recorded at capture. All animal handling procedures were approved by University of Saskatchewan Animal Care Committee (protocol # 20000088).

2.2 Marking and radio-telemetry

At initial capture, skunks were ear-tagged (Monel #3, National Band and Tag Co., KY) and equipped with a 60 g VHF radio-transmitter (Telonics Inc., Mesa, AZ) that contained a motion-sensor to identify mortality (animal motionless > 8 hours). I relocated skunks daily from September to December and from April to end of July each year; due to winter inactivity, animals were monitored monthly from January to March.

2.3 Body composition

All animals were weighed to the nearest g with an electronic scale (Sartorius PT6, Germany) to obtain total body mass (TBM) and measured for body fat using a

Bioelectrical Impedance Analysis (BIA) analyzer. Resistance (R_s) and reactance (Xc) were recorded with the Model 101A analyzer (RJL Systems, Detroit, Michigan) which reads 0 – 10000 ohms with a resolution of 1 ohm and an accuracy of ± 0.5 %. The use of BIA was validated for use in striped skunks (Hwang et al. 2005). Skunks were placed in sternal recumbency in a standard position on a dry plastic sheet. The plastic sheet was used to prevent possible loss of electrical current to the ground from wet animals. Needle electrodes (21 g, Vacutainer® needles) were used with the short end inserted subcutaneously into the animal and the long end clamped to the impedance meter's cable. Snout-to-vent (SVL) measurement was taken dorsally and chest circumference (CC) of was measured. See appendix A for complete methods and body fat predictive equations.

2.4 Necropsy

I retrieved dead skunks as soon as possible after detecting mortality and submitted carcasses for necropsy to the Canadian Cooperative Wildlife Health Centre at the Western College of Veterinary Medicine at Saskatoon, Saskatchewan. All animals, regardless of the proximate cause of mortality, were tested for rabies by the Canadian Food Inspection Agency in Lethbridge, Alberta, Canada.

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CHAPTER 3. WINTER TORPOR AND COMMUNAL DENNING IN A NORTHERN POPULATION OF STRIPED SKUNK

3.1 Introduction

Endotherms such as mammals maintain a relatively constant internal body temperature for optimal physiological function (McNab 1974). Endothermy requires high energy expenditure and water loss, especially at low ambient temperatures when high heat production is needed to compensate for large amounts of heat loss (Hudson 1978, Lyman *et al.* 1982, Wang and Wolowyk 1988). During periods of food shortage, endotherms experience an energy deficit. In temperate environments, food resources are typically seasonal and highly variable within a year with the majority of primary productivity occurring during spring and summer. Consequently, in autumn and winter, animals that rely on seasonal foods must find ways to cope with prolonged food shortages during low ambient temperatures. Many mammals have employed physiological and behavioral strategies to overcome this period of energy deficit (Lyman *et al.* 1982, Karasov 1992, Humphries et al. 2003).

Torpor is a physiological strategy employed by mammals and birds to overcome periods of inclement weather or food shortages (Lyman *et al.* 1982, Wang and Wolowyk 1988, Geiser and Ruf 1995). Torpor is characterized by substantial reductions of body temperature (T_b), metabolic rate (MR), and other body functions to achieve substantial energy and water conservation (Lyman *et al*. 1982, Wang and

Wolowyk 1988). There are two distinct patterns of torpor: daily torpor and hibernation (Geiser and Ruf 1995). Daily torpor is a shallow reduction of metabolism typified by short duration (< 24 h), with mean minimum T_b between 10 to 25 ^oC, and mean minimum oxygen consumption rate (VO_2) of roughly 30% of basal metabolic rate; seasonal hibernation is characterized by long torpor bout duration ranging from several days to weeks, with a mean minimum T_b of less than 10 ^oC, and a significant reduction of mean VO_2 to 5% of basal metabolic rate (Hudson 1973, Wang and Wolowyk 1988, Geiser and Ruf 1995). Although daily torpor represents only a shallow reduction in metabolism for energy conservation, it is likely to have significant energetic importance because shallow reductions in T_b conserve relatively more energy than reductions of the same increment at lower T_b due to Q_{10} effects (Studier 1981, Webb et al. 1993, Barclay et al. 2001, McNab 2002).

Animals may adapt to food shortages or inclement weather by physically avoiding areas with unsuitable microclimate, changing resting postures to decrease thermal conductance (Morrison and Tietz 1957), increasing insulation (Pearson 1960, Kenagy and Pearson 2000), building nests (Redman et al. 1999), taking refuge in shelters (Arnold *et al.* 1991), and or huddling to decrease heat and water loss by decreasing exposed surface to volume ratio (Vogt and Lynch 1982, Hayes et al. 1992, Bazin and MacArthur 1992, Kirkwood and Robertson 1999). Depending on the severity, predictability and length of energy deficit due to cold ambient temperature or food shortages, physiological and behavioral strategies are sometimes used separately or together for energy conservation (Karasov 1992, Dausmann et al. 2004). Behavioral thermoregulation by huddling has been studied in many species. It is commonly assumed that group living in wintering mammals is driven by physiological benefits such as reduced energy and water requirements that would accrue to individuals living in groups (Punzo 1975, Vickery and Millar 1984, Madison 1984, Hayes et al. 1992). Physiological benefits probably favoured the evolution of sociality in mammals (Alexander 1974, Madison 1984, Arnold 1990, Armitage 1999).

Torpor has been documented in many mammal species and there is increasing acceptance that endothermic heterothermy is plesiomorphic (i.e., ancestral) and did not evolve independently on multiple occasions (Geiser 1998). There is intra-specific variation in torpor expression (Humphries et al. 2003); however, the capacity to use torpor is not considered to vary intra-specifically. Many life-history traits of organisms vary both inter- and intra-specifically on a geographic and climatic gradient (Harlow 1997, Buck and Barnes 2000, Angilletta 2001, Niewiarowski 2001). Thus, the capacity and extent of torpor may also vary with latitude and altitude.

In the Order Carnivora, physiological processes linked with hibernation have been studied mostly in larger (>75 kg) animals such as bears (*Ursus* spp.). However, many constraints on torpor are directly related to body size (Morrison 1960, Geiser and Ruf 1995), and studies of large carnivores may fail to yield insights into physiological or behavioral processes that exist in smaller carnivores (~ 3.5 to 12 kg) undergo winter inactivity, such as raccoon (*Procyon lotor* – Loetze and Anderson 1979), American badger (*Taxidea taxus* – Harlow 1981) or striped skunk (Mutch and Aleksiuk 1977). Striped skunks and badgers are active year-round in the southern distribution range; however, many studies have documented winter inactivity in the northern parts of these species' distributions (Allen 1939, Mutch and Aleksiuk 1977, Harlow 1981). Study of these northern populations of small carnivores could elucidate the mechanism of torpor and influences of environmental factors on torpor characteristics (Humphries et al. 2002).

Although most carnivores like skunks are mainly solitary, there is evidence that skunks congregate during autumn and winter and undergo winter inactivity in communal dens in northern locations (Gunson and Bjorge 1979). In contrast, in the southern range of distribution, striped skunks are exclusively solitary animals throughout the year except during mating season in February and March. It is assumed that use of communal dens was driven by physiological benefits of social thermoregulation (Madison 1984).

At the northern part of its range, striped skunks have mean body temperatures of 34.4 ºC while they are dormant in den sites (Mutch and Aleksiuk 1977). Striped skunks in the north experience a doubling of body mass in the autumn, and subsequently lose 18 – 40% of their body mass over winter (Wade-Smith and Verts 1982). Body fat reserves after den emergence are vital to survival and reproduction as food availability remains low for the entire spring period. Many animals depend on body fat reserves to sustain daily activities until food resources become more abundant during spring and summer.

My objectives were to examine the winter physiology and the role of communal denning on the physiology and survival. I hypothesized that small carnivores such as skunks over-winter in communal dens in the north for the purpose of social thermoregulation in order to survive the long period of cold temperature and food shortage. To test this hypothesis, I examined the physiological responses of skunks over-wintering in communal and solitary dens in conditions mimicking those observed in the wild. I predicted that solitary skunks would use torpor whereas grouped skunks would use huddling to conserve energy. Furthermore, I predicted that dens with larger skunk groups possess thermoregulatory advantages over dens with only a solitary skunk, specifically, temperatures in winter dens of larger groups would remain warmer than those of solitary animals. Skunks in groups that experienced physiological benefits of huddling would emerge from winter dens in better condition (i.e., higher body fat) than solitary skunks, hence directly affecting reproduction and survival in the spring.

3.2 Methods and Materials

3.2.1 Animal Use and Experimental Design

The study was conducted at the Delta Marsh (50^{o} 10’ N, 98^{o} 22’ W) in Manitoba, Canada, during the winter of 2002-2003. Snow cover was on the ground from end of October to early April with a monthly average snow depth of 17.8 cm.

Twenty captive striped skunks (14 females, 6 males) were separated into two experimental categories, communal and solitary. Four adults (3 females, 1 male) were wild-caught in the area during April 2002; 16 (11 females, 5 males) were juveniles born from the wild-caught females in captivity from 1 – 14 May 2002. I monitored 4 groups of 4 individuals, and 4 solitary animals ($n = 4$ replicates for each treatment). Groups consisted of 1 male and 3 females, whereas solitary animals included 3 males and 1 female. Within the groups, males and females were not related; however, two of the three females from each group were siblings. Housing and care of animals are fully described elsewhere (Larivière et al. 2004).

Abdominal body temperature from captive animals was obtained every 2 hours using surgically implanted miniature dataloggers (Thermochron iButton® DS1921, Dallas Semiconductor Corp., Dallas, Texas 75244, USA). Surgical implantation of miniature temperature probes was performed on 30 October 2002 and all probes were removed on 28 March 2003. Dataloggers were implanted into the peritoneal cavity of the animals (Hwang et al. 2005). Dataloggers weigh 5 g and measured 17.4 mm in diameter and 5.9 mm in thickness and measure temperature from -20 °C to 85 °C in 0.5 °C increments and are able to log up to 2048 consecutive temperature measurements in non-volatile memory. The accuracy of dataloggers for temperature measurement is ± 1 °C from -20 °C to +70 °C and internal clock of dataloggers is ± 2 min per month from 0 °C to 45 °C.

From August to October, food was provided in excess to allow animals to gain sufficient body reserves to overwinter. Skunks were relocated to winter facilities at the end of October, and housed in groups or kept solitary. To simulate natural conditions, I gradually reduced food portions when the weather became colder and there was snow on the ground in early November. I offered regular food portions for 2 weeks beginning November 1, 50% for one week, 25% for one week, and then food was withdrawn completely. Water was provided *ad libitum* throughout the acclimation period, but both food and water were discontinued after November 30. Animals had access to water after November 30 in the form of ice in the water dish and snow on the ground in the outdoor enclosures. In the winter facilities, two to three square bales of hay and straw were provided in nest boxes and outdoor enclosures for skunks to build nests. All protocols were approved by the institutional and provincial Animal Care and Use Committees (University of Saskatchewan protocol #20000088, Manitoba Wildlife Animal Care Committee #2002-03).

3.2.2 Nest box and ambient temperature

Winter facilities were constructed inside a non-heated building. They consisted of adjoining wire outdoor enclosures with a concrete base (1.9 m X 5.2 m) in an enclosed building. Inside the building, I built nest boxes designed to house skunks during winter. Access tunnels (15 cm in diameter; PVC sewer pipe) connected the outdoor enclosure to the nest box inside the building. Tunnels were connected with a 45^{o} angle to prevent wind from directly entering nest boxes. Animals had access to the outdoor enclosure at all times and were exposed to natural photoperiod and ambient temperature throughout the experiment.

Nest boxes were 1 m^3 in size (1 m X 1 m X 1 m**)** and constructed of plexiglass to allow winter observations. However, the large amounts of grass and complexity of tunnels built by the skunks made visual observations difficult. Nest boxes had a hinged lid so that they could be opened for cleaning or animal capture in spring. All nest boxes were covered with an opaque cover to provide darkness.

Ambient and nest box temperatures were measured using temperature dataloggers (HOBO® H08-002-02, Onset Computer, Bourne, MA, USA 02532) and external sensors (TMC6-HB, Onset Computer, Bourne, MA, USA 02532). HOBO® dataloggers can store up to 8000 readings in non-volatile memory. The dataloggers have a temperature measurement range from -20° to 70°C with an accuracy of ±0.7° at 21°C. Dataloggers were approximately 29 g, with a dimension of 6.0 x 4.8 x 1.9 cm. All temperature dataloggers were programmed to measure temperature at 15-minute intervals. To measure ambient temperature, I deployed three temperature dataloggers, two were set to measure temperature outside the winter facility and one was set to measure temperature inside the facility. Within each nest box, a temperature datalogger was deployed to measure the temperature of the skunk den, with sensors inserted 6 cm below the center of the top lid inside the nest box.

3.2.3 Data Analyses

I measured torpor, torpor bouts, and torpor frequency for each individual throughout the winter season. I defined torpor as $T_b < 31^oC$. The operational definition of torpid T_b is justified by the 5^oC difference between normothermic T_b including $1\text{-}2^oC$ fluctuation in normothermic T_b (Barclay et al. 2001, Willis and Brigham 2003). Average abdominal body temperature of active striped skunks in July was 37.7 ^oC (Mutch and Aleksiuk 1977) and in November was 36.4 ^oC (Mutch and Aleksiuk 1977) and 36.1 ^oC (this study; n = 342). The normothermic T_b readings were obtained when average ambient temperatures were 19.1 ^oC (July) and -5.2 ^oC (November), respectively.

During the winter season, time of day for each entry into torpor was measured as the point at which T_b declined below stable normothermic T_b, and arousal was measured as the point at which the T_b rose above 31 ^oC. I divided the day into four 6-h periods of observations begin at midnight (0000 h). I used these data to test for randomness of starting time for both entry into torpor and arousal from torpor (Zervanos and Salsbury 2003). A chi-square analysis was performed assuming an expected equal distribution of starting times within each 6-h period.

I calculated torpor bout length as the period from when T_b declined below 31 °C to when T_b rose above 31°C. Torpor frequency was calculated as the number of times T_b dropped below 31°C from December 1 to March 28 (~ 120 days). Minimum body temperature was the lowest body temperature recorded for each animal throughout the experiment. Because I tried to minimize disturbance to animals, it was not possible to weigh and perform BIA on them during winter. Therefore, I estimated daily fat loss through winter by subtracting post-winter body fat from pre-winter body fat and dividing by length of the winter season. For comparison among individuals, I calculated percent daily fat loss (%) through winter by dividing daily fat loss (g day^{-1}) by pre-winter body fat (g) of individuals. For individuals in groups, I averaged the physiologic responses before comparing with solitary individuals. I used a Mann-Whitney U test to examine the effects of communal denning on torpor length, torpor frequency, minimum T_b, and percent daily fat loss. I used the Wilcoxon sign-rank test to assess the effect of communal denning on nest box temperature. Due to a small sample size for statistical analyses, I set the significance level at 0.10. All values shown are mean ± SE.

3.3 Results

During winter, skunks exhibited the characteristic pattern of daily torpor after December 10 (Fig. 3.1.a & b). Individuals in the solitary category tended to enter torpor between 0000 h and 0600 h ($\chi^2 = 88.8$, df = 3, $P < 0.001$) and aroused from torpor from 0600 h to 1200 h ($\chi^2 = 85.9$, df = 3, $P < 0.001$). Grouped individuals entered torpor from 0600 h to 1200 h ($\chi^2 = 33.1$, df = 3, $P < 0.001$) and aroused from 1200 h to 1800 h ($\chi^2 = 12.4$, df = 3, $P = 0.006$). See Table 3.1 for a summary of results.

All solitary individuals employed daily torpor; however, not all grouped individuals entered torpor. One male from grouped den escaped the winter facility in early March before I can obtain its body temperature data. Three grouped males did not enter torpor during winter, but all grouped females did. Torpor frequency differed ($U = 1.5$, $n_s = 4$, $n_g = 4$, $P < 0.001$) between solitary and grouped animals. During winter (~120 days), solitary animals entered torpor on average 50 times (range = 15 to 73 times) compared to 6 times (range = 0 to 17 times) for grouped animals. For skunks that entered torpor, mean torpor bout length was similar between solitary (7.8 h ± 0.22) and grouped (5.4 h ± 0.97) animals ($U = 22.5$, $n_s = 4$, $n_g = 4$, $P = 0.47$). Torpor length ranged widely between individuals in both categories, from 2 to 20 h. Solitary skunks underwent deeper torpor, with mean minimum T_b of 26.8 ^{o}C compared to 30.9^{o}C for grouped skunks ($U = 0.00$, $n_s = 4$, $n_g = 4$, $P = 0.001$).

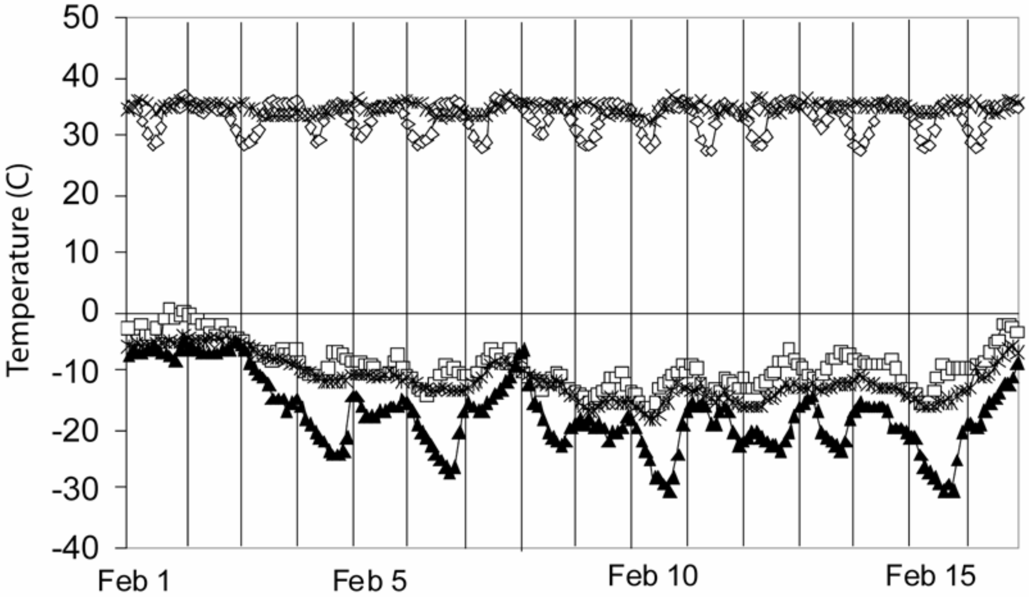

Figure 3.1.a Examples of body temperature (T_b) variation in captive striped skunks under experimental conditions from 1 - 16 Feb 2003 at Delta Marsh, Manitoba, Canada. Graph illustrates T_b of two male striped skunks, one individual that over-wintered solitarily (◊) and one individual that over-wintered in a group (x). Ambient temperatures (▲), temperatures of solitary nest box (∗) and group nest box (□) were also plotted. Vertical solid lines represent 0100h for each day plotted. Animals with $T_b < 31$ °C were defined as having entered torpor.

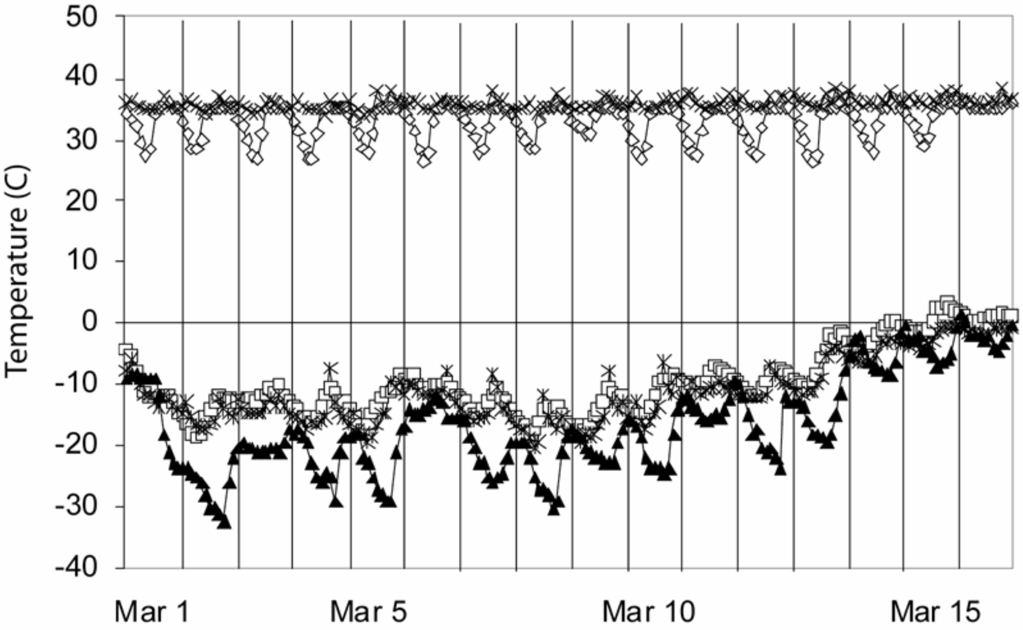

Figure 3.1.b Examples of body temperature (T_b) variation in striped skunks under experimental conditions from 1 - 16 March 2003 at Delta Marsh, Manitoba, Canada. Graph illustrates T_b of two male striped skunks, one individual that over-wintered solitarily (◊) and one individual that over-wintered in a group (x). Ambient temperatures (▲), temperatures of solitary nest box (∗) and group nest box (□) are also plotted. Vertical solid lines represent 0100h for each day plotted. Animals with $T_b < 31$ °C were defined as having entered torpor.

Table 3.1 Comparison of body mass, body fat, percent body fat and physiologic responses of striped skunks over-wintered in solitary and group category in captivity at Delta Marsh, Manitoba, Canada from November 2001 to March 2002. All values presented are means ± SE. Asterisk denotes significant differences ($P \leq 0.10$, Mann-Whitney U test).

	Solitary			Group[a]			
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	P
Body mass (kg)							
November	4	2.88	0.07	4	3.33	0.73	--
March	4	1.12	0.04	4	1.67	0.22	--
Body fat (kg)							
November	4	1.44	0.14	4	1.65	0.24	--
March	4	0.10	0.06	4	0.47	0.17	--
Percent body fat (%)							
November	4	50.1	4.2	4	49.1	1.9	1.00
March	4	9.3	5.3	4	25.5	5.6	0.08*
Percent daily fat loss (%)	4	0.71	0.063	4	0.56	0.091	0.04*
Torpor frequency (times/120 days)	4	50.0	12.4	4	6.19	1.20	0.03*
Torpor length (h)	4	7.75	0.22	4	5.38	0.97	0.11
Minimum T_b (^oC)	4	26.8	0.32	4	30.90	0.23	0.03*

[a] Group responses are presented as averaged values of each group.

Solitary and grouped skunks had similar ($U = 30.0$, $n_s = 4$, $n_g = 4$, $P = 0.89$) percentage of pre-winter body fat. After a winter season of no food and cold temperature, individuals from communal dens emerged with a significantly higher ($U = 6.0$, $n_s = 4$, $n_g = 4$, $P = 0.056$) percentage of body fat compared to solitary individuals. In spring, grouped skunks had on average 25.5% (± 5.62) body fat compared to 9.3% (± 5.32) for solitary skunks. Similarly, percent daily fat loss (%) differed ($U = 1.0$, $n_s = 4$, $n_g = 4$, $P = 0.043$) between social categories. Solitary individuals lost more body fat per day compared to group individuals. On average, solitary individuals lost 0.71% (± 0.063) of body fat per day compared to group individuals that have lost 0.56% (± 0.045) per day over 130 days of fasting and low ambient temperature.

During the winter season, mean nest box temperature was slightly warmer in communal versus solitary nest boxes ($-3.1^{o}C \pm 1.56$ versus $-6.8^{o}C \pm 0.60$; $t = -2.20$, $df = 3.88$, $P = 0.10$). From 1 December to 28 March, mean ambient temperature measured at the winter facility was -10.9 ^{o}C (min = -32.5 ^{o}C). I opportunistically observed that solitary skunks had larger straw nests compared to group skunks. Solitary skunks were often observed inside nest tunnels built inside nest boxes whereas group skunks were more active and often rested on top of the nest material.

3.4 Discussion

My results demonstrate that solitary skunks use daily torpor during winter. Body temperature of one solitary skunk during torpor reached 26.0 ^{o}C, the lowest ever reported for a carnivore during winter. For comparison, larger black bears (*Ursus americanus*) also experience torpor during winter but their body temperature has not been recorded below 31.2 ^{o}C (Hock, 1957, 1960). My results also revealed a different strategy for animals in groups: when skunks are in groups, they benefit from huddling to reduce the need to undergo torpor. These skunks have a thermoregulatory benefit by denning in groups in the reduction of torpor expression with infrequent torpor bouts and shallow torpor temperature range compared to solitary skunks. However, within group, there was variation in torpor expression. Males in groups did not use torpor even though females in the same group underwent shallow torpor. Male skunks in group probably want to be physically alert to defend the females in the winter den against other male skunks that might be roaming in search of mates. In addition, there is physiological cost of low body temperature to reproduction (i.e., spermogenesis -- Arnold and Dittami 1997, Fietz et al. 2004). Skunks often breed in February or early March, prior to emerging from winter dens. Thus, male skunks that overwinter in groups would be physiologically prepared to breed when females in the group are receptive. Consequently, huddling provided an additional fitness benefit to skunks.

Behavioural adaptations of skunks are not limited to communal denning. All animals in the study build elaborate nests using the straw and hay made available to them. Nest insulating properties probably created a more favourable microclimate conditions for the solitary animals (Gebczynska and Gebczynska 1971). However, I was unable to detect any significant difference in temperature of nest boxes. Possibly, the lower temperature of the nest boxes were due to the fact that I was not measuring microclimate immediately around the animals as I had only inserted the temperature sensor 6 cm from the top of the nest boxes. Possibly, the temperature surrounding the animals in the nest was probably much higher and likely above 0 ^{o}C.

Timing of daily torpor should depend on the animal's ecology and the prevailing environmental conditions (Kortner and Geiser 2000). Arousals are the most energetically expensive part of torpor, and costs could be minimized if torpid animals arouse during the warmest part of the day (Ortmann, Schmid, and Ganzhorn 1996, Lovegrove, Körtner, and Geiser 1999). To accurately assess the energetic cost of arousal in solitary and grouped skunks, oxygen consumption rates of the individuals need to be measured during the arousal phase. Thus, I limited my inferences about arousal costs to the ecology of skunks. Solitary skunks entered torpor from midnight to dawn, which represent the nocturnal activity phase of skunks, and aroused from dawn to midday. Torpor during the activity phase was used to minimize energy loss. Grouped skunks that were torpid entered torpor from dawn to midday, and aroused from midday to dusk. Torpor rhythm coincided with their normal rest phase and was probably an extension of sleep (Körtner and Geiser 2000).

My results suggest that northern populations of striped skunks have the capability of entering torpor during periods with low ambient temperature and food shortage**.** Thus, my results showed the influence of climate and food resources on torpor characteristics for this species. By allowing the animals to overwinter in groups, I found plasticity in the expression of torpor, probably due to increasing the energy available to grouped skunks by decreasing the energetic demand of low ambient temperature and food shortage (Humphries et al. 2003). The flexibility of torpor use by these animals further suggest that the evolution of daily torpor and hibernation was derived according to ecological and physiological requirements such as body size and diet, not merely due to phylogeny (Geiser 1998).

To conclusively demonstrate that physiological benefits are the ultimate cause of grouping, laboratory results must be indicative of natural conditions (Berteaux et al. 1996, Geiser and Ferguson 2001). The winter facility was designed to allow animals to be exposed to natural fluctuations in ambient temperatures, snowfall, wind, and photoperiod. In contrast to many laboratory studies, the animals were not restrained in metabolic chambers and/or exposed to controlled environmental cues. Also, I provided the animals with hay for nesting material which is often used by skunks in the wild. Animals were able to build their own nest in the boxes by bringing in nesting material from the outdoor enclosures. Furthermore, I synchronized the period of food withdrawal with observations from a winter field study of free-ranging striped skunks concurrent to this study. Therefore, conditions and design of "winter dens" mimicked conditions regularly observed in the wild, so I am confident that the results reflect natural conditions.

Physiological benefits from social thermoregulation should translate directly into fitness benefits (Berteaux et al. 1996), which in turn imply that animal should maintain higher body fat reserve in the spring to ensure better survival and reproduction (Huber et al. 1999). Gebczynska and Gebczynska (1971) demonstrated a significant energetic benefit for groups of bank voles (*Clethrionomys glareolus*) without a nest, but this benefit was insignificant when a nest was available. Many studies of grouping benefits might have overestimated the benefits of huddling. Berteaux et al. (1996) examined winter sociality in meadow voles (*Microtus pennsylvanicus*) in a natural setting and suggested that winter sociality confers no physiological benefits in terms of higher body condition for voles in groups. I detected direct physiological benefits of gregariousness in striped skunks as animals from communal dens generally emerged from winter inactivity with a higher percentage of body fat compared to solitary skunks. For species inhabiting relatively high latitude, spring represents a period of unpredictable food resources due to low primary productivity. Therefore, for many species, body fat reserves are critical in the spring when animals are active and not using any physiological strategies to conserve energy (Tietje and Ruff 1980, Farley and Robbins 1995). However, the fitness benefits of spring body fat are probably higher in females than males because of higher reproductive cost incurred by females for pregnancy, parturition, and lactation. The benefits of communal denning in females probably outweigh the cost of communal denning (i.e., disease and parasite transmission). For males, the cost of communal denning outweighs the benefit of higher body fat in spring. Thus, not all skunks den communally; females overwinter in communal dens and males overwinter in solitary den.

Previous work documented a loss of 18% - 40% body mass overwinter (Wade-Smith and Verts 1982), in my study, skunks lost an average of 50% - 60% body mass overwinter. The estimate of body mass loss in skunks was attributed to body fat loss over the winter period. The low estimates of mass loss in other studies were probably due to measuring spring mass later in the season after skunks had the opportunity to feed. Even though my study animals lost 50 - 60% body mass (or 25% - 40% body fat), all females in communal dens with males reproduced successfully in the spring (Hwang et al. 2005).

In conclusion, I found that striped skunks have the ability to use daily torpor as an over-wintering strategy in the absence of social thermoregulation. For individuals in communal dens, thermoregulatory advantages reduce torpor expression and these individuals only expressed shallow and infrequent torpor periods. Social thermoregulation probably plays an important role in influencing winter sociality in this solitary carnivore species. The cost of communal denning is probably restricted to disease transmission, especially rabies (Sargeant et al. 1982, Rosatte 1984, Guerra et al. 2003), between communal nest mates. However, the benefit of communal denning translates into higher fitness advantages in terms of higher body fat reserve in the spring which is directly related to spring survival and reproduction (Tietje and Ruff 1980, Farley and Robbins 1995). I argue that skunks have successfully adapted to the northern climate by using winter torpor and social thermoregulation. The capability of using torpor during winter for energy conservation probably resulted in their wide geographic distribution in northern North America.

3.5 References

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CHAPTER 4. LANDSCAPE METRICS AND SELECTION OF HABITATS SURROUNDING DEN SITES OF STRIPED SKUNKS

4.1 Introduction

Habitat selection theory predicts that animals use habitats differentially to meet life requisites and maximize fitness. Consequently, biotic and abiotic factors influence fitness potential and selection patterns on each individual (Martin 2001). Understanding the ecological basis for habitat preference may help natural resource managers protect, modify, or enhance habitats important to species. In addition, knowledge of how fluctuating environments affect habitat selection may further our understanding of which resources is limiting and critical to individuals and populations (Rettie and Messier 2000, McLoughlin et al. 2004).

Individuals select habitat at multiple spatial scales, from geographic range to home ranges, to non-random use of habitats within home ranges, and to selection of microsites (Johnson 1980, Morris 1992, Jones and Hudson 2002, Chamberlain et al. 2003). Within the established home range, selection of a nest, den, and retreat for resting, parturition or over-wintering site is especially critical because of the direct influence of these choices on survival and/or reproduction. For mammals, selection of den sites may be influenced by availability of den structures (Bulova 2002, Bakker and Hastings 2002), microclimate (Arnold et al. 1991, Wilbert et al. 2000, Bulova 2002), and life history requirements such as parturition and refuge from predation (Larivière and Messier 1998a, Spencer 2002, Zabala et al. 2003). For example, when considering thermoregulatory quality of dens, selection of daily resting sites during the warmer months may not be critical, whereas daily resting sites during colder spring or autumn months may be highly affected by fitness costs of poorly insulated dens.

Selection of habitats surrounding dens may also influence den use, because it may affect safety from predators or disturbance (Grand 2002, Mitchell and Lima 2002, Spencer 2002) and access to critical resources (Rubin et al. 2002, Lyons et al. 2003). Dens may be of unequal value because habitats may affect survival differentially (Messier et al. 1990). In response to spatial and temporal differences in climate and interference from competitors and predators, individuals have to adjust their den site use to maintain energy balance and survival (Lima and Dill 1990, Morris 1992, Wilbert et al. 2000, Martin 2001). Therefore, examining the habitats that surrounds den sites may reveal important cues traditionally ignored in den selection studies (Orians and Wittenberger 1991, Henner et al. 2004).

My project examined the influences of the surrounding habitats on den use by mammals at northern latitudes, where animals are subjected to fluctuating seasonal environments. Thus, I predicted that selection of dens would differ among seasons. Specifically, in autumn/winter, animal would use dens that provide insulative quality; in spring/summer, females would use dens that are more secure for reproduction whereas males have less restriction in den use. Secondly, I predicted that den sites should be selectively situated in habitats composed of foraging areas that provide consistent food and water resources (Yahner 1988, Dijak and Thompson 2000).

I examined the seasonal landscape and habitat selection patterns of striped skunks. Southern Canada represents the northern limit of distribution for the species, and striped skunks have adapted to the harsh climate (Allen, 1939, Mutch and Aleksiuk 1977a). In contrast to skunks in the southern distribution that remain active all year (Wade-Smith and Verts 1982), skunks at the northern latitude undergo winter dormancy and communal denning to conserve energy during the long period of non-feeding and cold temperature (Mutch and Aleksiuk 1977, Hwang et al. submitted 2004a).

4.2 Methods and Materials

4.2.1 Den use analysis

From 15 April to 1 December, radiocollared skunks were located daily by triangulation and homing to identify diurnal retreats. From December to March, animals were radio-located once a month. Locations of resting skunks were recorded using a Global Positioning System (GPS, ± 5 m). At each den site, I identified den structure and habitat type. Den structures were categorized as: underground burrow, building, rock pile, and miscellaneous (< 5% frequency of occurrence in study area), which included brush piles, old cars, old buses, and culverts.

I defined the biological year into two main intervals: autumn/winter from 22 September to 31 March, and spring/summer from 1 April to 21 September. I developed a log-linear model to test the predictions that den structure use differed with respect to gender and season (Feinberg 1977). Striped skunks reuse dens in different seasons. Some den structures were used by both male and female skunks multiple times during the same or different seasons. Thus, I performed an analysis of variance to examine whether the number of dens used by striped skunks varied with gender and season.

4.2.2 Landscape metrics of dens

I described skunk den sites with landscape level metrics derived by using the Patch Analysis (Elkie et al. 1999) extension of ArcView® Geographic Information System (GIS) Software (Environmental Systems Research Institute, Inc., Redlands, California, USA). Den locations were plotted on a land-cover map of the study area that contained information on habitat type, area and perimeter of each habitat patch. The land-cover GIS was provided by Saskatchewan Research Council and Prairie Farm Rehabilitation Administration. I classified habitat patches into 5 classes: crop field, woody (shrub and tree vegetation), grassy (pasture, grassland, and hayfield), water body (wetland and stream), and other (farmsteads and miscellaneous land use). I buffered each den site with a 50-m circular buffer to examine resource selection at local and landscape levels. Skunks can distinguish den sites and food resources at a scale of several meters (Nams 1991, Pedlar 1994, Larivière and Messier 1998b, Henner et al. 2004), so I assumed that this buffer would also include habitat elements and features used by skunks to select den sites.

I calculated landscape metrics to describe composition and structure of buffered areas around dens (McGarigal and Marks 1995; Henner et al. 2004). Specific metrics included mean patch size, total edge, and edge density. I calculated similar landscape metrics for an equal number of random sites generated from a uniform distribution using the Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcView®.

I developed a logistic regression model to determine whether landscape metrics could be used to classify locations as dens (1) or random points (0). An equal number of random and den sites ensured a prior probability of group membership of 0.5. Variables were selected using stepwise backward selection procedures with a 0.05 significance level for entry and retention in SPSS (Version 12.0, SPSS Inc., Chicago, Illinois, USA) to build models.

4.2.3 Distance to landscape features

I used ArcView® to determine distances (m) from each den site or random point to nearest road, water, crop field, and habitat edge (distance to a different habitat type) to examine the relationship between den selection and distance to landscape features. I used analysis of variance (Version 12.0 SPSS) to examine differences in distance measures between den sites and random sites.

4.2.4 Habitats surrounding dens

I used an arbitrary delineation of the entire study area for measuring habitat available to skunks (Johnson, 1980). I estimated availability of habitats using ArcView® GIS. I subsequently used each den site buffered by 50 m to examine habitat selection relative to the availability of habitats. Availability of habitats within each den buffer was determined by summing the area for each habitat and dividing it by the total area of habitats within each den buffer. I used compositional analysis (Aebischer et al., 1993) to determine whether habitat selection occurred at the level of den site buffer and whether selection differed between genders or seasons.

I created ranking matrices (Aebischer et al., 1993) to assess relative habitat preferences. Subsequently, I used multiple analysis of variance (MANOVA) to detect gender- or season-specific differences. If differences were detected, I created a separate ranking matrix for each group.

4.3 Results

4.3.1 Den use analysis

I tracked 52 male and 72 female skunks from September 1999 to June 2003, for a total of 4323 encounters at 803 den locations (Table 4.1). Number of dens used by skunks varied significantly by season ($F_{1,175} = 187.3$, $P < 0.001$) and gender ($F_{1,175} = 29.4$, $P < 0.001$). In autumn/winter, skunks used an average of 4.7 (SD = 3.4) dens compared to 15.7 (SD = 9.0) dens in spring/summer. Females generally used fewer dens ($\bar{x} = 6.7$) than males ($\bar{x} = 8.1$) during both season. Den structure was related to gender and season ($\chi^2 = 149.2$, df = 13, $P < 0.001$). Both males and females tended to use buildings and culverts as den structures during winter (Table 4.2), whereas females used rock-piles and underground burrows more often than males, particularly during parturition and young-rearing period. Males used more above-ground retreats throughout spring and summer.

Table 4.1. Use of den structures by striped skunks in southeastern Saskatchewan, Canada, 1999 – 2003. Den structures used multiple times by different skunks were only represented once.

Den structures	n	Percentage	Frequency of use	Percentage of use
Above-ground retreat	299	37.2	360	8.3
Building	119	14.8	1321	30.6
Rock pile	44	5.5	179	4.1
Underground burrow	288	35.9	2010	46.5
Miscellaneous[a]	53	6.6	453	10.5
Total	803	100	4323	100

[a] Miscellaneous den structures include brush piles, old cars and buses, and culverts.

Table 4.2. Seasonal use and reuse of den structures by striped skunks in southeastern Saskatchewan, Canada, 1999-2003.

	Female		Male	
Den Structure	Autumn/ Winter	Spring/ Summer	Autumn/ Winter	Spring/ Summer
Above-ground retreat				
N	45	68	96	107
% of structure[a]	14	22	30	34
% of season[b]	18	23	38	56
Building				
N	75	44	57	16
% of structure	39	23	30	8
% of season	31	15	22	8
Rock pile				
N	5	34	8	3
% of structure	10	68	16	6
% of season	2	11	3	2
Underground burrow				
N	102	128	71	56
% of structure	29	36	20	16
% of season	42	43	28	29
Miscellaneous[c]				
N	18	24	22	10
% of structure	24	32	30	14
% of season	7	8	9	5

[a] Proportion of all dens used.
[b] Proportion of total den use during respective season.
[c] Miscellaneous den structures include brush piles, old cars and buses, and culverts.

4.3.2 Landscape metrics and distances to habitat features

I used 803 den sites and an equal number of random locations to develop a model of den-site selection relative to landscape metrics. Five of 15 parameters were retained in the final model excluding an intercept term (Table 4.3). Probability of a location being a den site was related positively to crop field total edge, woody mean patch size, water total edge, and farmstead total edge. However, probability of a location being a den site was negatively related to crop field mean patch size. Den sites were situated closer to water bodies ($F_{1, 1507} = 53.76$, $P < 0.001$), habitat edges ($F_{1, 1507} = 74.27$, $P < 0.001$), roads ($F_{1, 1507} = 5.71$, $P = 0.017$) and crop fields ($F_{1, 1507} = 11.47$, $P = 0.001$) relative to random sites (Table 4.4).

4.3.3 Habitat selection surrounding den sites

Habitat composition surrounding den sites differed from the composition of the study area ($F_{4, 982} = 727.24$, $P < 0.001$). I found both gender- ($F_{4, 979} = 4.28$, $P = 0.002$) and season-specific differences ($F_{4, 979} = 14.95$, $P < 0.001$) in habitat composition surrounding dens. In order of relative importance, dens used by females were surrounded by grassland/pasture, farmsteads, crop field, woodland, and water bodies. Dens used by males were often surrounded by habitats of grassland/pasture, farmsteads, water bodies, crop field, and woodland. During autumn/winter, habitat surrounding dens often consisted of grassland/pasture, farmsteads, crop field, woodland, and water bodies. In contrast, during spring/summer, dens were surrounded by farmsteads, grassland/pasture, woodland, water bodies, and crop field.

Table 4.3. Parameters retained in the final model of a logistic regression to determine landscape metrics that can be used to characterize den sites of striped skunks in southeastern Saskatchewan, Canada 1999-2003.

Parameter	β	SE	χ^2	df	P
Intercept	-0.015	0.11	0.02	1	0.89
Crop field mean patch size	-2.26	0.43	27.73	1	<0.001
Crop field total edge	0.003	0.001	13.9	1	<0.001
Woody mean patch size	1.41	0.34	16.9	1	<0.001
Water total edge	0.001	0.0001	6.75	1	<0.001
Farmstead total edge	0.003	0.001	3.43	1	0.06

Table 4.4. Means (and standard errors) for landscape variables associated with striped skunk den sites (n = 741) and random locations (n = 768) in southeastern Saskatchewan, Canada, 1999-2003.

Variable (m)	Den sites	Random sites
Distance to nearest source of water	224 (8)	316 (10)
Distance to nearest macro-habitat edge	47 (2)	80 (3)
Distance to nearest road	230 (7)	254 (7)
Distance to nearest crop field	46 (4)	64 (4)

4.4 Discussion

My results demonstrated that the habitat surrounding den sites influences den use by striped skunks. At the local level, skunks exhibited differential season- and gender-specific use of den structures. In the colder months, skunks were selectively using buildings as den sites whereas in the warmer months, skunks displayed gender-specific use of den structures, with females using rock piles and males using above-ground retreats. The shift in den structures may be related to several factors. First, buildings may provide better thermoregulatory qualities compared to other den structures (Storm 1972, Spencer 1987). Second, northern skunks aggregate in the autumn to over-winter in groups forming communal dens (this study, Gunson and Bjorge 1979), and buildings may offer more space for communal groups. Because both male and female skunks are faced with similar constraints in the winter, i.e. thermoregulation and energy conservation, it was not surprising to find that there was no gender-specific difference in den structures used for over-wintering. Finally, because inactive skunks may be more vulnerable to predation (Larivière and Messier 1996c), buildings may offer better protection from predators.

Den sites used during spring and summer differed from the winter season. During spring and summer, females are faced with reproductive constraints such as parturition and rearing young, whereas after breeding during February to early April, males are relatively unrestricted in movement because they provide no parental care (Wade-Smith and Verts 1982, Larivière and Messier 1998a). Males used mainly above-ground retreats in the summer, whereas females selectively used rock piles as den sites during parturition and when rearing their young. I assumed that above-ground retreats offer little or no protection from predators, which is particularly risky for juveniles when the female is away foraging. In contrast, rockpiles represent safe den structures due to the limited entrance opening size, limiting access by potential predators such as coyotes (*Canis latrans*) or badgers (*Taxidea taxus*).

Season- and gender-specific den structure use are consistent with previous studies (Storm 1972). However, I did not find that females selectively uses buildings as maternity dens, a trend reported from a study area located ca. 400 km further northeast (Larivière et al. 1998). This lack of use of buildings during summer could be a result of selective use of building dens in the winter, decreasing the availability of buildings as suitable dens in the summer due to parasite and excrement build-up (Butler and Roper 1996).

My results also highlight the influence of surrounding habitat and landscape features on den use by skunks. Given that skunks might be restricted in their selection of habitat characteristics due to the location of dens, I limit my inferences of my discussion of habitat surrounding den sites to use instead of selection. However, due to the large number of dens available in the study area and the high reuse of certain dens, there is some level of choice exhibited by skunks for landscape and habitat characteristics surrounding den sites. Although my model did not allow perfect classification of used and random sites, patch analysis of the habitat surrounding den sites revealed the influence of wetland edges on den use, a finding previously highlighted for foraging activities (Larivière and Messier 2000, Phillips et al. 2003). The prairie landscape is fragmented in southern Canada, and striped skunks are resource generalist; as a result, den sites probably encompass a wide range of habitats, both desirable and undesirable. The presence of these resources potentially contributed to greater misclassification of used sites. There is a positive relationship between total edge of water bodies (i.e., wetlands and streams), crop field, and farmstead, and mean patch size of woody area with den use. This could explain the propensity of skunks to den near edges and small patches.

Den sites used by striped skunks were closer to water bodies, habitat edge, road, and crop field compared to random sites. Previous research into the activity patterns of skunks in the northern prairie during the summer months showed that skunks prefer to forage in wetland-agriculture margins (Phillips et al. 2003) and avoided foraging in large patches of grassland (Larivière and Messier 2000). The result of this study demonstrates that skunks choose to den in proximity to water and habitat edges.

The Canadian prairies have been highly fragmented by agriculture during the last 100 years. Animals living in the prairies now have numerous habitat options available, and habitat preferences for foraging are typically obvious (Larivière and Messier 2000 for *Mephitis mephitis;* Phillips et al. 2003 for *Vulpes vulpes* and *Mephitis mephitis*). My analyses of the denning habits of striped skunks revealed that the habitat surrounding den sites has a clear influence on den use. For example, striped skunks used dens surrounded by grasslands/pastures and farmsteads probably because of consistent availability of food resources in these habitats (Larivière and Messier 2000). Also, skunks used dens in habitats with large amounts of wetland, woodland, cropfield, and farmstead edge. The proximity of den sites to water bodies may reflect the greater use of these habitats for foraging (Larivière et al. 1998). These results support predictions that den use by striped skunks occurs in habitats that provide consistent food and water resources. Increasing habitat fragmentation in the prairies and elsewhere has had tremendous influence on mesocarnivore communities (Yahner 1988, Dijak and Thompson 2000, Sovada et al. 2000). My study indicates that habitats surrounding den sites may influence patterns of den use as much as the local habitat and den sites characteristics. With ever increasing attention devoted to understanding the ecology of species in fragmented habitats, multi-resolution assessment of den sites enables the incorporation of the surrounding habitats into habitat selection studies.

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CHAPTER 5. SEASONAL MOVEMENTS AND SPATIAL ORGANIZATION OF THE STRIPED SKUNK IN THE CANADIAN PRAIRIES

5.1 Introduction

Animal movement is often associated with foraging, avoiding predators, finding mates, seeking favourable microclimate, and interacting with other individuals (Greenwood and Swingland 1983). Some animals migrate long distances due to changes in environmental conditions that result in reductions of critical resources such as food. Animals also disperse away from natal sites to establish breeding home ranges, presumably to reduce inbreeding with close relatives (Greenwood 1980, Armitage 1991, Berggren 2001). At smaller scales, animals move within their home range to fulfill life requirements, and occasionally venture outside their home range for exploratory excursions (Greenwood 1980; Messier 1985). Movement distances often scale with ecological factors, such as territoriality, mating systems, and resource availability, which may determine the density and dispersion of individuals across the landscape (Sutherland et al. 2000). Therefore, movement patterns influence the spatial organization and distribution of animals (e.g., *Vulpes vulpes* -- Poulle et al. 1994), and affect the connectedness between populations in fragmented landscapes (Dijak and Thompson 2000, Sutherland et al. 2000, Gehring and Swihart 2004).

In North America, striped skunks are of special interest to waterfowl managers due to their role as a predators of duck eggs (Greenwood 1986, 1993, Phillips et al.

2003). With increased agricultural development in the Canadian prairies, native habitat is increasingly fragmented, forcing waterfowl and other grassland birds to nest either in the few remaining patches of natural vegetation or in cultivated fields (Clark and Diamond 1993), often increasing their vulnerability to predators. Recent findings suggest that high predation rates are linked to high predator densities, and not to specialized foraging by specific individuals (Larivière and Messier 1998b). Thus, factors that affect the distribution and aggregation of predators in the landscape may have critical implications for mitigating nest predation.

Moreover, striped skunks are the major terrestrial reservoir of rabies in the northern prairies (Rupprecht et al. 1995, Hayles and Dryden 1970, Gremillion-Smith and Woolf 1988, Schubert et al. 1998). Because space use of animals play a major role in disease transmission (White et al. 1995, Caley et al. 1998, Totton et al. 2002), there are concerns regarding the potential of increased contact rate between individuals in the population. Spatiotemporal aggregation of skunks affects the contact rate between rabid and susceptible skunks. To control or prevent rabies epizootic and spillover effects into other mammals, wildlife vaccination programs have been initiated in many locations including Ontario (Broadfoot et al. 2001, Totton et al. 2002) and Arizona (Engeman et al. 2003). In France, a rabies vaccination program in red fox (*Vulpes vulpes*) was successful in eliminating rabies in the area (Charlton et al. 1992, Chautan et al. 2000). However, to have an efficient oral-bait vaccination program, it is imperative to have an understanding of proximate factors that influence the spatial dispersion of the target group.

Social system may affect contact rates among individuals. In contrast to striped skunks in southern areas, northern striped skunks are social during winter (Wade-Smith and Verts 1982). Skunks in southern latitudes are solitary all year,while skunks in northern latitudes congregate during winter (Selko 1938, Terres 1940, Mutch and Aleksiuk 1977). At northern latitudes, many skunks den communally, where one adult male may den with >5 females (Sunquist 1974), (Gunson & Bjorge 1979), (Houseknecht & Tester 1978). In contrast, juvenile males often remain solitary in winter. Because striped skunks are polygynous (Wade-Smith and Richmond 1978), denning habits in winter have implications for reproduction during spring. In spring, skunks in communal dens breed prior to emergence from the winter den (Wade-Smith and Verts 1982). Winter communal dens act as spatial and temporal “hot-spots” for skunk aggregations on the landscape (Hwang et al. submitted 2004b). The movement patterns from winter den sites (both solitary and communal dens) could potentially influence the spatial dispersion of skunks across the landscape in the following spring and summer. Striped skunks are not territorial and often have extensive overlap in home range (Rosatte and Gunson 1984, Larivière and Messier 1998c, Bixler and Gittleman 2000). After winter den emergence, if skunks move short distances (~1 – 2 km) away from winter dens, areas surrounding communal dens would have a high aggregation of skunks with extensive overlapping home ranges. If a waterfowl nest is located close to a communal den from the previous winter, the nest will likely be within the home ranges of several striped skunks, perhaps reducing the chance of nest survival (Sugden and Beyersbergen 1986).

I examined the movement patterns of striped skunks from winter dens to subsequent home ranges and investigated how this relationship affects the spatial organization of skunks during the following seasons. I hypothesized that communal winter den location influences the spatial distribution of skunks. I predicted that communal winter dens might cause spring-summer aggregation of striped skunks due to extensive home range overlap between members of communal winter dens as compared to skunks that over wintered solitarily. In the northern prairies, buildings are preferred for parturition and rearing dens, and are often used as resting sites (Larivière and Messier 1998a, Larivière et al. 1999, Hwang et al. submitted 2004). I hypothesized that movement patterns are affected by winter den location and den structure. I predicted that maternity den sites are located close to winter den sites. Thus, females that use underground burrows as maternity dens settle closer to winter dens than females that use buildings, because underground burrows can be dug anywhere whereas suitable buildings for denning are not as common.

5.2 Materials and methods

5.2.1 Home range estimation

I tracked radiocollared skunks via triangulation using vehicle-mounted 5-element antenna (Heezen and Tester 1967), and via ground-based homing using two-element hand-held H-antenna. I obtained radio locations for each animal three times per night with a minimum 2-hour interval between successive relocations. Because skunk can move throughout their home range within a 2-hour period, I believe my nightly locations for each animal is independent. Each animal was radiolocated 2 nights (separated by several days) per week to generate at least 60 activity locations for the season (3 months). I obtained 3-5 bearings as quickly as possible (within 5-8 min) to reduce telemetry error (White and Garrott 1990). I calculated the standard deviation of bearing error (Lee et al. 1985) and used the standard deviation to calculate 95% confidence ellipses in the microcomputer program LOCATE II (Nams 1990). Locations were determined using the maximum likelihood estimator available in LOCATE II software.

I estimated 100% and 50% (core) minimum convex polygon (MCP) home ranges using nighttime activity locations. Minimum convex polygon home ranges were generated by using Animal Movement Extension (Hooge and Eichenlaub 1997) for ArcView® Geographic Information System (GIS) Software (Environmental Systems Research Institute, Inc., Redlands, California, USA).

5.2.2 Den location and group composition

From September to early December, I radiolocated skunks every day until they entered winter dens. From December to March, animals were radiolocated once a month. A winter den was identified as such when one of two criteria were satisfied: fidelity of use for > 3 consecutive days after December 1, and collection of grass for preparation of the nest chamber (Allen 1939, Allen and Shapton 1942). From middle to late November, I determined group composition of winter dens by setting traps immediately outside den entrances for consecutive days until new individuals were no longer captured. Because all captured animals were equipped with radio-transmitters, I could determine if skunks were transient individuals or if they belonged to the winter group. From my intensive trapping effort, I assumed that I had captured and radiocollared all skunks in my study area.

From early April to the end of July, I relocated skunks daily at their diurnal retreat (maternity dens or resting sites). A maternity den was defined as any retreat for which at least two of the following criteria were satisfied (Larivière and Messier 1998a): fidelity of use for > 3 consecutive days during the parturition/rearing period, collection of grass for preparation of the nest chamber, and presence of young during the rearing period.

5.2.3 Seasonal movement

Seasonal movements of striped skunks were calculated as the shortest straight-line distance (m) from the winter den site to the center of the MCP home range in the following summer season. I also calculated seasonal movement distance (m) of female skunks from the center of the summer home range to the winter den site in the following season. A survey of all dens used by radiocollared skunks in the study area was plotted in Arcview to calculate the average distances (m) between two closest den sites using Nearest Features extension (Jenness 2004) in ArcView. All den sites in the study area were classified as either underground burrows or anthropogenic dens (including rockpiles, brushpiles, old cars, and farm buildings). The average distance between anthropogenic dens (or underground burrows) was used in conjunction with the movement distances to examine the assumption that underground burrows were common and widely distributed, whereas buildings and other anthropogenic structures were sparse and relatively far from each other. Nearest distances between den sites were analyzed using the Mann-Whitney U test. In addition, I calculated straight-line distance (m) between winter and the first maternity den for pregnant females. Females tend to have more than one maternity den during the summer for parturition and rearing of young. They change maternity dens after occupying them for approximately 1 month, usually when young are able to venture out of dens (Hwang unpubl. data). Therefore, movement distances for pregnant females were calculated as straight-line distance from winter den to the first maternity den.

Seasonal movement distances were compared between gender and winter grouping using two-way ANOVA. For movement distances between winter and maternity dens, I examined the influence of maternity den structures on the movement of pregnant females away from winter dens using a t-test.

5.2.4 Home range overlap

Spatial organization of striped skunks was assessed by examining the extent of overlap among home ranges of neighboring skunks. I calculated the percent overlap of home ranges, number of overlaps, number of male overlaps, and number of female overlaps for each individual for both 100% and 50% (core) MCP home ranges. I compared these variables between gender, age, and winter group using Mann-Whitney U tests. MCP-50% home ranges were square-root transformed to generate data normality. Home range sizes (MCP-50% and -100%) were analyzed using two-way ANOVA (gender and winter grouping). All values presented are mean ± standard error (SE).

5.3 RESULTS

5.3.1 Seasonal movement

From 2000 to 2003, I radiolocated 9 male and 21 female skunks from winter dens to summer home ranges. In addition, during 2001 - 2003, I followed 11 females in the summer to the following winter den. I found 16 solitary (7 underground burrow, 9 anthropogenic) winter dens and 17 communal (8 underground burrow, 9 anthropogenic) winter dens during 2000 - 2003. Solitary dens were typically occupied by a lone male. Winter group size of communal dens ranged from 2 to 8 (mean = 4, SD = 1.6). Communal dens usually consisted of one male and multiple females. Distance from winter den site to center of established home range in summer was similar ($F_{1, 30} = 0.29$, $P = 0.60$) between males (1.37 km ± 0.34) and females (1.28 km ± 0.18). Skunks traveled similar ($F_{1, 30} = 0.85$, $P = 0.37$) distances from communal (1.24 km ± 0.16) and solitary (1.56 km ± 0.48) winter dens to establish home ranges in the summer. Distance traveled was similar ($F_{1, 30} = 0.16$, $P = 0.70$) between skunks that over-wintered in underground burrows (1.25 km ± 0.22) and anthropogenic den structures (1.38 km ± 0.23). Seasonal movement from winter to summer (1.30 km ± 0.16) and summer to winter (1.56 km ± 0.30) did not differ ($F_{1, 40} = 0.65$, $P = 0.43$).

The distance to the next nearest den was similar ($U = 29862$, $n_1 = 288$, $n_2 = 219$, $P = 0.31$) between underground burrows (269 m ± 17.7) to that of anthropogenic dens (293 m ± 22.4). Thus, the assumption that underground burrows were more common and close to each other compared to anthropogenic dens was not substantiated. Skunks most often chose buildings for winter dens (Hwang et al. submitted 2004a), but distances between neighboring buildings (422 m ± 45.0) used by striped skunks were not significantly different ($U = 15364$, $n_1 = 288$, $n_2 = 119$, $P = 0.10$), than distance between underground burrows (269 m ± 17.7). Pregnant females on average traveled 1.3 km (± 0.21) from winter dens to establish maternity dens. Females that overwintered in underground burrows and building dens moved similar ($t = -0.60$, $df = 14$, $P = 0.56$) distances to maternity dens. Females that established maternity dens in anthropogenic den structures traveled similar ($t = -1.4$, $df = 14$, $P = 0.18$) distance from winter dens (1.0 km ± 0.21) as did females with maternity dens in underground burrow (1.6 km ± 0.39).

5.3.2 Spatial organization

In the summers of 2001 and 2002, I estimated 100% and 50% MCPs for 37 (10 male and 27 female) skunks (Table 5.1). Home ranges were similar (100% MCPs; $F_{1,30} = 0.011$, $P = 0.92$) between males and females when winter grouping was accounted for. Core home ranges (50% MCPs) were similar ($F_{1,37} = 0.36$, $P = 0.55$) between males and females when winter grouping was accounted. Skunks from winter communal dens had smaller ($F_{1,37} = 6.89$, $P = 0.01$) average 100% MCPs (3.9 km^2 ± 1.05) than skunks from solitary dens (10.2 km^2 ± 1.30) when gender effect was accounted for. Core home ranges (50% MCPs) were similar between skunks from communal dens and skunks from solitary dens. Percent overlap of 100% MCPs were similar ($U = 82.5$, $n_1 = 10$, $n_2 = 27$, $P = 0.072$) between males and females. However, percent overlap of 100% MCPs were significantly different ($U = 43$, $n_1 = 7$, $n_2 = 30$, $P = 0.015$) between winter

Table 5.1. Summary of striped skunk summer home range overlap results for gender (10 males, 27 females) and winter grouping (7 solitary, 30 communal). Data collected in southeastern Saskatchewan, Canada from 2000 to 2003. All values presented are means ± SE. Asterisk denotes significant differences ($P < 0.05$, Mann-Whitney U test unless stated otherwise).

Variables	Gender			Winter Grouping		
	Male	Female	P	Solitary	Communal	P
MCP[a, b, c] (km^2)						
100%	7.1 ± 1.2	3.8 ± 0.66	0.92	10 ± 1.3	3.9 ± 1.1	0.01*
50%	1.1 ± 0.25	0.45 ± 0.14	0.27	1.4 ± 0.27	0.58 ± 0.22	0.43
Percent overlap (%)						
100%	20 ± 5.4	32 ± 3.6	0.072	14 ± 6.2	32 ± 3.2	0.015*
between male-male	9.1 ± 4.2	----		8.9 ± 5.0	0.94 ± 0.90	
between male-female	24 ± 6.8	41 ± 6.2		18 ± 7.0	41 ± 5.6	
between female-female	----	22 ± 3.1		----	19 ± 3.0	
50%	18 ± 8.8	28 ± 7.6	1.0	17 ± 1.2	28 ± 6.9	1.0
between male-male	0.60 ± 0.60	----		0.90 ± 0.86	0.033 ± 0.030	
between male-female	14 ± 8.4	13 ± 5.5		16 ± 12.2	13 ± 5.0	
between female-female	----	8.6 ± 4.1		----	7.7 ± 3.7	
Number of overlap						
100%	5.5 ± 1.2	4.3 ± 0.45	0.27	4.9 ± 1.6	4.6 ± 0.45	0.78
50%	1.0 ± 0.33	1.2 ± 0.24	0.85	0.57 ± 0.30	1.2 ± 0.22	0.23
Number of male overlap						
100%	1.6 ± 0.58	1.4 ± 0.20	0.83	2.0 ± 0.76	1.4 ± 0.20	0.58
50%	0.10 ± 0.10	0.33 ± 0.092	0.29	0.14 ± 0.14	0.30 ± 0.09	0.53
Number of female overlap						
100%	3.9 ± 0.86	2.8 ± 0.36	0.23	2.9 ± 0.94	3.2 ± 0.39	0.81
50%	0.90 ± 0.31	0.81 ± 0.23	0.60	0.43 ± 0.20	0.93 ± 0.22	0.51

[a]Minimum convex polygon calculated in Animal Movement Extension in ArcView GIS. [b]Two-way ANOVA. [c]Least-square means.

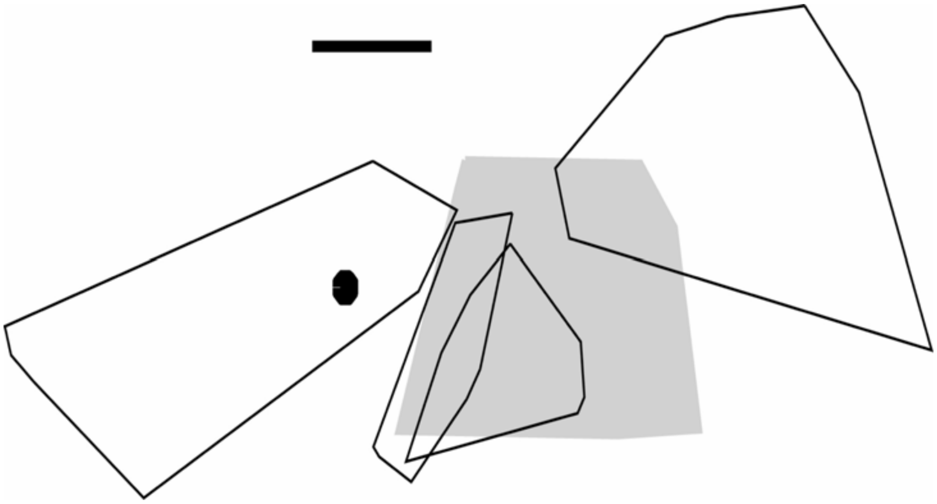

Figure 5.1.a Summer home range overlap of five skunks (1 male, 4 females) from a building winter communal den in Saskatchewan, Canada. Black dot (●) marks the location of the winter communal den, the grey shaded polygon is the home range of the male skunk, and the clear polygons are female home ranges. Scale bar is 1 km.

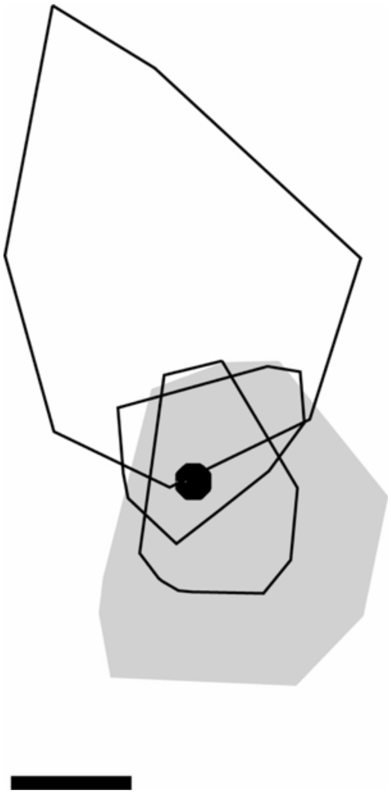

Figure 5.1.b Summer home range overlap of four skunks (1 male, 3 females) from an underground burrow winter communal den in Saskatchewan, Canada. Black dot (●) marks the location of the winter communal den, the grey shaded polygon is the home range of the male skunk, and clear polygons are female home ranges. Scale bar is 1 km.

grouping. Skunks from communal dens had higher percentage of home range overlap (32% ± 3.2; see Figure 5.1a & b) when compared with skunks from solitary dens (14% ± 6.2). Percent overlap of core home ranges was similar ($U = 135$, $n_1 = 7$, $n_2 = 30$, $P = 1.00$) between skunks from solitary and communal winter dens.

5.4 DISCUSSION

For animals that become inactive during winter, the choice of over-wintering site may have implications for the distribution during the following spring. This impact is even greater for animals that over-winter in groups such as striped skunks. In spring, skunks lost ~25% to 40% body fat (Hwang et al. 2004b). Thus, extensive movement in spring when resources are still limited is energetically costly to the animal. My results clearly indicate that the spatial location of the winter den used by skunks denning communally has direct implication on the distribution of summer home ranges of the skunks within the group and thus, winter dens affect the distribution of striped skunks in the landscape during other seasons.

Winter communal dens act as centers for dispersal or movement across the landscape for other species (Brown & Parker 1976, Graham et al. 2000). In species that share a winter den with potential mates, successful mating may pose additional evolutionary pressure (Douglas et al. 1976). Among mammals, for example, males of promiscuous species have disproportionate and highly variable mating success (i.e., a few males breed with most of the females in the population). Consequently, even if a winter den is valuable, the aggregation of kin in the den in the next winter may decrease its value to males (Bronson 1989). Alternately, females may benefit from remaining close to winter dens due to the increased risk in long-distance movement, and presumable benefit from greater familiarity with neighbors, good foraging sites, and shelters (Ratnayeke et al. 2002). Therefore, I predicted that males would move further from winter dens in the spring than females. Contrary to my predictions, all striped skunks moved short distances, often less than 1.4 km from winter dens irrespective of gender, age, and winter grouping. Instead of the early spring dispersal reported for North Dakota (Sargeant et al. 1982, Greenwood et al. 1985), I found juvenile males dispersing in late summer (July) and again during autumn (October -- Hwang unpubl. data). Adult males in my study area stayed in the general area in consecutive summers, and in one instance an adult male returned to the same winter communal den with some of the same female from previous winter and her young (Hwang unpubl. data). In my population, as is the case elsewhere (Verts 1967), turnover rate is high; 50-70% of juveniles do not survive the first year. Therefore, the evolutionary pressure on males to disperse is lower where the chances of males to over-winter and breed with their offspring are lower. With limited movement from winter dens in the spring, area surrounding winter communal dens represent a spatial “hot-spot” for skunk activities.

Movement distances from summer to winter were similar to spring movement distances. Female skunks in close vicinity to each other often over-winter in the same winter communal den. In Alberta, males moved a mean distance of 2.75 km (± 0.41) and females moved 2.51 km (± 0.50) in autumn during the pre-winter denning period (Gunson and Bjorge 1979). My study revealed that the average movement distance data from summer to winter was ca. 1.56 km, which is lower than previously reported in the literature. Possibly, this difference is because other studies often measured dispersal or movement distance from place of capture to the diurnal retreat that is furthest from origin (Gunson and Bjorge 1979, Rosatte and Gunson 1984). I measured distance from the center of summer home range to winter den site. With limited movement of females from summer to the following winter, the presence of winter communal dens influence the distribution of skunks across the landscape during other seasons.

The spatial organization of mustelids involves extensive intersexual overlap and limited intrasexual overlap, especially of males (Powell 1979, Hornocker et al. 1983). In polygynous mating systems, intrasexual overlap among males is often rare (e.g., *Mephitis mephitis* -- Wade-Smith and Verts 1982). The skunks in northern prairie exhibited extensive inter- and intrasexual overlap in home ranges. This is consistent with findings of Larivière and Messier (1998) on intrasexual overlap among females and Bixler et al. (2000) on intrasexual overlap among males. In my study, core areas of male and female ranges also overlapped extensively. Male skunks exhibit extensive range overlap with neighboring males and females. Skunks from winter communal dens had a higher percentage of home range overlap compared to skunks from solitary dens. This is probably due to the limited movement from winter dens, thus, causing spatial aggregation surrounding winter communal dens which leads to higher home range overlap between communal members.

In conclusion, my results support the hypothesis that communal winter dens influence the spatial dispersion and organization of striped skunks during summer. Due to restricted dispersal from winter to summer dens, a 2-km radius surrounding winter dens contains the highest concentration of skunk activity. Winter dens result in spatial aggregation of striped skunks in the prairies. For mitigation of nest predation on duck nests, proximity of winter dens to nesting areas may impact nest survival. Duck nests located closer to winter dens could potentially be within home ranges of several skunks, which could in turn decrease nest survival.

Aggregations of skunks in winter dens may represent major focal points of rabies transmission due to the apparent aggressive interactions between adult males in seeking communal dens with multiple females (Verts 1967). In the spring, skunk mating behaviour could also potentially increase the transmission of rabies in the population. The extensive overlap of home ranges surrounding a winter den could facilitate the spread of rabies epizootic because rabid skunks often move similar distances as non-rabid skunks (Storm and Verts 1966), thus, neighboring skunks could be potential targets. Rabies virus is transmitted through biting from infected individuals. If there is spatial aggregation of skunks in the landscape, the contact rate between neighboring skunks could potentially increased, thus, increasing the potential for spreading rabies in endemic population.

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CHAPTER 6. EFFECTS OF WINTER SEVERITY, INFECTIOUS DISEASES AND INDIVIDUAL CHARACTERISTICS ON SURVIVAL OF STRIPED SKUNKS

6.1 Introduction

Dynamics of animal populations are influenced by extrinsic environmental variables and intrinsic individual characteristics. Environmental variables may include climate (Weladji and Holand 2003), food resources (Wauters and Lens 1995), diseases (Kohler and Hoiland 2001, Cavanagh et al. 2003), parasites (Ives and Murray 1997, Tompkins and Begon 1999), predation (Banks and Powell 2004, Sundell 2003) and competition (Banks and Powell 2004). Intrinsic characteristics include gender, age (Singer et al. 1997), body condition (Hill et al. 2003, Schmutz and Ely 1999), and reproductive status (Jorgenson et al. 1997, Pilastro et al. 2003). For example, pregnant females may experience greater mortality because of energy allocated to parturition and nursing of young. In contrast, males do not face reproductive constraints during summer, and thus typically experience higher survival (Berteaux 1993, Cransac et al. 1997, Fancy et al. 1994, Toïgo et al. 1997).

Survival is affected by environmental conditions, and when these vary seasonally the variation in resource availability may magnify such constraints. Seasonality in resources is directly affected by environmental factors such as periodic fluctuations in precipitation and temperature, and provide both a direct effect on animals, and an indirect effect through fluctuations in other selective forces such as abundance or distribution of predators and disease agents. Disease agents and parasites influence the dynamics of animal populations either in a density-dependent (Anderson et al. 1981) or density-independent manner. The occurence of disease could be related to periods of the year when there is a high level of population mixing (i.e., breeding period), where susceptible individuals might be more exposed to infection. For example, raccoon rabies often peaks in the spring due to increased contact rate between individuals during breeding in late January and February (Fischman et al. 1992).

For animals living in northern environments, winter severity itself is a strong determinant of survival (Loison and Langvatn 1998, DelGiudice et al. 2002). Deep snow impedes mobility of animals (Crête and Larivière 2003) and reduces their foraging efficiency (Moen 1976). Cold ambient temperature increases energetic demands (Lyman et al. 1982), and may reduce access to or availability of food resources.

Individual characteristics also may affect survival. For example, males and females have different life requirements and strategies during the year, and the constraints imposed by parturition and nursing on females, or by mate seeking and breeding on males, may result in gender differences in survival (Norrdahl and Korpimäki 1998, Rödel et al. 2004). Age may also influence survival, as juveniles and adults are confronted by different mortality factors (Farand et al. 2002, Jorgenson et al. 1997, Millesi et al. 1999, Schwarz and Stobo 2000).

Effects of ecological pressures and individual characteristics likely do not act independently. For example, sub-lethal parasite loads may increase mortality when animals experience harsh environmental conditions (Murray et al. 1997). These effects can be accentuated in species that become inactive during winter. For such species, the ability to store body fat rapidly during a short period to sustain prolonged (≥ 6 months) winter inactivity is critical (Murie and Boag 1984). Animals that live in an environment with seasonal periods of predictable food shortage often experience hyperphagia to increase body fat reserve (Klenner and Kroeker 1990, Messier et al. 1992, Messier et al. 1994). Thus, these animals are more susceptible to poor body condition in the autumn and winter, and this usually translates directly into lower survival or reproduction. Hibernating mammals living in seasonal environments exhibit seasonal changes in body condition ranging from limited fat deposition in the summer to lipid storage comprising more than 20% of the body mass during autumn (Mech et al. 1968, Armitage et al. 1976, Adamczewski et al. 1992). The amount of body fat reserves represents a critical factor in survival.

Northern populations of striped skunks experience extreme seasonality in food resources, long periods of winter inactivity, and consequently display physiological and behavioral adaptations to living in the north (Hwang et al. submitted 2004a). Striped skunks enter daily torpor throughout the winter months (Hwang et al. submitted 2004a), they store fat reserves often equal in mass to their lean mass (Wade-Smith and Verts 1982), and often sleep in groups (e.g., communal denning) to facilitate thermoregulation for energy conservation (Hwang et al submitted 2004a). However, group denning may facilitate transmission of infectious diseases such as rabies, a significant mortality factor for prairie skunks (Hayles and Dryden 1970, Greenwood et al. 1997). Northern populations of striped skunks represent an ideal system to examine the interactive effects of environmental seasonality, disease, and individual characteristics on survival.

I hypothesized that winter survival (September to March) is mainly affected by extrinsic variables. I predicted that winter severity and rabies negatively impact winter survival. I investigated the effects of extrinsic and individual characteristics on the survival of striped skunks in the Canadian prairie from 2000 to 2003. The study coincided with the onset of a major rabies epizootic in skunks in my study area in 1999 and 2000, and lasted through its gradual recovery during 2001, 2002, and 2003.

6.2 Materials and methods

I estimated winter survival from September to March (190 days) for skunks that I had monitored from 2000 to 2003 in the study area. I used a multivariate Cox proportional hazards model (Cox 1972) to estimate survival of skunks on the basis of extrinsic and intrinsic covariates. In the proportional hazards model, the cumulative survival function $S(t)$ is expressed as a hazard function, which is the instantaneous probability of death:

$$h(t) = dS(t)/dt \qquad [1]$$

The proportional hazards model is:

$$h(t) = h_o(t)e^{[\beta 1\chi 1 + \beta 2\chi 2 + \ldots + \beta i\chi i]} \qquad [2]$$

where h_o is the baseline hazard function, e is the base of the natural logarithm, β_1 to β_i are regression coefficients, and χ_1 to χ_i are model covariates (see Cox 1972, Cox and Oakes 1984, Therneau and Grambsch 2000).

The null model is the survival function in the absence of covariates. I selected a suite of covariates related to survival to be included the model. I believed that increased winter severity would reduce survival. Also, rabies infection in skunks often peaks in the autumn (Hayles 1970); therefore, the incidence of rabies was considered in the model. Individual characteristics such as age and gender affect energetic requirements, movement patterns, and behaviours that might influence survival producing age- and gender-specific survival patterns. Hence, extrinsic covariates included in the survival analysis were winter severity index (WSI -- DelGiudice et al. 2002) and rabies; intrinsic covariates included gender, age, and body condition. WSI was calculated by adding the number of days with 15 cm or more snow on the ground to the number of days when minimum temperature were ≤ – 15 ^{o}C between December 1 to March 31 (Environment Canada). Rabies was a categorical variable of high (1) or low (0) incidence of skunk rabies in the study area from 2000 to 2003. High incidence is when there is skunk rabies epizootic in the study area; low incidence is when no skunk rabies cases were reported in the study area. Gender and age were categorical variables. Body condition was the percent body fat for each individual measured in the autumn using BIA. The full regression model for winter survival included effects of WSI, rabies, gender, age, and body condition.

I used Akaike's information criterion (AIC) to select the model that optimized goodness of fit and parsimony (Burnham and Anderson 1998). AIC is based on log-likelihood estimates and is defined as -2log*L* plus 2 times the number of parameters. AIC was used to identify the model that best represented the data with the fewest parameters. Due to small sample size, I used the modified criterion, AIC_c (Burnham and Anderson 1998). Subsequently, I ordered the set of possible models from "best" (i.e., lowest AIC_c) to "worst" (i.e., highest AIC_c). Model parameters were fitted by using SPSS (Version 12.0, SPSS Inc., Chicago, Illinois, USA).

I reported ΔAIC_c (= AIC_{ci} – min AIC_c) to compare the different models. Models with $\Delta_i \leq 2$ are considered to have substantial support, models with Δ_i of about two to seven have considerably less support. Models with $\Delta_i \geq 10$ have essentially no support. I calculated the normalized AIC weight (ω_i) for each model, which is considered as a measure for the weight of evidence in favour of model *i* as being the actual best model in the set (Burnham and Anderson 1998). For models with $\Delta AIC_c < 2.0$, I used model-averaging for parameter estimation (Burnham and Anderson 1998). Unconditional standard errors were estimated for the model-averaged coefficients (Burnham and Anderson 1998). All values presented are means ± SE.

6.3 Results

I radio-tracked 99 skunks (43 males, 56 females) from September to March 2000-2003. Body condition of skunks during autumn was similar ($t = -1.46$, $df = 97$, $P = 0.15$) between males (37.6% ± 1.68) and females (40.4% ± 1.06). However, adult skunks were in better ($t = -3.85$, $df = 58$, $P < 0.001$) body condition (42.3% ± 0.84) than juveniles (34.8% ± 1.76).

Model selection using AIC_c suggested that three models for winter survival had strong support (Table 6.1). The model-averaged regression model for winter survival was expressed with regression coefficients as (Table 6.2):

$$h(t) = h_0(t)e^{[0.067\,(WSI)\,-\,0.10\,(condition)\,-\,1.74\,(rabies)\,+\,0.77(gender)\,+\,0.69(age)]} \qquad [3]$$

Winter survival can be predicted using equation 3 as follows. Consider a year with winter severity index of 40 (i.e., 40 days with either $\leq$-15°C and/or $\geq$15 cm of snow on the ground) and no rabies cases in the area. For a period of 190 days (i.e., from early September to end of March), eqn. 3 would predict that for male juvenile skunks with 40% body fat reserve, $h(190) = 0.09$, where $h_0(190) = 0.453$. Converting to $S(190)$, skunks with these parameters could be expected to survive 190 days 91.3% of the time. In contrast, male juvenile skunks with 10% body fat reserve could expect to survive 190 days 15.9% of the time (Figure 6.1.a). Thus, winter survival is positively related to body condition of skunks. Furthermore, WSI has an inverse relationship with winter survival rates (Figure 6.1.b), with high WSI leading to lower winter survival in skunks. During a rabies outbreak and with WSI of 40, juvenile males with 20% body fat have $h(190) = 3.85$, where $S(190) = 2.1\%$; in contrast, with no rabies, $h(190) = 0.68$, and $S(190) = 50.9\%$ (Figure 6.1.c). In general, adult females had higher survival rates compared to juvenile females, and males (see Figure 6.1.d).

Table 6.1. Rank of models (using Akaike's Information Criterion [AIC_c] adjusted for sample size) used to estimate Cox proportional hazard functions for winter survival of striped skunks in southeastern Saskatchewan, Canada, September to March 2000-2003. The best-approximating model results in the lowest AIC_c; ΔAICc of >2.0 was representative of a significant decrease in the fit of the model. The number of estimable parameters (K) and Akaike weights (ω), which indicate the relative likelihood of a model given the data and the set of candidate models are provided.

Model	K	AIC_c	ΔAIC_c	ω_i
WSI + Condition + Rabies	3	287.91	0.00	0.31
WSI + Sex + Age + Rabies	4	287.91	0.00	0.31
WSI + Condition + Sex + Age + Rabies	5	288.93	1.01	0.19
WSI + Condition + Rabies + Age	4	289.92	2.00	0.11
WSI + Rabies	2	291.41	3.49	0.05
WSI + Condition	2	295.24	7.32	0.01
WSI + Condition + Age + Sex	4	295.85	7.93	0.01
WSI + Age + Condition	3	297.27	9.36	0.00
WSI + Sex + Age	3	301.57	13.66	0.00
Rabies + Sex + Age	3	302.80	14.89	0.00
WSI + Sex	2	303.06	15.14	0.00
Condition + Age + Sex + Rabies	4	304.10	16.18	0.00
Rabies + Sex	2	304.97	17.05	0.00
Rabies + Condition	2	305.00	17.08	0.00
Sex + Condition	2	305.65	17.73	0.00
Age + Condition + Rabies	3	306.82	18.91	0.00
Rabies + Age	2	307.24	19.32	0.00
Sex + Age + Condition	3	307.42	19.51	0.00
WSI + Age	2	307.77	19.85	0.00
Condition	1	308.28	20.37	0.00
Sex + Age	2	310.30	22.38	0.00
Age + Condition	2	310.37	22.45	0.00
Sex	1	311.58	23.67	0.00
Null	0	316.33	28.42	0.00
Age	1	316.86	28.95	0.00

Table 6.2. Model-averaged coefficients (β) of the three best AIC_c models ($\Delta AIC_c < 2.0$) of the Cox proportional hazard function for winter survival of striped skunks in southeastern Saskatchewan, Canada, September to March 2000-2003. Model coefficients, 95% upper (95UCL) and lower (95LCL) confidence limits estimated from unconditional standard errors are provided.

Parameters	β	95UCL	95LCL
WSI	0.067	0.10	0.038
Rabies	-1.7	-0.51	-2.8
Condition	-0.10	0.043	-0.18
Gender	0.77	1.1	0.40
Age	0.69	1.1	0.28

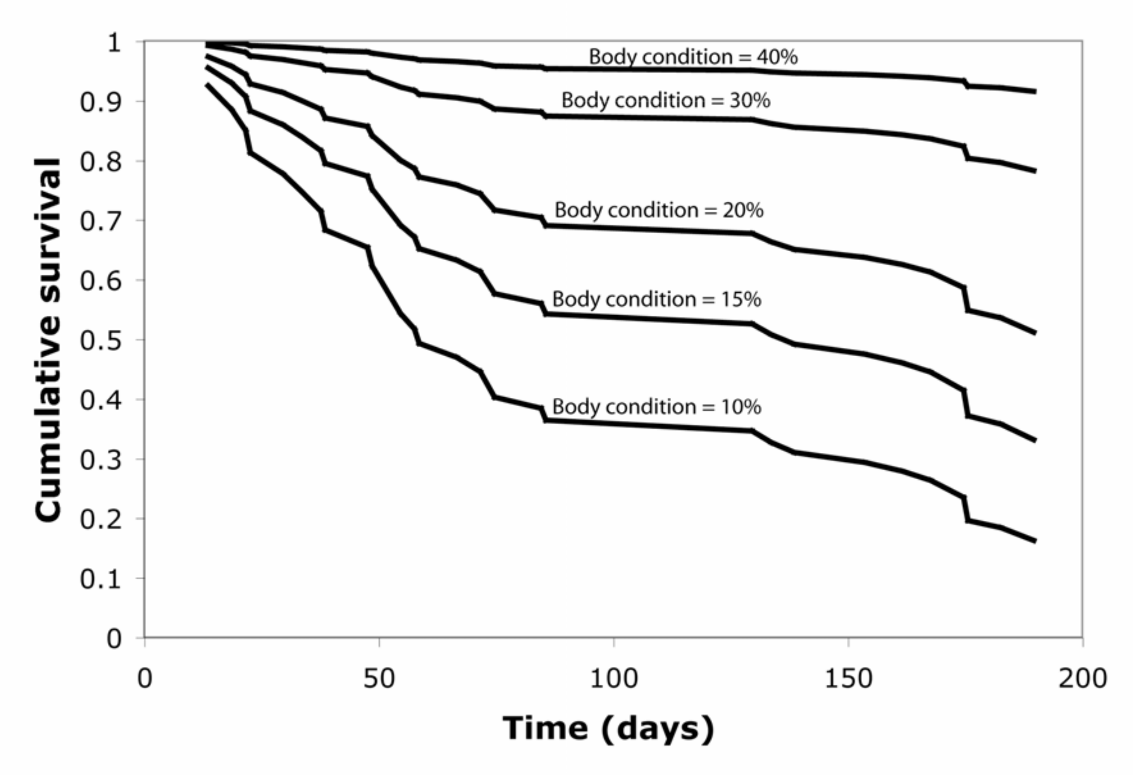

Figure 6.1.a. Prediction of winter cumulative survival using equation 3 [$h(t) = h_0(t)e^{[2.4 - 0.10 (condition)]}$] where covariates (i.e., male, juvenile, WSI = 40, and low prevalence of rabies) were held constant with varying levels of body condition (i.e., 10%, 15%, 20% 30%, and 40%).

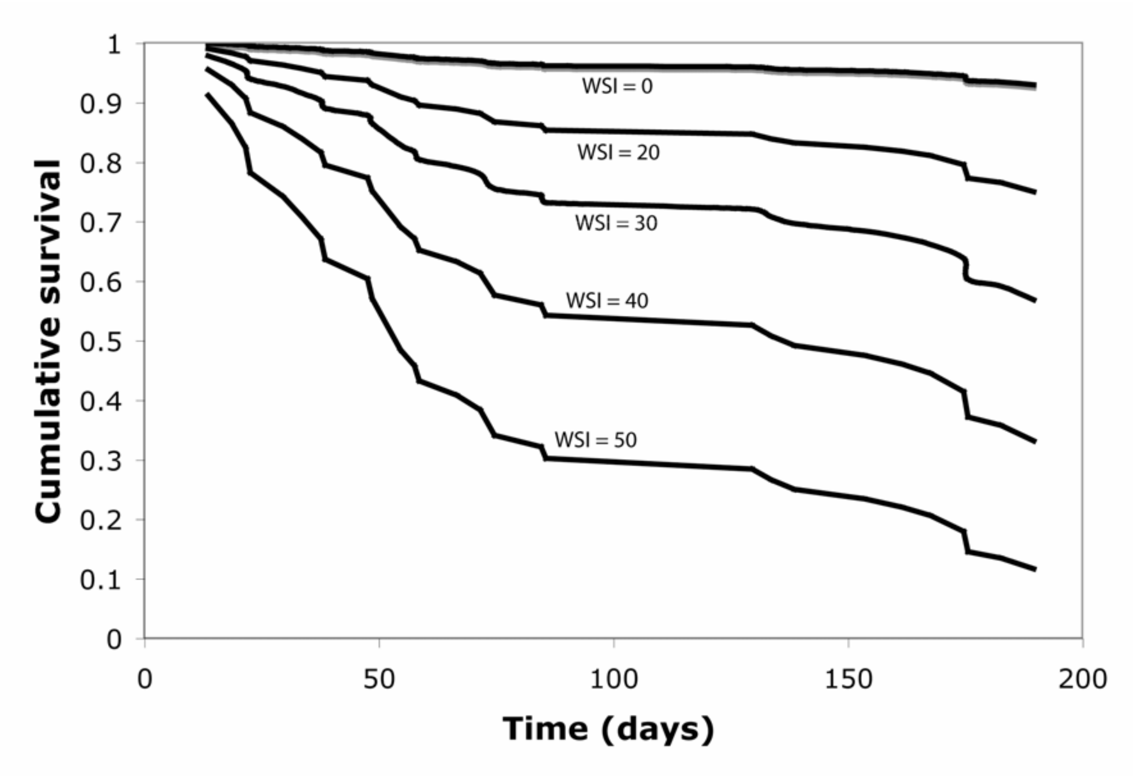

Figure 6.1.b. Prediction of winter cumulative survival using equation 3 [$h(t) = h_0(t)e^{[0.067\,(WSI) - 1.78]}$] where covariates (i.e., male, juvenile, low prevalence of rabies, and 15% body condition) were held constant with varying levels of WSI (i.e., 0, 20, 30, 40, and 50).

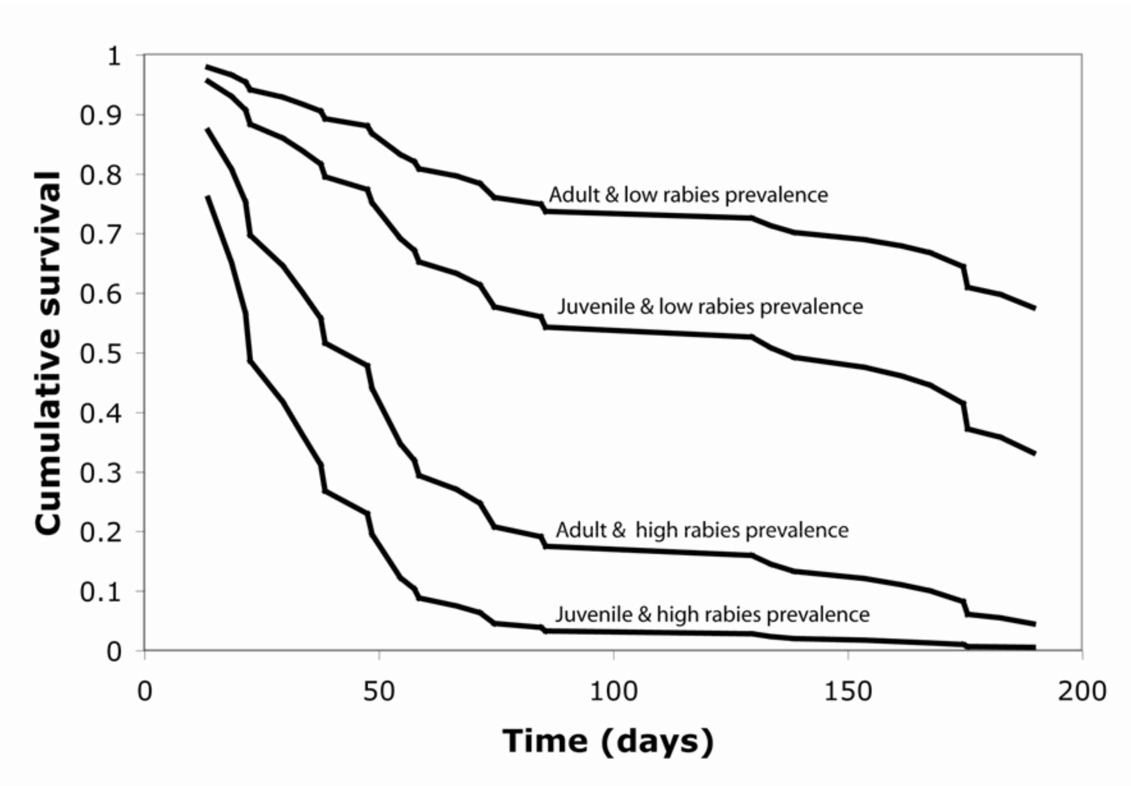

Figure 6.1.c. Prediction of winter cumulative survival using equation 3 [$h(t) = h_0(t)e^{[0.69\ (age) - 1.7\ (rabies) + 1.9]}$] where covariates (i.e., males, WSI = 40, and 15% body condition) were held constant with varying parameters of age and rabies (i.e., adult and low rabies prevalence, juvenile and low rabies prevalence, adult and rabies, and juvenile and rabies).

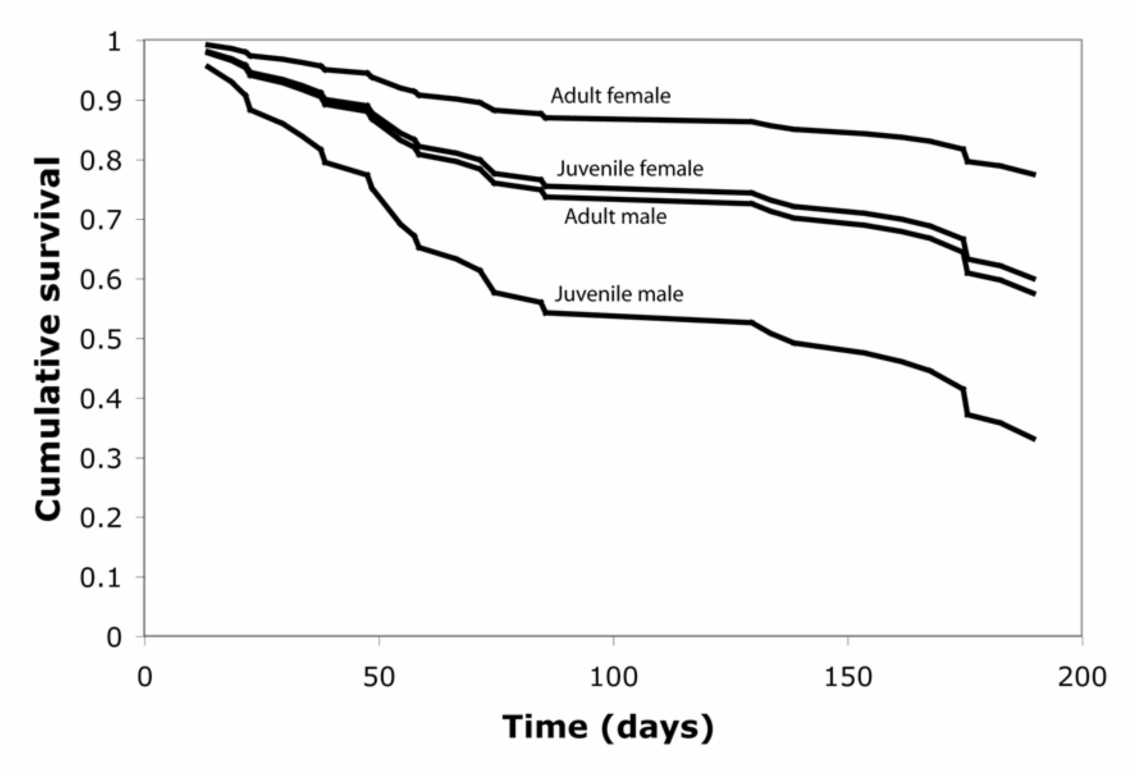

Figure 6.1.d. Prediction of winter cumulative survival using equation 3 [$h(t) = h_0(t)e^{[0.77\,(gender)\,+\,0.69\,(age)\,-\,0.56]}$] where covariates (i.e., WSI = 40, low prevalence of rabies, and 15% body condition) were held constant with varying parameters of gender and age (i.e., adult males, juvenile males, adult females, and juvenile females).

6.4 Discussion

My results demonstrate that winter severity and rabies negatively affect winter survival of striped skunks. Severe winter conditions significantly reduced winter survival of skunks, irrespective of gender and age. Winter condition (e.g., snow depth and low ambient temperature) may impedes mobility of skunk and increased metabolic energy requirements. Early snowfall and accumulation in autumn would decrease foraging attempts of skunks to store body reserves in anticipation of periods of food shortage. Deep snow throughout winter also prevents skunks from venturing out of den sites in search of food. In addition, low ambient temperature during winter creates high ambient-to-body-temperature gradient, thus, increasing metabolic energy requirement and rate of depletion of body reserves. Furthermore, skunks enter daily torpor in the winter. Hence, the size of body reserves has to be greater than the rate of depletion of the reserve times the length of winter. After a long and severe winter, skunks should emerge from winter inactivity with lower body condition, which directly influence their survival during spring when food resources are still scarce.

Rabies transmission requires direct contact between infected and susceptible individuals, and it probably acts in a density-dependent manner in regulating population. Due to spatial aggregation of skunks in the autumn and early winter, rabies is an important mortality factor during outbreak years. During rabies epizootics, males have lower survival compared to females probably due to their increased roaming in the autumn to find suitable den sites and the apparent agonistic behaviour between males which results in increased transmission (Verts 1967).

Although body condition was an important factor in influencing winter survival as shown by AIC model selection procedure, the body condition coefficient was not statistically significant. This is probably because the average percent body fat of skunks captured in the autumn was 39.3% (SD = 9.45, n = 99), with few individuals having either 0% or 53.8% body fat. With such low variation in autumn body condition, it represents the physiological adaptations of skunks where animals have adapted to winter severity of the northern climate by increasing fat deposition in the autumn, thus, increasing their over-winter survival. My results indicate that there is a threshold in early autumn body condition (i.e., > 30% body fat reserve) of skunks that allows for high winter survival even in years with high winter severity. Therefore, body condition of skunks represents a biologically if not statistically significant factor in influencing winter survival.

Moreover, gender differences in winter survival were probably caused by the different over-winter strategies of males and females. During the winter, females experienced higher survival rates than males. In the autumn, females often aggregate and form communal winter den where they use social thermoregulation to conserve energy (Hwang et al. submitted 2004b). In these winter communal dens, there is only one adult male with the female groups (Hwang et al. submitted 2004b). Thus, juvenile and adult males often over-winter solitarily and would have higher energetic demand compared to communal members (Hwang et al. submitted 2004a), thus, lowering their winter survival. Furthermore, juveniles tend to have lower survival compared to adults. Juveniles have only a short period of time in the summer after weaning to gain enough body fat reserve (~20 - 30%) to survive the period of winter inactivity and fasting.

Also, juveniles might be less experienced in finding food resources, suitable den sites, and making insulating nests (Gebczyòska and Gebczyòska 1971). This emphasizes that pressures linked to seasonality can have a compounding effects on other stresses on animals.

My study helps further the understanding of the link between climate and biogeography of species that undergo winter inactivity, specifically skunks (Humphries et al. 2002). With climate change, the Northern Hemisphere is experiencing increased temperature and decreased precipitation, with freeze-free periods lengthening and a 10% decrease in snow cover and ice since 1960s (Climate Change 2001). By understanding the effects of winter climate on the population dynamics of hibernating or torpid species, one could further project the ecological responses to climate change (Walther et al. 2002). Winter severity probably poses a limit on the northern distribution of the species. These results add support to the growing body of literature that suggest that disease/parasite effects are compounded when environmental conditions are severe or body condition of animals is poor (Murray et al. 1997). Because winter survival is closely correlated to winter climate and body condition (Sœther 1997, Diaz and Alonso 2003, Post and Stenseth 1999), with climate change and the subsequent warming of winter in northern latitudes, dynamics of many animal populations will be significantly affected.

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CHAPTER 7. SYNTHESIS

Striped skunks occupy a large geographic range in North America, occurring in many different ecosystems in which they have evolved to exploit seasonal resources. From physiological and ecological perspectives, I examined the processes and strategies developed during the three critical periods: pre-winter, winter, and post-winter emergence of skunks. In so doing, I have illustrated some of the adaptations and strategies which enable this small carnivore to survive in the northern part of their distribution.

7.1 The significance of daily heterothermy in carnivores

During a period when skunks do not have access to food, they are capable of using daily torpor (Chapter 3). In the Order Carnivora, bears (*Ursus*) also hibernate (Watts 1981), and there are suggestions that American badgers (*Taxidea taxus*) may also enter torpor during winter (Harlow 1981). Torpor occurs in at least nine mammalian orders (Geiser and Ruf 1995, Geiser 1998). Unlike ectotherms, daily heterotherms and hibernators have precise body temperature control during hypothermia (Lyman et al. 1982, Geiser and Ruf 1995, Geiser 1998). It has been proposed that torpor is likely pleisiomorphic (ancestral) in mammals, but it is not functionally primitive (Geiser 1998). The capacity for torpor has been lost in lineages of mammals that can survive without the requirement for periods of heterothermy for energy conservation, and retention of torpor may be determined by diet and body size

(Geiser 1998, Lovegrove et al. 1999). In bears, there are intraspecific variation (related to latitudinal gradient) in torpor expression, for example, in the south, only pregnant females hibernate, whereas in the north, both sexes hibernate (Rogers 1999). In the southern U.S.A and in Mexico, skunks are active year round. However, this study has shown that in the north, some skunks use daily torpor for energy conservation. The intraspecific variation in torpor expression suggests that torpor is a pleisiomorphic trait in mammals, with animals that have no seasonal requirement for energy conservation to have lost or not express the trait, rather than having heterothermy evolving multiple times across and within taxa. In order to fully examine the intraspecific variation of torpor in skunks, it would be imperative to study the capability of torpor expression in a southern population of striped skunks by transplanting individuals to the north and observing their physiological responses during winter.

During autumn, skunks forage extensively to store body fat and may reach extremely obese proportions, some individuals possessing as much as 500 to 600 g of fat per kg of lean body mass (Chapter 3 and Appendix A). This apparent hyperphagy and obesity is a physiological adaptation to prepare for winter torpor. The cost of excessive fat storage (Witter and Cuthill 1993, Gosler et al. 1995) such as difficulty in mobility and increased energetic requirement while foraging is mitigated by increased survival during winter (Chapter 6). Because skunks undergo winter torpor, the selection of den sites during this critical life history stage probably represents a strong selective force (Chapter 4). With anthropogenic activity changing the prairie landscape, skunks have adapted to habitat fragmentation by using abandoned farm buildings, specifically, old farm houses and sheds, as winter den sites. These den structures provide safe and relatively large spaces to accommodate groups of animals that hibernate communally during winter.

Furthermore, the importance of winter severity as a parameter influencing the population dynamics of skunks was clearly emphasized by the results of my research (Chapter 6). Winter conditions negatively affect winter survival, with severe winters causing high mortality. However, there is a physiological benefit to torpor and huddling in skunks. If skunks have reached the threshold body condition of ~30% total body fat, they would be able to survive the winter irrespective of environmental conditions. This clearly demonstrates the adaptations developed by northern population of skunks in surviving the long periods of winter and fasting.

7.2 The significance of winter sociality for a solitary carnivore

Skunks are solitary throughout the year, except during winter, when animals aggregate in communal dens (Chapter 3 and 5). This behavioural adaptation enabled animals in communal dens to huddle and conserve energy expenditure by decreasing the exposed surface area to reduce heat loss to the environment. Winter sociality in skunks occurs only in the northern latitudes where winter is harsh and resources are seasonal. In southern range of the species, skunks are solely solitary except during breeding season (Wade-Smith and Verts 1982). The following question remains: are physiological benefits the main contributing factor in winter sociality of small solitary carnivores? There are detriments to group living, namely, increased intensity of resource competition such as for food and mates, increased likelihood of disease and parasite transmission, and increased conspicuousness which makes the group more vulnerable as prey (Alexander 1974). In contrast, there are some benefits to group living, although they are neither universal or automatic (Alexander 1974). Some of these benefits include protection from environment by huddling, decreased predation by increased predator detection rate, and cooperation in finding and defending resources (Alexander 1974). Group living would only have evolved if the benefits to the animals can be translated directly into fitness potential and outweigh the cost of group living. Predator of skunks in the prairies is the coyote (*Canis latrans*). In the winter, there was no incidence of coyote predation at winter den sites in the study area from 1999 - 2003. Skunks do not feed in the winter, thus, there is no competition for food between group members. Consequently, in northern populations of skunks, the cost of group living is mainly increased disease and parasite transmission between communal members.

I have demonstrated a physiological benefit of group living in skunks, which can be translated into increased body condition in the spring when resources are still unavailable, thus directly increasing fitness potential of group members (Chapter 3). Although I was unable to examine the genetic composition of communal members to elucidate the genetic structure of the population, there is evidence of reproductive fitness benefits in winter communal grouping. The skewed sex ratios in winter communal dens of one adult male and multiple females indicate the potential role group living plays in reproduction. Because skunks are able to reproduce at 10 months of age (Wade-Smith and Richmond 1978), juvenile female skunks in winter groups are potential mates for the adult male. The breeding season is from late February to early March, at which time burrow entrances could sometimes still be under snow and ice making it impossible for skunks to emerge to find mates (Hwang unpubl. data). In years with late snow melt, deep snow also may impede the ability of skunks to find mates in the area. Thus, by having a group of females and male over-winter together, they could mate in late winter, irrespective of winter or spring conditions. Reproductive advantages and physiological benefits of winter group living probably contribute to the evolution of winter sociality in a solitary carnivore living in the north.

Winter group living of animals also affects the spatial distribution of the population in the following summer (Chapter 5). Due to limited movement from winter dens, skunks from winter communal dens have greater overlap in home ranges than skunks from solitary dens. The consequences on genetic structure of northern population of striped skunks are unknown. Furthermore, winter dens act as "hotspots" in the landscape, and could potentially influence nest predation and disease transmission, specifically rabies in the area (Chapter 5).

7.3 Concluding remark: climate change and resource seasonality

Climatic variation (local or global) affects life-history and population dynamics of animal populations (Post and Stenseth 1999, Weladji and Holand 2003). Energetic constraints are used commonly to explain animal distributions and biogeography (Humphries et al. 2002, Walther et al. 2002). The recent rate of climate warming has been greater than at any other time during the last 1000 years (Climate Change 2001). With this recent climate change, mid- and high latitude regions of the Northern Hemisphere are experiencing changes in precipitation and temperature regime (Climate Change 2001). There is evidence of ecological responses to recent climate change (see review Walther et al. 2002) with earlier spring and later onset of autumn phenological events (i.e., timing of seasonal activities of animals and plants), consequently changing the seasonality of resources. Because physiology and ecology of organisms are highly linked to resources, climate change could potentially affect the range and distribution of species, the composition of and interactions within communities, and the structure and dynamics of ecosystems (Walter et al. 2002)

With the current changes to the climate of the earth and the associated warming of the northern environments, I can only speculate on the implications for hibernating species and their distribution in these northern areas. In the short-term, the rise in temperature in northern environments would be detrimental to the hibernating species (i.e., bats, marmots and ground squirrels) because it would raise the hibernaculum temperature several degrees above that predicted to be optimal for energy conservation (~ 2 ^{o}C; McNab 1974). Thus, hibernating species would not be able to achieve the minimum metabolic rate; consequently, increasing the energetic demands and the risk of deficit in fat storage during hibernation. However, in the long-term, with increasing temperature and precipitation, perhaps food resources will be available and the animals would not have to hibernate due to food shortages. Arguable, the next century will have profound effects on the lives and distribution of species adapted to hibernation and torpor to survive periods of energy conservation when resources are unavailable.

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APPENDIX A. EVALUATING BODY CONDITION OF STRIPED SKUNKS USING NONINVASIVE MORPHOMETRIC INDICES AND BIOELECTRICAL IMPEDANCE ANALYSIS

(Wildlife Society Bulletin 2005, in press)

A1. Introduction

Assessment of body composition and body condition of animals in the wild is an important aspect of animal ecology. In northern environments food availability varies with season, with most primary productivity occurring during spring and summer. Animals that rely on seasonal foods must find ways to cope with prolonged food shortages by migrating to areas with predictable food resources, caching food, or becoming dormant to decrease energy consumption. In anticipation of food shortages, animals often experience hyperphagia and increase body fat reserves (Virgil and Messier 1992, Messier et al. 1992). As a result mammals inhabiting the northern environments exhibit seasonal changes in body condition ranging from limited fat deposition in the summer to more than 20% fat deposition in autumn (Mech et al. 1968, Armitage et al. 1976, Adamczewski et al. 1992).

Body composition is the quantification of ingesta-free components such as water, fat, protein, and ash or mineral of the animal (Robbins 1993). Measure of body composition can be accurately obtained through direct carcass analysis (Reynolds and Kunz 2001) and estimated indirectly through nondestructive methods (Speakman 2001).

Body condition is used as a term to describe the variation in body composition (Krebs and Singleton 1993) and is a measure of the abundance of potential energy stored in the body fat of an animal relative to its body size (Woolnough et al. 1997, Cattet 2000). The term body condition is an indication of the animal's energetic state (Schulte-Hostedde et al. 2001) and is assumed to relate to a wide range of attributes, including health and aspects of ecological performance, such as fitness, ability to avoid or fend off predators, ability to hold a territory, and ability to forage and reproduce successfully (Adamczewski 1993, Noyce and Garshelis 1994, Atkinson and Ramsay 1995, Jakob et al. 1996, Hodges et al. 1999).

Techniques for accurately measuring body composition may allow animal ecologists to assess the relationship between body condition and survival, productivity, and behavior in populations (Walsberg 1988, Green 2001). Direct assessment of body composition is time consuming, tedious, and expensive (Reynolds and Kunz 2001). Also, the greatest limitation in estimating body composition by direct analysis is the inability to conduct measurements on live animals.

Noninvasive measurements of body composition involve the development of a condition index based on morphometric measurements. Three commonly used condition indices are ratio index, slope-adjusted ratio index, and residual index (Jakob et al. 1996). Ratio index is obtained by dividing body mass by a linear measure of body size (e.g., body length), or by linear measure raised to the power of 2 or 3. Sloped-adjusted ratio index differs from ratio index only in that the slope of the line is generated from independent data instead of being assumed on the basis of general relationship in body shape (Le Cren 1951). In contrast, residual index is obtained by regressing body mass on body size so that residuals are independent of body size.

These indices often are not validated and are incapable of quantifying the fat reserves of an animal (Walsberg 1988, Cattet 1990, Krebs and Singleton 1993, Green 2001, Hayes and Shonkwiler 2001). The ratio between body mass and body length assumes that body mass and size scale isometrically, and an animal with a higher ratio is in better condition than an animal with lower ratio. The rationale for ratio index where body mass divided by body length raised to the power of 3 was based on the assumption that body mass should be related to the cube of length if mammals are like simple cylinders (Le Cren 1951, Krebs and Singleton 1993). However, many studies used an exponent of 2 and 3 without justification (Angerbjörn 1986, Wirsing et al. 2002). The cube law may not apply to all mammals and the exponent used in ratio indices often is not validated (Krebs and Singleton 1993). Also, ratio indices are not independent of body mass or size (Lidicker and Ostfeld 1991, Jakob et al. 1996). Alternatively, body mass can be regressed on body size and the residuals of this regression can be used as an index of body condition; an individual with a positive residual is in better condition than an individual with a negative residual (Dobson 1992, Dobson and Michener 1995, Guinet et al. 1998). Residual index, however often is not validated to reflect fat content. Studies that have evaluated the residual condition index have found negative results where indices do not explain any variation in fat content (Virgl and Messier 1992, Krebs and Singleton 1993). Validation of condition indices has been performed on 3 carnivores (*Martes americana* – Buskirk and Harlow 1989, *Alopex lagopus* – Prestrud and Nilssen 1992, *Canis latrans* – Huot et al. 1995), and each species had a different condition index that was the best predictor of its total body fat.

An alternative noninvasive method to estimate body composition is bioelectrical impedance analysis (BIA). Bioelectrical impedance analysis was initially developed for humans (Lukaski et al. 1986) and has been used for rats (*Rattus*) under laboratory conditions (Hall et al. 1989), and under field conditions for rodents (*Tamiasciurus hudsonicus* and *Marmota flaviventris* -- Wirsing et al. 2002), rabbits (*Lepus americanus* -- (Wirsing et al. 2002), martens (*Martes americana* – Raphael et al. 1991), wombats (Woolnough et al. 1997), seals (Bowen et al. 1999), bears (Farley and Robbins 1994), and moose (Hundertmark and Schwartz 2002). Bioelectrical impedance analysis offers a rapid, nondestructive, and objective means to estimate body composition. It measures the resistance to conduction (in ohms) of a low-level alternating current (800 µA at 50 kHz) in an organism (Van Marken Lichtenbelt 2001). Since the conductivity of body lipids is 4–5 % that of lean tissue, body fluids, and bone, the resistance measured by BIA is an indicator of body water content and lean body mass (Walsberg 1988, Hall et al. 1989). Body mass and other morphometric measurements are often used in conjunction with BIA measurements in multiple regression models to predict body composition (Lukaski et al. 1986, Farley and Robbins 1994, Woolnough et al. 1997).

I tested 5 standard morphometric body condition indices and BIA as potential estimators of body fat reserve in striped skunks (*Mephitis mephitis).* Striped skunks undergo periods of dormancy during winter as an adaptive strategy for food shortages (Mutch and Aleksiuk 1977). I were interested in understanding seasonal changes in body condition in order to investigate effects of the adaptive strategies on the life history of the animal. I determined whether condition indices and BIA measurements were significant predictors of body water and fat as measured by direct chemical analysis. The objectives of this study were 1) to test the validity of condition indices, and 2) to evaluate the validity of using BIA to measure body condition of striped skunks in the field.

A2. Methods

A2.1 Field procedure

I captured 26 wild skunks (12 males, 14 females) around farmsteads and homes surrounding the city of Saskatoon (52^{o} 10' N, 106^{o} 41' W), Saskatchewan, Canada. I captured animals from April – October 2001 in plastic live-traps (Minnesota Plasti-Catch, Mitlyng Development, Minn.) baited with canned cat food. Upon capture, I immobilized skunks with halothane (M.T.C. Pharmaceutics, Cambridge, Ont.) and Telazol® (Fort Dodge Animal Health, Fort Dodge, Ia.) following procedures of (Larivière and Messier 1996a). I applied halothane (8 ml) directly under the door of plastic traps (23 * 23 * 60 cm). I left animals undisturbed for 2–4 min in the trap. After animals were initially anesthesized by halothane, I began handling procedures by an intramuscular injection of Telazol® (standard dosage of 10mg/kg) at the shoulder of the animal.

I weighed all animals to the nearest gram with an electronic scale (Sartorius PT6, Goettingen, Germany) to obtain total body mass (TBM). I took snout-to-vent (SVL) measurement following the dorsal contour of the animal and also measured chest circumference (CC) of each animal. I subsequently measured skunks using the BIA analyzer. Resistance (R_s) and reactance (Xc) were recorded with the Model 101A (RJL Systems, Detroit, Mi.) which read 0–10000 ohms with a resolution of 1 ohm and an accuracy of ±0.5%. I placed skunks sternally recumbent in a standard position on a dry plastic sheet. The plastic sheet was used to prevent possible loss of electrical current to the ground for wet animals. I used needle electrodes (21 g, Vacutainer® needles; Becton Dickinson and Company, Franklin Lake, Nj.) with the short end inserted subcutaneously into the animal and the long end clamped to the impedance meter's cable. Electrode positions on skunks were standardized for consistency among all subjects (Farley and Robbins 1994). I measured impedance with the anterior electrode pair clamped to the upper lip (needles were not used) at the level of the canines. Good electrical contact was ensured by wetting the lips with water. I placed posterior electrodes on the needle inserted subcutaneous at the base of the tail with the current-carrying electrodes always placed on the right side of animal. To increase accuracy, I obtained multiple readings until 2 consecutive measures fell within 5% of each other (Hildebrand et al. 2000). I averaged these 2 readings to produce a final measure of resistance. Electrodes remained in place until readings of R_s and Xc stabilized (usually <5 s). The environmental temperature under which I took BIA measurements varied from 0^o to 27^oC. Because I were interested in studying a population of marked animals in the wild, I measured BIA before and after the application of 2 2*5-mm metal eartags (Monel #3, National Band and Tag Co., Kent.) to investigate whether metal eartags would affect results.

I then euthanized each animal with T-61® (0.3ml/kg; Hoechst Animal Health Benelux, Bruxelles, Belgium) injection into the heart. I carefully examined all skunks for injury post-mortem. After euthanasia, I individually triple-wrapped animals in plastic and stored them at –20°C to prevent water loss through storage.

A2.2 Lab procedure

Dissection. I removed ingesta within the gastrointestinal tract and anal scent glands. I skinned all animals and weighed total dissectible fat (TDF) with an electronic scale for comparison with total fat content measured using chemical extraction. Most of the dissectible fat was subcutaneous fat on the rump and back of the animal, and some was taken off surrounding internal organs, such as kidneys.

Complete chemical analysis. I homogenized the viscera, total dissectible fat, and ingesta-free carcass in a commercial grinder. Complete recovery of all tissue was ensured by thoroughly scraping the grinder between each homogenization. I retained subsamples (160 g) from each animal for chemical analyses. I obtained total body water (TBW) by oven-drying at 90°C for 5 days until consecutive weighing of samples in the oven produced constant values (Kerr et al. 1982). The dried homogenate aliquot subsamples (10 g) were finely ground in a coffee grinder and used for all subsequent chemical analyses. Total lipids (TBF) were extracted for >8 hours in a Soxhlet apparatus with petroleum ether as solvent (Dobush et al. 1985). I carried out all assays in duplicate (differences between duplicates were less than 5%) and used means in all calculations. I determined lean dry mass (LDM) by subtracting TBF and TBW from TBM (Reynolds and Kunz 2001).

A2.3 Statistical analysis

Body condition indices. I assessed the accuracy of 5 standard body condition indices to estimate body fat by least-square linear regression. I obtained ratio index by dividing body mass by body length (Jakob et al. 1996). I obtained additional ratio indices by dividing body mass by body length raised to the power of 2 and 3. I obtained slope-adjusted ratio index by first regressing body mass on body length after both variables were ln transformed (Le Cren 1951, Jakob et al. 1996). I then used slope of the regression line in the ratio index by dividing body mass by body length raised to the power of the slope. I obtained residual index by regressing ln-transformed body mass against ln-transformed body length (Kreb and Singleton 1993, Schulte-Hostedde et al. 2001).

Bioelectrical impedance analysis. Conduction of an electric current is proportional to the water and electrolyte distribution within an animal. Resistance (R_s) and reactance (Xc) can be used to calculate impedance (Z), where

$$Z\ (\Omega) = (R_s^2 + Xc^2)^{0.5} \qquad [1]$$

Biological impedance varies inversely with the volume and water composition of the body (Bowen et al. 1999). Impedance is related to bioelectrical conductor volume as follows:

$$\mathrm{Vol}\ (\mathrm{cm}^2/\Omega) = (L^2/Z) \qquad [2]$$

where L is body length (cm). Because electrodes were placed on the snout and vent, L is replaced by SVL for further analyses (Hall et al. 1989). Since the magnitude of reactance is small relative to resistance, and resistance is a better predictor of impedance than is reactance (Lukaski et al. 1986, Hall et al. 1989, Bowen et al. 1999), resistance can be used in place of Z and the equation above becomes

$$\text{Vol (cm}^2/\Omega) = (L^2/R_s) \qquad [3]$$

I analyzed BIA measurements before and after application of metal eartags using a paired-sample t test. I used analysis of variance (ANOVA) to test for sex and season differences in TBM. I used simple linear and multiple linear regressions to develop predictive equations. Also, I used standard errors of the estimates (SEE) and coefficients of determination to compare predictive equations. I used backward stepwise regression to generate models predicting TBW, LDM, and TBF in striped skunks. Variables available for inclusion in the models included TBM (kg), SVL (cm), CC (cm), Z (Ω), L^2/R_s (cm^2/Ω), TBM/SVL, TBM/SVL^2, TBM/SVL^3, TBM/SVL$^{3.47}$, and residual index. For condition indices, I used linear regression to generate models to predict TBF using each ratio index (i.e., mass/length, mass/length^2, mass/length^3, slope-adjusted index, and residual index). I used Akaike's Information Criterion (AIC) weights to compare the efficacy of all possible models that included BIA measurements and standard condition indices to predict TBF (Burnham and Anderson 1998).

A3. Results

Total body mass of striped skunks in this study ranged from 0.55–6.17 kg (mean = 3.09, SD = 1.35, *n* = 26). Fat mass, as determined by direct chemical analysis, in striped skunks ranged from 0.02–3.23 kg (percent body fat ranged from 2.43–55.60%), which probably included the extremes of body condition found in the wild. Total body mass was not significantly different between the sexes ($F_{[1,22]} = 0.49$, $P = 0.49$), but did vary between seasons ($F_{[1,22]} = 14$, $P = 0.001$) with skunks being leaner in summer and fatter during autumn. I found a significant linear relationship between percentage body fat and percentage body water as determined by direct chemical analysis (Figure A.1.a).

Bioelectrical impedance analysis measurements did not differ before and after the application of metal eartags ($t = 0.43$, df = 25, $P = 0.67$). Therefore, subsequent analyses were based on impedance values after the application of eartags to estimate body composition. Bioelectric volume and chest circumference were the best predictor of total body water (equation 4; $r^2 = 0.91$, SEE = 0.15, $P < 0.001$). The variable that best explained lean dry mass was total body mass (equation 5; $r^2 = 0.63$, SEE = 0.13, $P < 0.001$).

$$\text{TBW} = -1.1 + 0.058\ (\text{CC}) + 0.25\ (\text{L}^2/\text{R}_\text{s}) \qquad [4]$$

$$\text{LDM} = 0.26 + 0.12\ (\text{TBM}) \qquad [5]$$

I then obtained estimates of total body fat by using the following formula (Reynolds and Kunz 2001):

$$\text{TBF} = \text{TBM} - \text{TBW} - \text{LDM} \qquad [6]$$

Estimates of total body fat furnished by equation 6 were related significantly to observed fat mass derived from ether extraction (Figure A.1.b; $r^2 = 0.94$, SEE = 0.21, $P < 0.001$). Total body water determined by BIA (from equation 4) was related significantly to observed total body water from desiccation (Figure A.1.c; $r^2 = 0.91$, SEE = 0.14, $P < 0.001$). Total dissectible fat (kg) obtained during dissection was significantly related to the total body fat measured using chemical extraction (Fig. A.1.d; $r^2 = 0.97$, SEE = 0.15, $P < 0.0001$), which probably suggests that fat reserves in

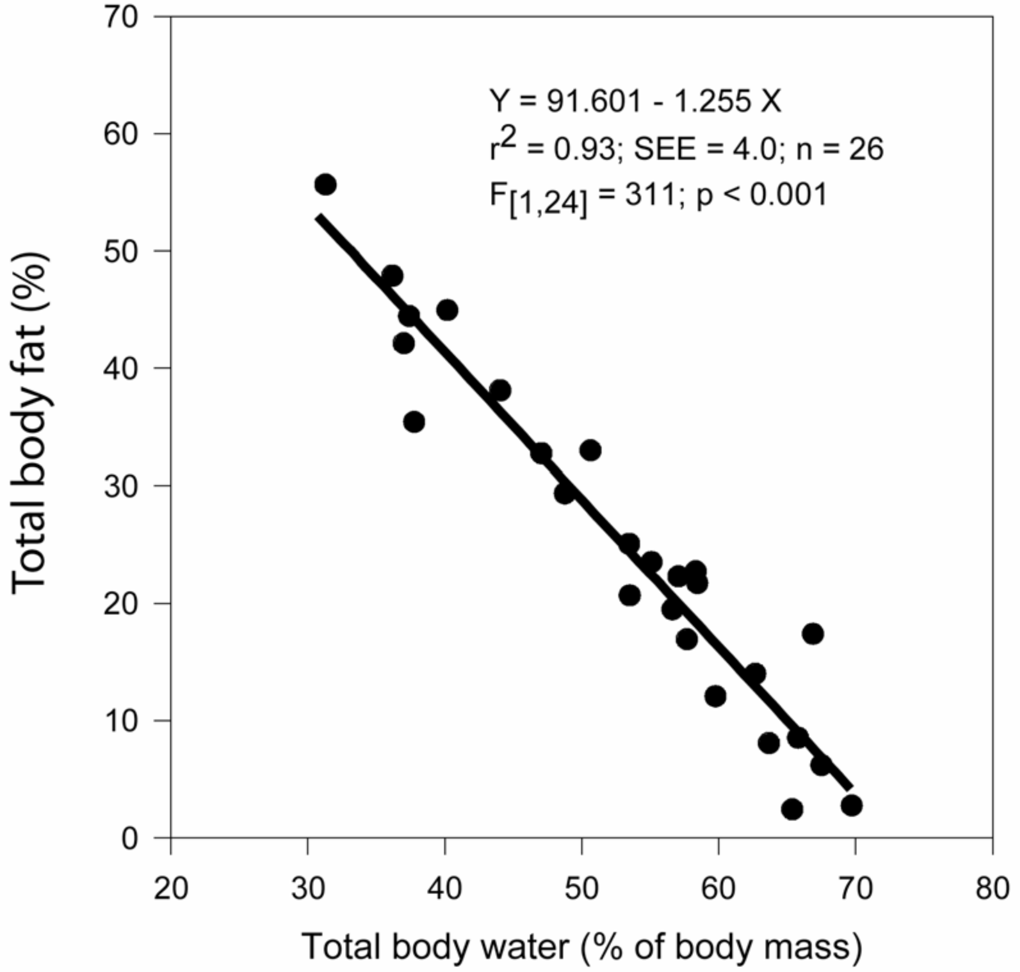

Figure A.1a. Relationship between percentage body fat and percentage body water determined by complete chemical analysis using 26 striped skunks (12 males, 14 females) collected in Saskatchewan, Canada from April to October 2001.

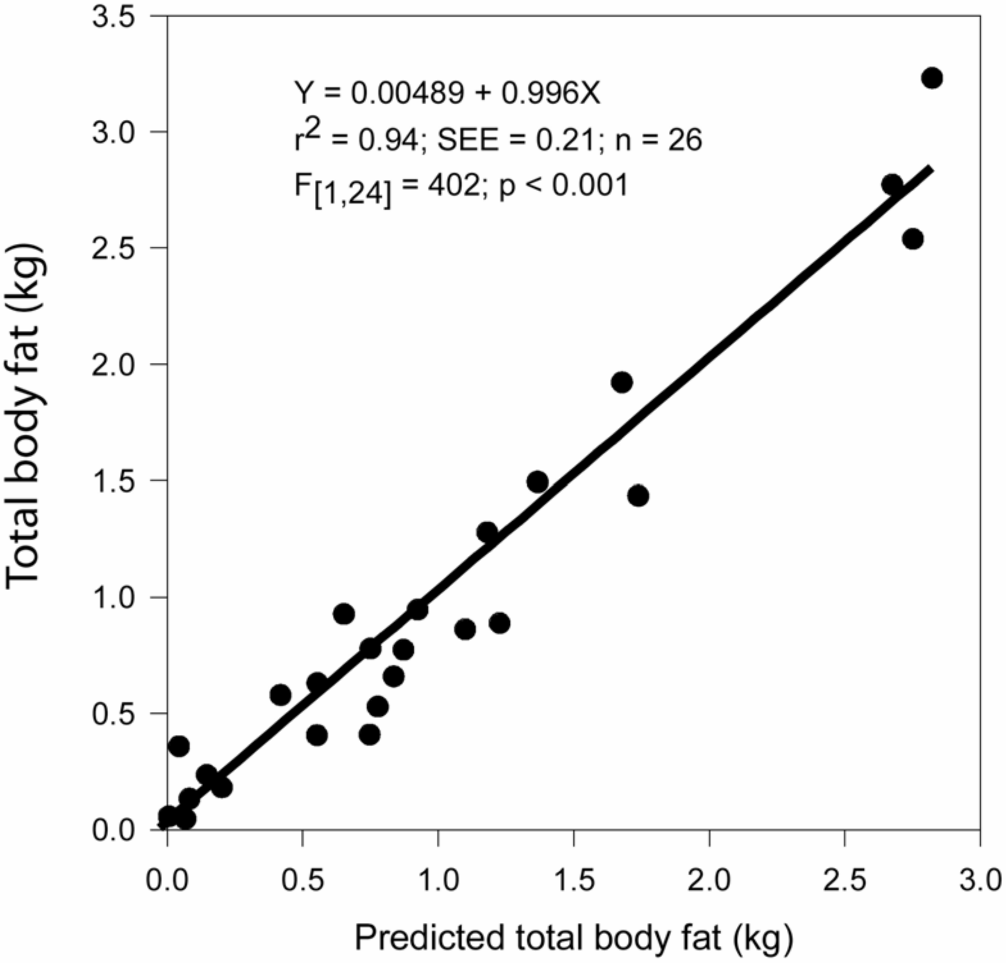

Figure A.1b. Relationship between total body fat (kg) estimated by direct chemical analysis and predicted total body fat (kg) estimated by BIA measurement (derived using TBW and LDM equations; see result section) using 26 striped skunks (12 males, 14 females) collected in Saskatchewan, Canada from April to October 2001.

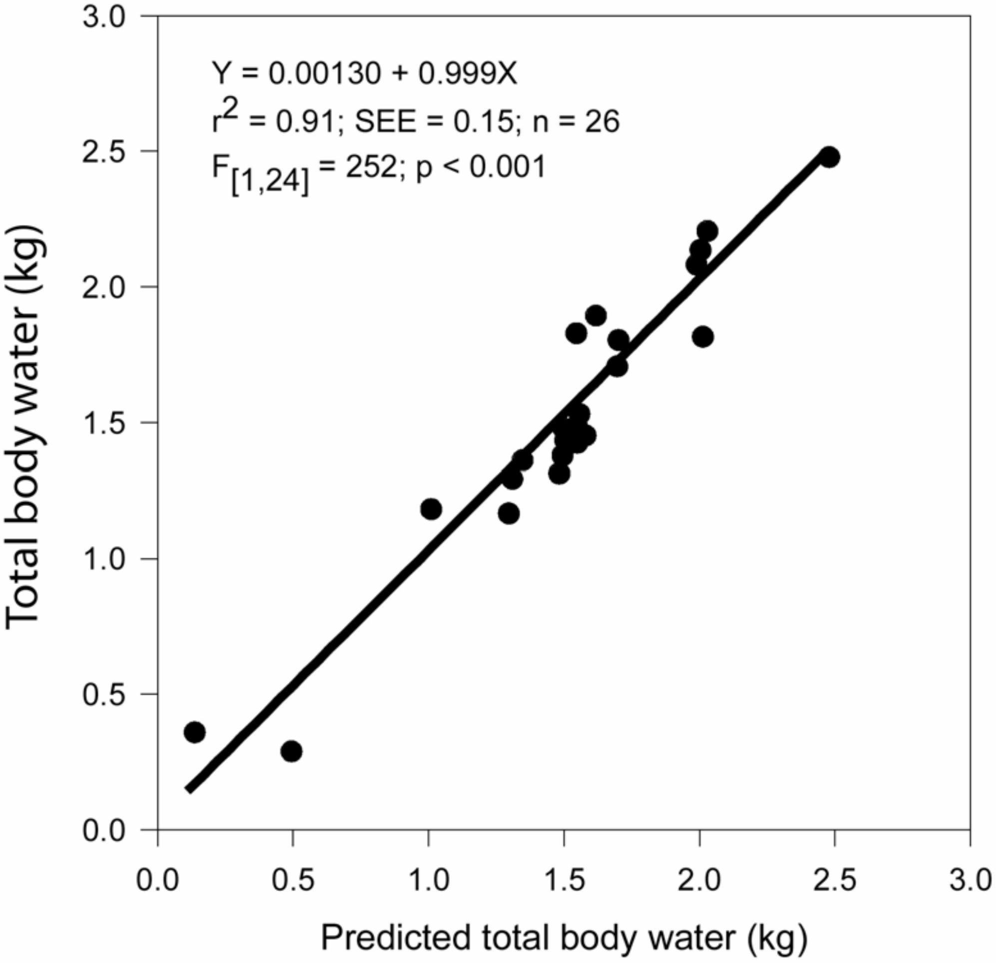

Figure A.1c. Relationship between total body water (kg) estimated by direct chemical analysis and predicted total body water (kg) estimated using BIA of 26 striped skunks (12 males, 14 females) collected in Saskatchewan, Canada from April to October 2001.

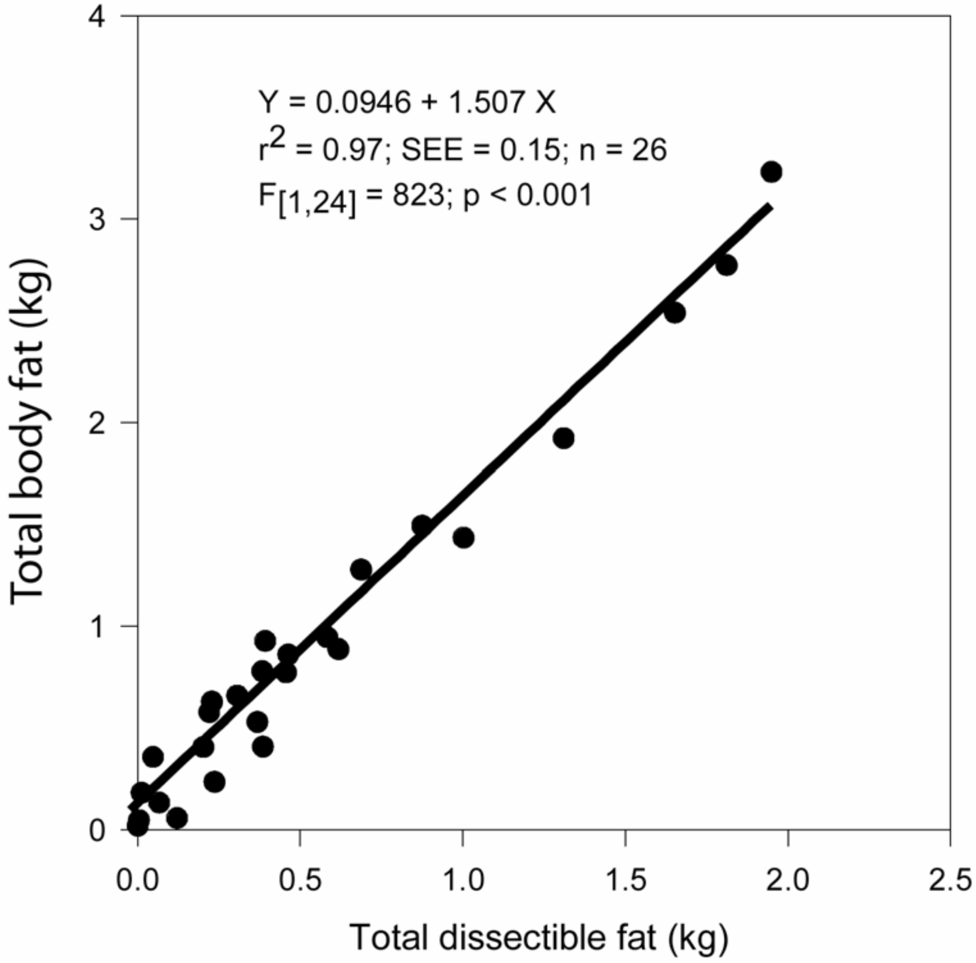

Figure A.1d. Relationship between total body fat (kg) estimated by direct chemical analysis and dissection of carcass using 26 striped skunks (12 males, 14 females) collected in Saskatchewan, Canada from April to October 2001.

skunks are mostly subcutaneous and in areas surrounding internal organs such as kidneys.

Bioelectric volume appears to be the most influential variable for TBF of striped skunks. The 2 best-ranked models with TBM, L2/RS, and CC had a high total Akaike weight of 0.76 (see Table A.1). Condition indices were not good indicators for TBF in skunks judged by the extremely low Akaike weight of 0.00006, with all models ranking the lowest in the 24 possible models in AIC analysis. Among condition indices, ratio index of dividing body mass by body length was the best predictor of body fat ($r^2 = 0.82$, SEE = 0.37, $P < 0.001$; see Table A.2). However, the data were not well explained by this ratio index because of the high standard error of estimate (SEE). For the slope-adjusted index, the exponent of 3.47 was the slope of the regression of ln-transformed body mass and length ($Y = -5.36 + 3.47 X$; $r^2 = 0.83$, SEE = 0.22, $P < 0.001$). Although regression equations for slope-adjusted index and residual index were significant ($p < 0.001$), they were both poor estimators of body fat, with explained variance of 22% and 24%, respectively (see Table A.2). The most commonly used ratio index of mass/length^3 was also a poor estimator of body fat with an explained variance of 41% and high standard error of estimate of 0.67 (Table A.2).

A4. Discussion

Techniques used for estimation of body composition in field situations should be quick and reliable. Compared to standard condition indices, my results show that BIA combined with morphometric measurements can be used to determine body condition of live striped skunks under field conditions. Total body fat can be obtained by

Table A.1. Rank of models (using Akaike's Information Criterion [AIC]) used to predict total body fat (TBF) of striped skunks from total body mass (TBM), chest circumference (CC), bioelectric volume (L^2/R_s), and snout-to-vent length (SVL) in Saskatoon, Saskatchewan, Canada, April to October 2001. The best-approximating model results in the lowest AIC_c; ΔAICc of >2.0 was representative of a significant decrease in the fit of the model. The number of estimable parameters (K) and Akaike weights (ω), which indicate the relative likelihood of a model given the data and the set of candidate models are provided.

Model	K	AICc	Δ_i	ω_i
TBM, L^2/R_s	2	4.8	0	0.59
TBM, CC, L^2/R_s	3	7.2	2.4	0.17
TBM, SVL, Z	3	8.5	3.7	0.09
TBM, Z	2	8.7	3.9	0.08
TBM, CC, Z	3	10.5	5.7	0.03
TBM, SVL, CC, Z	4	11.0	6.2	0.03
Ratio index (TBM/SVL) 0.00006	1	23.3	18.5	
Ratio index (TBM/SVL^2) 0.00000003	1	38.3	33.5	
Ratio index (TBM/SVL^3)	1	60.3	55.6	0
Slope-adjusted index[a] ($TBM/SVL^{3.47}$)	1	63.9	59.2	0
Residual index	1	67.4	63.6	0

[a] Exponent of the slope-adjusted index was the slope of the regression of ln-transformed body mass on body length ($Y = -5.36 + 3.47 X$; $r^2 = 0.83$, SEE = 0.22, $P < 0.001$).

Table A.2. Results of multiple regressions between total body fat (TBF) and condition indices of striped skunks ($n = 26$) sampled from Saskatoon, Saskatchewan, Canada, from April to October 2001.

Condition indices	Regression equation	r^2	SEE	*P*
Ratio index (mass/length)	TBF = –1.29 + 0.034 (mass/length)	0.82	0.37	<0.001
Ratio index (mass/length^2)	TBF = –1.69 + 1.93 (mass/length^2)	0.70	0.48	<0.001
Ratio index (mass/length^3)	TBF = –1.52 + 84.28 (mass/length^3)	0.41	0.67	<0.001
Slope-adjusted index[a] (mass/length$^{3.47}$)	TBF = –0.93 + 387.25 (mass/length$^{3.47}$)	0.22	0.77	<0.001
Residual index	TBF = 0.93 + 0.43 (residual)	0.24	0.76	<0.001

[a] Exponent of the slope-adjusted index was the slope of the regression of ln-transformed body mass on body length ($Y = -5.36 + 3.47 X$; $r^2 = 0.83$, SEE = 0.22, $P < 0.001$).

estimating total body water from bioelectric volume (obtained from BIA) and chest circumference, and lean dry mass. Mean absolute error in calculating predicted total body fat (from equation 6) was 0.16 ±0.06 kg (95% confidence interval). This means that BIA can detect with (95% confidence) differences in total body fat of more than 0.22 kg. The range of total body fat in skunks was 0.02–3.23 kg. Therefore, the resolution for detecting differences in total body fat was 6.9%. Total dissectible fat was highly related to total body fat estimated from direct chemical extraction. This implies that fat reserves in skunks are highly related to body condition since subcutaneous fat typically is utilized for daily metabolism as compared to bone marrow fat, which is utilized when other resources are exhausted (Cahill and Owen 1967).

In order to use BIA for estimating body fat content in striped skunks, it is necessary to obtain morphometric measurements such as total body mass, snout-to-vent length, and chest circumference, in addition to resistance values obtained from BIA machine. This is consistent with other studies that incorporate some morphometric measurements together with resistance and reactance values to obtain predictive equations for total body water and body fat. In black bears (*Ursus americanus)*, grizzly bears (*U. arctos),* and polar bears (*U. maritimus)*, snout-to-vent length, snout-to-tail length and body mass together with resistance values were necessary to predict body water (Farley and Robbins 1994). In grey seals (*Halichoerus grypus*), only body length and resistance values were necessary to predict body water (Bowen et al. 1999). Also, body length, mass and sex were used to predict body water content in moose (Hundertmark and Schwartz 2002). In humans, height, body mass and reactance values were used to predict body fat content (Lukaski et al. 1986). With larger animals such as bears and large ungulates, body mass measurement and consistent positioning of the anesthetized animals often is difficult to achieve; thus, the utility of BIA is questionable (Hundertmark and Schwartz 2002). With striped skunks, however, I do not have these problems.

As an alternative to BIA, ratio index (body mass/body length) appears to be a poor estimator of body fat. The ratio index and body mass were highly correlated and were not independent ($r^2 = 0.96$, SEE = 0.24, $P < 0.001$); thus, this index carries little information besides body mass (Lidicker and Ostfeld 1991, Piersma and Davidson 1991). Residual index for striped skunks also has proved to be an unreliable estimator similar to other studies (Virgl and Messier 1992, Krebs and Singleton 1993, Green 2001, Schulte-Hostedde et al. 2001). The use of ratio index of dividing body mass by length raised to the power of 2, 3, or slope of regression line in striped skunks was a poor estimator of body condition, probably due to the inherent correlation with body mass.

In summary, I found BIA to be a good and promising method to estimate body fat content in striped skunks compared to morphometric condition indices. The BIA machine is relatively cost-effective (i.e., cost US$2000), highly portable and light weight (<1 kg), and requires only a 9-volt battery for operation. Bioelectrical impedance analysis offers a rapid, nondestructive, and objective means to estimate body composition. Furthermore, I found that BIA measurements were not affected by metal eartags. This is important because I are interested in using BIA measurements in longitudinal studies where the body conditions of subjects are measured over different seasons. With this technique, I can assess the relationship between body condition and survival, productivity, and behavior in long-term population studies.

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APPENDIX B. CAUSE-SPECIFIC MORTALITY OF STRIPED SKUNKS

Table B.1. Cause-specific mortality of 61 skunks (31 males, 30 females) in Saskatchewan, Canada from 1999 to 2003. Necropsies performed by veterinarian pathologists at the Canadian Cooperative Wildlife Health Center at the Western College of Veterinary Medicine at Saskatoon, SK.

	Female		Male	
Cause-specific mortality	Juvenile	Adult	Juvenile	Adult
Diseases	2	2	3	2
Rabies	1	4	3	8
Emaciation	2	0	2	0
Human	2	5	1	5
Predation	2	3	2	2
Unknown	3	4	2	1
Total	12	18	13	18

Table B.2. Cause-specific mortality of 61 skunks in autumn/winter and spring/summer from 1999 to 2003 in Saskatchewan, Canada. Necropsies performed by veterinarian pathologists at the Canadian Cooperative Wildlife Health Center at the Western College of Veterinary Medicine at Saskatoon, SK.

	Autumn/Winter				Spring/Summer		
Cause-specific mortality	1999/2000	2000/2001	2001/2002	2002/2003	2001	2002	2003
Disease	3	3	0	2	0	1	0
Rabies	6	8	0	0	2	0	0
Emaciation	0	0	0	0	1	2	1
Human	0	1	4	2	2	2	2
Predation	0	2	3	1	0	2	1
Unknown	1	7	1	0	0	0	1
Total	10	21	8	5	5	7	5