

WINTER ECOLOGY OF THE NORTH AMERICAN BADGER (*TAXIDEA TAXUS JEFFERSONII*) IN THE CARIBOO REGION OF BRITISH COLUMBIA

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE IN ENVIRONMENTAL SCIENCE

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March 2013
Thompson Rivers University
Kamloops, British Columbia, Canada

Stephen Anthony Symes, March 2013

DEDICATION

TO DEBORAH KRAUSS

"People come - they stay for a while, they flourish, they build - and they go. It is their way. But we remain. There were badgers here, I've been told, long before that same city ever came to be. And now there are badgers here again. We are an enduring lot, and we may move out for a time, but we wait, and are patient, and back we come. And so it will ever be."

- Kenneth Grahame, *The Wind in the Willows*, Ch. 4



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ACKNOWLEDGEMENTS

First and foremost, I would like to thank my supervisor, Dr. Karl Larsen, for taking a chance on me and for providing me with an opportunity to study such amazing creatures. His support and guidance has helped me grow as a wildlife ecologist, and by challenging me with this project, I have learned a great deal. Secondly, without Richard Klafki's previous work, this project would not have been a success. Richard provided an enormous amount of advice and help with the study, navigating bureaucracy, and providing the impetus for my research. Similarly, Roger Packham is also credited with starting and supporting all the Cariboo badger research. He provided funding, support, and advice through both winters. Brent Persello from the BC Ministry of Transportation and Infrastructure also deserves recognition for championing this project and providing much valued funding. Thank you to my committee members Dr. Nancy Flood and Dr. Darryl Carlyle-Moses for their feedback and support, particularly during the design of the study. Further, I'd like to thank my external examiner Richard Weir for his comments on the final version of this thesis.

My fellow lab mates, Nicole Bassaraba, Jocelyn Garner, Jessica Gosling, Dexter Hodder, Richard Klafki, Emily Lomas, and Eric Stromgren, all deserve a thank you for their advice and encouragement. You made this experience fun and I only wish I had had more time to spend with you all. Next time I'm doing a summer study!

I am extremely appreciative of the help I received in the field; often it was volunteer and unpaid. Jonquil Crosby and Cara Lamont assisted with the winter field work. In addition, Melvin Louis and the Canoe Creek First Nation provided excellent support by regularly re-locating one of my female badgers at the very south of the study area. Kayla Straume provided extremely valuable assistance with burrow measurements in the summer. I'd also like to thank Hamish Nicolson and Mike Packham who conducted cursory winter tracking in 2007/2009 and 2008/2009, prior to my involvement with the project. Similarly, I'd like to thank Nicole Heim for her contribution to the examination of seasonal burrows. The Witt's End Gust Ranch (Tom and Danielle, Doug and Pat Witty) provided a comfortable place to sleep and escape from the cold: thank you. Stoli and Blackbean, you kept me sane at the cabin. I love you with all my heart! Despite missing home, struggling with days upon days

of field work, and nights spent mulling over research ideas and statistical problems, it was all worth it to have found Blackbean.

John and Alison Trulsen, I am indebted to you for all you've done for Cristen and I in the years leading up to and through my graduate research. I am forever grateful! My parents and sisters, you introduced and encouraged me to explore the natural world. I'm blessed to have had the opportunities I had growing up with exposure to wilderness. You have always been supportive of my pursuit for knowledge, thank you!

Finally, I owe my beautiful wife Cristen Symes, more than she will ever know. Her support through the entire process has helped me accomplish a major goal in my life. It was she who pushed me to pursue a graduate degree and led me to work on this project. Her words of encouragement built me up and kept me strong when I needed it the most. I truly love you!

Last but not least, I would like to thank all the landowners that allowed access to study the badgers. They made me feel welcome, offered coffee breaks, and even helped me get unstuck on occasion. It is people like you who enjoy having badgers on your land that deserve a lot of credit for the preservation of this species. I'd also like to thank all the people in the Cariboo Region who have reported badger sightings, these data have helped us to conduct our research and have given us valuable information about the species.

The B.C. Ministry of Transportation and Infrastructure, B.C. Ministry of Environment (Ministry of Natural Resource Operations), Natural Sciences and Engineering Research Council of Canada, and Habitat Conservation Trust Fund all provided funding and support for this project. This work was conducted under the British Columbia Ministry of Environment permit number WL10-65208. All protocols for capturing, handling, and researching the badgers were approved by the Thompson Rivers University Animal Ethics Committee (protocol no. AUP 2009-30R)

Thesis Supervisor: Karl W. Larsen (PhD)

ABSTRACT

The purpose of this study was to examine the winter activities and burrow characteristics of North American badgers (*Taxidea taxus jeffersonii*). At the northern range-limit of these animals (British Columbia, Canada) winter is long and harsh and habitat patchy and atypical; thus, badgers may respond to winter differently here than elsewhere. Using radio-telemetry and remote-cameras, I documented winter activities of 16 badgers (12♀, 4♂) between 2007 and 2011. Similar to limited and anecdotal data collected elsewhere, badgers during winter reduced home range 3.5 (SD = 0.6) km^2 and movements 110.5 (SD = 12.2) m /day and intensively used burrows 1.3 (SD = 0.8) burrows per winter. Total winter burrow stay averaged 34 days (SD = 25.0) per winter and this use coincided with the onset of torpor (first week in January). Despite intensive burrow-use, badgers emerged frequently (0.30 ± 0.07 events/camera-night) and displayed foraging behaviour (mean foray length: 46.70 ± 65.44 min). Burrow emergence was not related to temperature or snow depth; rather it was best explained by the amount of time elapsed since the badger entered the burrow in mid-winter (Julian Day). Despite these trends, winter activity was quite variable among individual badgers. I also compared the thermal properties of the burrows used by the badgers to those previously used in summer or for rearing offspring (natal). As expected, all burrow temperatures remained relatively mild and constant throughout the winter; however, winter burrows were significantly cooler during this time than burrows that had been used in the previous summer, albeit a small difference (average 1.9°C). Snow depth at winter burrows did not differ from ‘summer burrows’, yet natal burrows had significantly less snow. Analysis revealed that soil fan size, number of entrances, horizontal cover, presence of infrastructure, and a coarse description of habitat differentiated seasonal burrow types relatively well. I suggest that individual variation (strategies) may be a response to local conditions. Relatively small, patchy, atypical habitat, in combination with extremely large summer home ranges may limit the ability of some animals to gain sufficient fat reserves, thus necessitating additional foraging during winter. Moreover, my research suggests that seasonal burrows differ with respect to measurable habitat features that can be used to identify and protect important burrows (natal and winter burrow). This study has been the

first dedicated winter ecology study of free ranging North American badgers and has expanded our knowledge about the winter activities, movements and burrow use of this endangered species. As winter is a critical time in the life history of many mammals, an effective management plan will require an understating of species ecology across all seasons.

Keywords: *Taxidea taxus*, winter, activity patterns, badger, critical habitat, species at risk, burrow, den.

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Chapter 1. General Introduction and Background

Winter as a Critical Time for Wildlife

Winter is a critical time for mammals inhabiting temperate regions (Pruitt 1960, Campbell *et al.* 2005). Animals in this region must cope with the high costs of thermoregulation, compounded by scarce food resources, cold temperatures, and restricted mobility due to snow cover (Formozov 1946, Pruitt 1957, Pruitt 1960, Telfer and Kelsall 1984, Buskirk and Harlow 1989, Marchand 1996). Ultimately, it is often temperature, snow depth, snow density, and snow duration that determine the severity of winter and consequently the demographics of populations (Jones and Pomeroy 1998, Hwang 2005) and the fitness of individuals. Winter severity, most notably snow depth, but also lower temperatures, has been linked to increased mortality. For example, increased mortality during winter, compared to other seasons, has been relatively well studied in ungulates (*e.g.*, white-tailed deer, *Odocoileus virginianus*; mule deer, *O. hemionus*; moose, *Alces alces*; mountain goats, *Oreamnos americanus*; Cederlund *et al.* 1991, DelGiudice *et al.* 2002, Baccante and Woods 2010, White *et al.* 2011). Moreover, winter severity has also increased mortality in carnivores such as raccoons (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), coyotes (*Canis latrans*), and striped skunks (*Mephitis mephitis*) (Kamler and Gipson 2004, Gehrt 2005, Pitt *et al.* 2008). For instance, in Eurasia, Bartoń and Zalewski (2007) found that variation in density of red fox (*Vulpes vulpes*) was best explained by winter temperatures and variation in seasonality¹ and snow depth. Overall, increased mortality of northern mammals during winter can lead to reduced densities where these winter effects are strong.

Despite the link between winter, fitness and population dynamics, this period in the life history of many northern mammals has been relatively understudied compared to the snow-free season. There are at least three reasons for this imbalance: (1) an assumption that

¹ Boyce (1979) explains that climatic seasonality is created through the year by variation in weather (*e.g.* temperature, humidity, rainfall, cloud cover, wind patterns, *etc.*) which, in turn create temporal variation in environmental components that affect populations. As such, increasing seasonality would see more pronounced temporal variation in environmental components.

biological activity slows during winter, (2) field seasons tend to coincide with the academic calendar, thus reducing the availability of students and researchers to conduct winter investigations, and (3) the logistical difficulties associated with conducting winter research in cold temperatures and deep snow (Campbell *et al.* 2005). Overcoming these hurdles, particularly the third one, is not easy, but it is essential that more in-depth winter studies (in applicable latitudes) are undertaken to improve our general understanding of animal ecology. Moreover, to craft effective management strategies for species-at-risk it may be particularly important to understand their winter habitat requirements and their adaptations to a winter environment.

Mammalian Adaptations to Winter and Strategies for Survival

Temperate-zone endothermic animals have adapted to winter by using one of three primary strategies, (a) migration, (b) resistance, and (c) hibernation (Marchand 1996). Hibernators and resisters face the challenge of maintaining their body temperature within narrow limits despite harsh winter conditions (Marchand 1996). Indeed, endothermic animals (*i.e.*, birds and mammals) must maintain their body temperatures by metabolizing food or fat reserves to balance heat lost to the environment (Marchand 1996). However, because resources are scarce or of limited quality during winter, endotherms must either continue (or perhaps elevate) food intake, switch to less nutrient-rich but more readily available foods, or rely on fat reserves. Furthermore, they may maintain and conserve heat by modifying their behaviour, morphology, or physiology (Pruitt 1984, Telfer and Kelsall 1984, Marchand 1996, Aitchison 2001, Pruitt 2005).

Mammals in temperate regions show a variety of tactics to cope with winter. For example, small mammals that display intraspecific aggression during the summer may modify their behaviour in winter to conserve heat through communal nesting (*e.g.*, voles - *Microtus* spp., West and Dubun 1984, Madison 1984; northern flying squirrels - *Glaucomus sabrinus*, Cotton and Parker 2000; bats - *Myotis* spp., Boyles *et al.* 2008). Morphological adaptations to maintain and conserve heat include the ability to undergo a physical change that improves an individual's ability to cope with winter. A well-known example is the thick fur and white pelage that snowshoe hares (*Lepus americanus*) acquire by moult prior to winter. The thicker fur and a lack of pigment in hair follicles may lower conductivity by

increasing the amount of air trapped near the body, thereby increasing insulation with the added benefit of providing cryptic colouration (Irving 1972). A more extreme example is found in some small mammals, (*e.g.*, shrews, *Sorex* spp.) in which an actual change in body size occurs with the approach of winter, through the shrinking of organs and body length (Pucek 1970, Merritt 1986). This process, known as Dehnel's phenomenon, is thought to increase the insulative properties of the body hair by increasing its density (Mezhzherin 1964).

Despite behavioural and morphological adaptations, the ability of mammals to maintain body temperature in the cold is limited. At a particular body temperature, known as the Lower Critical Temperature (LCT), metabolic rate must increase to balance heat loss (Marchand 1996). At this point, physiological adaptations such as non-shivering thermogenesis (*i.e.*, increased heat production from increased muscular activity and metabolism of brown fat²) are used (Marchand 1996). As a last resort, mammals may shiver to produce heat, although this is energetically expensive (Marchand 1996). Further to these physiological mechanisms, some mammals (*e.g.*, Columbian ground squirrels, *Urocitellus columbianus*; yellow-bellied marmots, *Marmota flaviventris*; bats, and bears, *Ursus* spp.) have evolved the ability to hibernate. This process involves body temperatures and metabolic rates being simultaneously reduced such that individuals enter a torpid or lethargic state and thereby conserve energy (Lyman *et al.* 1982). Although a continuum of body temperatures, metabolic rates, and length of torpor bouts exists, some mammals (*e.g.*, ground squirrels and marmots) enter a deep, prolonged sleep during which their body temperature remains only slightly above freezing (true hibernation or deep torpor). This is a contrast to carnivores, whose body temperature and metabolic rate are reduced for a much shorter time, typically 24 hours (*i.e.*, shallow or daily torpor; Lyman *et al.* 1982, Geiser and Ruf 1995, Wilz and Heldmaier 2000). Whereas true hibernation is associated with deep torpor (individuals often cannot be roused), shallow or daily torpor enables animals to take advantage of times when foraging conditions are more favourable, which often occur in fluctuating environments (Newman *et al.* 2011). These states allow mammals to reduce

² **Brown fat** is capable of a higher rate of metabolism due to its high level of mitochondria, higher O₂ consumption, density of nerve cells and blood veins.

thermoregulatory costs through the metabolism of fat reserves accumulated in the fall (Buskirk and Harlow 1989).

Hibernating or torpid mammals can further conserve heat by occupying insulated microhabitats such as burrows or dens that mitigate cold temperatures (Pruitt 1960, Vose and Dunlap 1968, Stephen 1969, Brocke 1970). Below-ground shelters provide thermal insulation (Geiger 1950, Marchand 1996) that is further enhanced by snow cover (Formozov 1946, Marchand 1996, Pomeroy and Brun 2001, Campbell *et al.* 2005). Despite hindering the ability of wildlife to move or access food, snow cover benefits those living in the subnivean by creating a humid, relatively-warm environment that is separated from the dry, very cold, fluctuating air mass above (Formozov 1946, Pomeroy and Brun 2001, Campbell *et al.* 2005). Snow, along with other insulating materials such as shrubby vegetation (Campbell *et al.* 2005) and thick litter layers, can create a warm environment allowing species such as active small mammals or hibernating species to survive the cold winter. Animals occupying sites such as burrows with good thermoregulatory properties (insulation) will likely have higher over-wintering survival than those that inhabit sites with poor properties (Webb *et al.* 1996). Thus, selection of winter burrows (or dens) with good insulation value may be important (perhaps critical) for an individual's survival and, ultimately, its fitness.

Previous Research on Temperate Carnivores

The winter ecology of mammalian carnivores (Order. Carnivora) has been the subject of a considerable amount of study. This includes work on bears (Folk *et al.* 1972, Mitchell *et al.* 2005), coyotes (Ozoga and Harger 1966, Murray *et al.* 1994, Gantz and Knowlton 2005), Canada lynx (*Lynx canadensis*, Murray *et al.* 1994, Kolbe *et al.* 2005, Maletzke *et al.* 2007), red fox (Van Etten *et al.* 2007, Silva *et al.* 2009), and Gray wolves (*Canis lupus*, Ciucci *et al.* 2003, Alexander *et al.* 2005). The Family Mustelidae in particular has been the subject of a number of winter ecology studies, including those on Eurasian badgers (*Meles meles*, Lindsay and Macdonald 1985, Fowler and Racey 1988, Tanaka 2006, Sidorchuk and Rozhnov 2008, Kowalczyk *et al.* 2009), fisher (*Martes pennanti*, Powell 1994), marten (*Martes americana*, Drew 1995, Porter *et al.* 2005, Mowat 2006, Goszczynski *et al.* 2007), small weasels (*Mustela* spp., Polderboer *et al.* 1941, Mowat and Poole 2005), and the wolverine (*Gulo gulo*, Copeland *et al.* 2007). Research on the carnivores has been broad and

has examined such topics as winter habitat, home range, diet, locomotion, activity and movement, hunting behaviour, and physiology.

Although many temperate carnivores simply tolerate winter stress by continuing to actively hunt through the winter, within the group there are recognizable adaptations for coping with the harsher conditions of the season. For example, Canada lynx possess large paws and long limbs enabling them to be suited for travel in snow (Murray and Boutin 1991). Although true hibernation has not been demonstrated in this group, some species such as certain bears (*Ursos arctos* and *U. americanus*; Hock 1960), or raccoons and skunks (Aleksiuk and Stewart 1977, Harlow 1981) will den up and demonstrate ‘carnivore lethargy’, even allowing their body temperatures to drop. In addition to all of these adaptations, carnivores that remain active over winter (even partially) must still demonstrate high predator efficiency as well as resistance to the cold. For example, Gray wolves have shown to effect higher kill rates (biomass/wolf/day) during winter than summer (Jędrzejewski *et al.* 2002, Metz *et al.* 2012) and these kill rates have been positively correlated to snow depth (Huggard 1993, Jędrzejewski *et al.* 2002). Similarly, Eurasian lynx (*Lynx lynx*) also have been observed to have higher kill rates during winter, particularly in years and areas with deep snow (Nilsen *et al.* 2009). Efficiency during winter may be partly explained by prey vulnerability (body condition and difficulty of prey traveling in deep snow) but also because of the ability of some predators to travel efficiently in snow due to lighter foot loading (Telfer and Kelsall 1984).

Winter Strategies of Mustelids

High predatory efficiency is especially important to members of the Family Mustelidae (the so-called ‘weasels’), making their winter ecology particularly interesting. Many members of this family (in particular true weasels, stoats: *Mustela erminea*, European polecat: *Mustela putorius*, sable: *Martes zibellina*, marten, fisher, American mink: *Neovison vison*, and North American river otter: *Lontra canadensis*) are long and thin, and therefore have a large surface-to-volume ratio that is costly in terms of heat loss (Brown and Lasiewski 1972, Casey and Casey 1979). This heat loss is further compounded by a general lack of insulation compared to other mammals such as canids, ursids, and bovids (Scholander *et al.* 1950). However, mustelids may benefit from the possession of an elongated body structure

by being able to more easily access confined spaces, allowing higher predatory efficiency on subnivean or burrowing prey, along with the added benefit of being able to escape predators (Brown and Lasiewski 1972, Casey and Casey 1979). This improved efficiency in turn allows the animals to meet metabolic demands more easily (Casey and Casey 1979, King and Powell 2007).

The lower critical temperature (LCT) for endotherms is the point at which the metabolism of an animal must increase to compensate for colder ambient temperatures. Mustelids as a group have relatively high LCTs: marten, for example, have an LCT that ranges between 16° C and 29° C (Drew and Bissonette 1997). However, as mentioned, most members of the family do not show the morphological or physiological adaptations that would allow them to offset thermal loss and reduce energy spent on metabolism during cold periods. In some mustelids (*e.g.*, weasels and stoats), the pelage turns white in winter to presumably allow increased predation efficiency and predator avoidance through cryptic colouration, yet there is little evidence that it improves heat retention. Also, unlike other Canadian mammals (Hart 1956), the winter pelage of least weasels (*Mustela nivalis*) and short-tailed weasels (*Mustela ermine*) is as short as it is in summer, has similar conductance in both seasons, and is a much poorer conductor than the pelage of similar-sized mammals (Casey and Casey 1979). Furthermore, because of their elongated shapes, some mustelids do not store additional fat nor do they enter torpor (Buskirk and Harlow 1989, King and Powell 2007, Newman *et al.* 2011). Despite high metabolic rates, poorly insulating fur, and lack of fat reserves, these species still are able to meet metabolic demands by spending a considerable amount of time foraging for food during winter (King and Powell 2007), often in very cold temperatures below their LCTs (Richardson *et al.* 1987, Taylor and Buskirk 1994), implying efficient prey capture.

Retreat-site selection is another important adaptation of northern mustelids. For example, weasels, stoats, ferrets and polecats rest in nests and burrows under the protective subnivean and further reduce heat loss from conduction by lining nests with grasses and fur (Polderboer *et al.* 1941, Blandford 1987, Richardson *et al.* 1987). Other mustelids, particularly martens and fishers, inhabit resting structures such as woody debris piles, coarse woody debris and rock piles under the subnivean, and cavities within snags and old trees (Buskirk 1984, Buskirk *et al.* 1989, Powell 1994, Taylor and Buskirk 1994, Wilbert *et al.*

2000). Other behavioural adaptations include adjustment of activities to coincide with favorable foraging periods (Thompson and Colgan 1994, Zub *et al.* 2009) and caching of food for later use (Polderboer *et al.* 1941, Richardson *et al.* 1987, Henry *et al.* 1990, Michener 2000, King and Powell 2007). In this way, resources can be consumed during periods when prey is less available or when ambient conditions make foraging in the open more costly.

One additional winter-adaptation, seen in almost all temperate mustelids, is delayed implantation of embryos (Ferguson *et al.* 2006). Here, the embryo is not immediately implanted in the uterus but instead enters a state of diapause (Lindenfors *et al.* 2003). This strategy allows the optimal times for (1) mating and (2) raising young to be separated by more than the gestation period. In high latitudes, mustelids often occur at low densities and have very large ranges (Ferguson *et al.* 2006). Delayed implantation allows mating to occur during the snow-free season when travel is easier and mates are more accessible. Parturition then follows early in the spring in time for more reliable and abundant food sources.

A minority of mustelid species do not possess a long, thin tubular shape, including the wolverine and the North American and Eurasian badgers (*Taxidea taxus* and *Meles meles*, respectively). The first of these is the mustelid most specialized to living in cold, high latitude environments. Unlike badgers that rely heavily on fossorial prey, wolverines are active hunters of small, mid- and large prey, and are adept at scavenging on winter kills. Their stout shape and thick pelage allow good retention of heat, allowing a LCT of -40°C during winter (Iverson 1972), and between -8° and 5°C during summer (Casey *et al.* 1979). Furthermore, their relatively large feet provide good foot loading, enabling easy travel on soft snow (Telfor and Kelsall 1984). Finally, female wolverines seem to seek out maternal dens where snowfall is retained late into spring, allowing them to use the subnivean to protect the kits from cold and predators (Magoun and Copeland 1998). The fact that badgers do not possess these adaptations may help explain why they do not occur as far north as the wolverine in either the Western or Eastern hemispheres. However, badgers still inhabit harsh seasonal environments where they must deal with winter conditions.

Winter Strategies of Badgers

As mentioned above, both Eurasian and North American badgers do not range as far north as wolverines, yet they still occur at latitudes with relatively severe winters (*e.g.*, Canada, Finland, Russia, *etc.*). Despite possessing a stout shape similar to wolverines, badgers do not appear to be as well suited for remaining active during winter. Both Eurasian and North American badgers increase fat reserves in the fall, which then slowly deplete over winter, in some cases by up to 50% (Harlow 1981a, Fowler and Racey 1988, Tanaka 2006, Kowalczyk *et al.* 2009). Daily activity is reduced to a point when Eurasian badgers are rarely active during December through February (Tanaka 2006, Kowalczyk *et al.* 2009). This inactivity has been known to last for an average of 96 days, but can vary from 79 to 116 days (Kowalczyk *et al.* 2009). During this time, they enter a period of winter lethargy characterized by mild hypothermia (Fowler and Racey 1988, Tanaka 2006). A continuum for this winter lethargy also exists. In southern portions of the Eurasian badger's range, body mass and activity remain relatively stable, whereas in the north, inactivity can persist for up to 6 months of the year and body weights can double (Kowalczyk *et al.* 2009). North American badgers show a similar pattern of inactivity and winter lethargy, reducing above-ground activity during winter by up to 93% with underground stays lasting up to 72 days (Lindzey 1978, Harlow 1979a, Harlow 1979b, Harlow 1981b, Messick and Hornocker 1981). In Minnesota (Sargeant and Warner 1972, Lampe and Sovada 1981) and in Idaho (Messick and Hornocker 1981) studies on telemetered badgers have shown reduced movements and home ranges during the winter months. This suggests that North American badgers remain underground to conserve heat and reduce thermoregulatory costs. Energy expenditures can be further reduced when North American badgers enter torpor, in which body temperature is lowered by 9° C and heart rate decreases by 50% (Harlow 1981b). However, unlike Eurasian badgers, there is no information on *Taxidea* regarding activity levels in relation to latitude.

During winter lethargy, both Eurasian and North American badgers occupy burrows that are relatively warmer and more stable in temperature than ambient (Harlow 1979b, Harlow 1981b, Fowler and Racey 1988, Roper and Kemenes 1997, Moore and Roper 2003, Sidorchuk and Rozhnov 2008). Eurasian badger burrows often contain bedding material for further insulation (Roper 1992). An important point to note here is that the Eurasian badger is a gregarious species (unlike its North America counterpart): denning is often communal

(several animals sharing 'setts'), and this likely contributes to warmer temperatures (Fowler and Racey 1988). Indeed, Fowler and Racey (1988) noted that winter setts of Eurasian badgers were up to 18° C warmer than ambient temperatures. Therefore, North American badgers that retreat during the winter are unlikely to see the energy savings associated with communal resting.

Eurasian and North American badgers may show little or no activity outside of burrows when critically low temperatures occur. For example, Kowalczyk *et al.* (2009) found Eurasian badgers in Eastern Poland did not emerge when the mean monthly temperature was below -4° C, and Lindsay and MacDonald (1985) found badgers in England did not emerge at temperatures below -1° C. Similarly, an apparent threshold of activity was noted in captive North American badgers that were held outdoors, where ambient temperatures below -17° C caused individuals animals to remain in their burrows where temperatures stabilized between 1° and 3° C (Harlow 1979b). Despite these demonstrations of winter inactivity, both *Meles* and *Taxidea* can be quite active during winter. Fowler and Racey (1988) noted that Eurasian badgers continue to forage, patrol or conduct other above-ground activities during winter, and Sargeant and Warner (1972) documented a female North American badger in Minnesota that was active in temperatures below -29° C.

What determines the winter activity patterns of badgers? Ultimately, it appears as though the availability and abundance of food drives winter activity levels of Eurasian badgers, although there is relatively little research for this species in the harsh winter conditions of continental Europe and Asia (Kowalczyk *et al.* 2009). In the case of North American badgers, we have yet to study the basic winter activity patterns, let alone the mechanism(s) driving them. Despite the plethora of winter research on carnivores, including even Eurasian badgers, surprisingly little has been conducted on the winter ecology and the life-history strategy of the North American badger.

Among the limited work done on the winter ecology of *Taxidea* are several studies that have radio-tracked low numbers of badgers during the winter (n=1; Sargeant and Warner 1972), often for only small portions of the winter (due to mortality or lost transmitters, *e.g.*, Lindzey 1978, Lampe and Sovada 1981, Messick and Hornocker 1981). Similarly, Harlow (1979a, 1979b) examined the winter activities and physiological adaptations of captive badgers; focusing on females within outdoor enclosures or in rooms exposed to outside

temperatures and photoperiods. To date, there have been no dedicated winter ecology studies of the North American badger in their natural environment. Descriptions of winter habitat use, at either a fine (burrow site, vegetation patch) or coarse scale (home range and landscape use), or studies that document activity patterns simply do not exist. The overarching purpose of this study was to remove this glaring gap in our knowledge of this species.

North American Badgers in the North

The North American badger (Figure 1.1) occurs as far north as 53° N Latitude, in habitats where relatively severe winters (snow season) lasts five months (Figures 1.2 and 1.3). Through the extensive range of the animals, badgers exhibit a solitary lifestyle (outside of brief mating bouts and maternal rearing of kits). Fossorial prey is generally targeted, including Columbian ground squirrels (*Urocitellus columbianus*) and yellow-bellied marmots (*Marmota flaviventris*) and northern pocket gophers (*Thomomys talpoides*), but other species such as mice and voles (*Cricetidae* spp.) are relied upon when more available (Errington 1937, Snead and Hendrickson 1942, Jense 1968, Messick and Hornocker 1981, Lampe 1982). Anecdotal and published observations suggest this trend holds true even in the more northern portions of the badger's range (Newhouse and Kinley 2000, Michener and Iwaniuk 2001, Hoodicoff 2003, Hoodicoff 2006, Proulx *et al.* 2011).

Taxidea is typically considered a grassland-obligate, but animals within the northern reaches of its western range (Cariboo region of B.C.; Figure 1.2) have been shown to utilize more atypical vegetation communities such as clearcuts, forests, alpine habitats, and wetlands (Rahme *et al.* 1995, Weir *et al.* 2003, *jeffersonii* Badger Recovery Team 2008; Figure 1.4). These northern animals maintain larger home ranges (at least in summer) than southern conspecifics (Sargeant and Warner 1972, Lindzey 1978, Lampe and Sovada 1981, Messick and Hornocker 1981, Newhouse and Kinley 2000, Hoodicoff *et al.* 2009). This disparity in home range size is likely due to either low population density (*i.e.*, lack of females on the landbase) or the lack of, or distance to, suitable habitat and prey base (*sensu* Minta 1993). Indeed, pocket gophers, which are an important and primary prey source of southern badgers (Todd 1980, Lampe 1982, Sovada *et al.* 1999), are absent at the extreme northwest limits of the species (Cariboo Region; Johnstone 1954). Habitat in this area is small and patchy



Figure 1-1. Top photo: Female North American badger (*Taxidea taxus jeffersonii*) emerging from a winter burrow. Bottom photo: Typical badger burrow during late fall/early winter in the Cariboo Region of British Columbia, Canada.



Figure 1-2. Geographic range map of the North American badger (*Taxidea taxus jeffersonii*) (Source: Patterson *et al.* 2007). The Cariboo Region of British Columbia (and location of study area) is indicated in red.

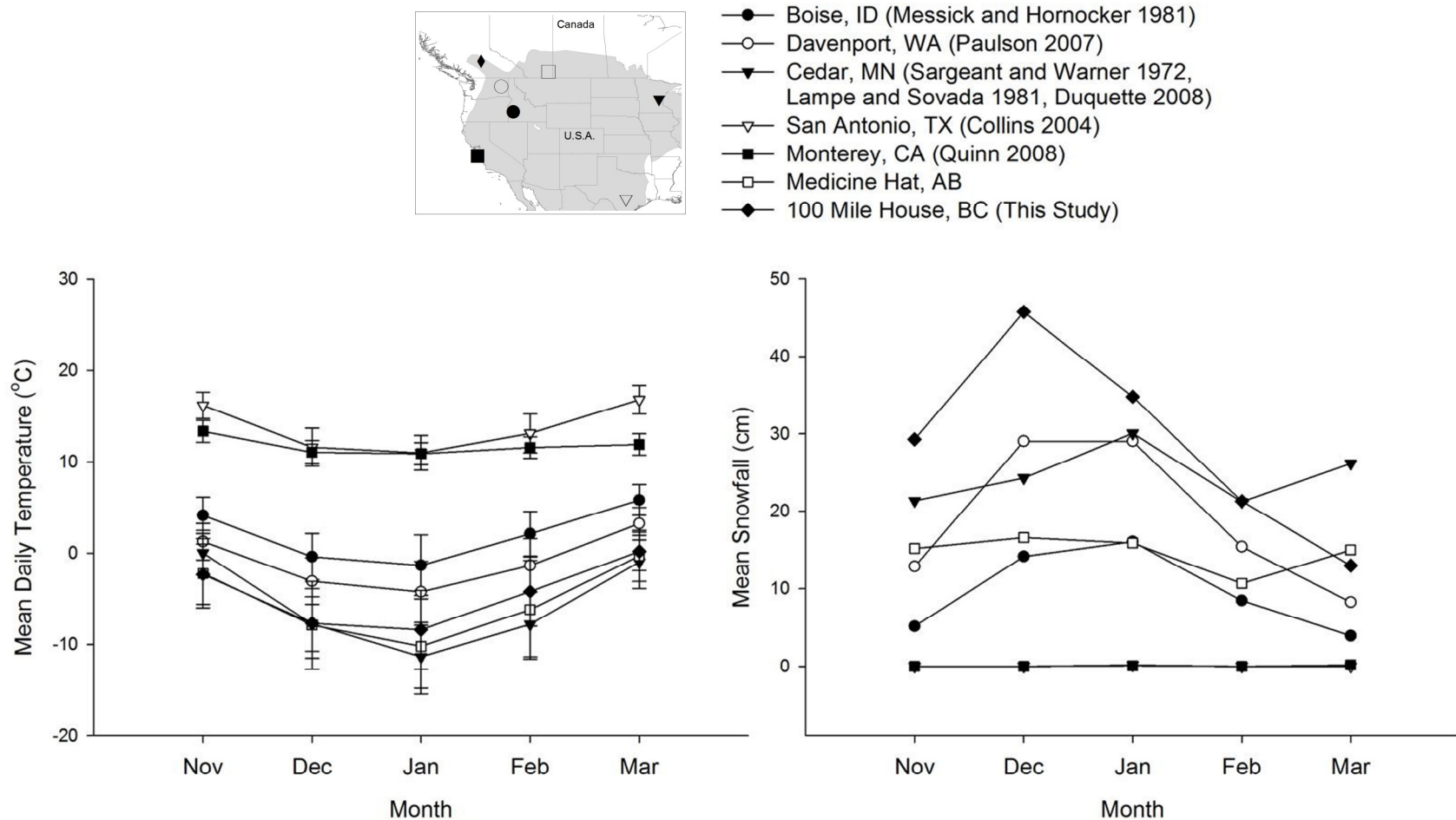


Figure 1-3. Mean daily temperature ($^{\circ}$ C) and mean snowfall (cm) for comparison of locations of previous North American badger research. Note that the northernmost location (the study area at 100 Mile House, BC) has the highest mean monthly snowfall and some of the coldest temperatures other than Medicine Hat, AB and Cedar, MN which are also in proximity to the northern and eastern range extents respectively. Data from 100 Mile House, BC and Medicine Hat, AB were taken from Environment Canada and based on a 30 year period between 1971 and 2000. (available at: <http://climate.weather.gc.ca>). Data for San Antonio, TX were taken from The Office of the State of Climatologist at Texas A & M University, (available at: <http://climatexas.tamu.edu/>). The remaining data (Davenport, WA: 1892-2012, Boise, ID: 1940-2006, Cedar, MN: 1962-2005, and Monterey, CA: 1906-2012) were taken from the Western Regional Climate Center (available at: <http://www.wrcc.dri.edu>).

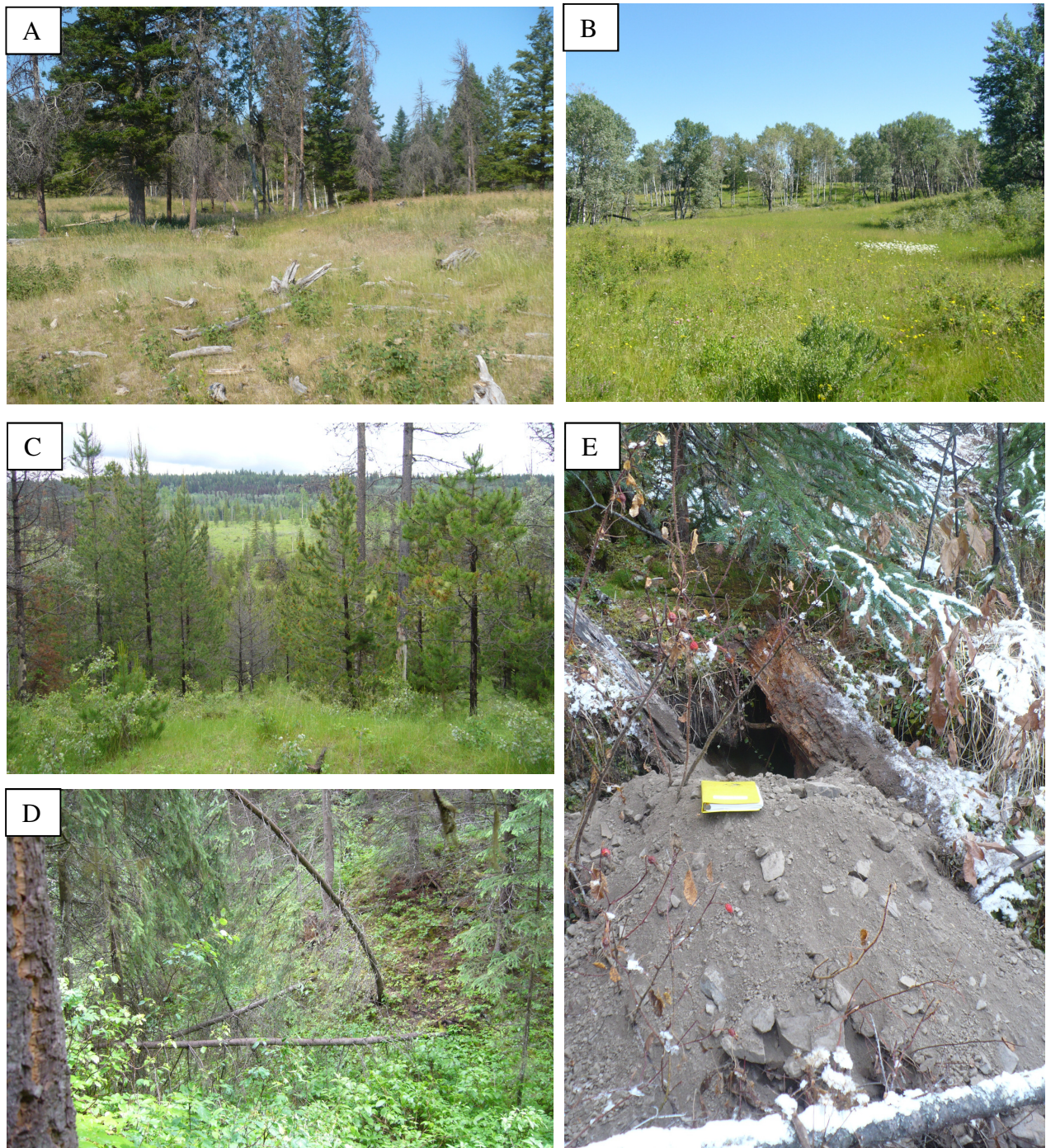


Figure 1-4. Photos of the grassland-forest matrix habitat (atypical for North American badgers *Taxidea taxus jeffersonii*) in the study area within the Cariboo Region of British Columbia, Canada. Photo A) typical open forest stand in the Interior Douglas-fir Zone (IDF), Photo B) typical pasture and aspen copse habitat, Photo C) typical lodgepole pine stand with cleared portions for grazing, Photo D) typical spruce stand in the Sub-Boreal Spruce Zone (SBS), and Photo E) atypical burrow location in a spruce stand. Note the relatively steep slope and large coarse fragments in the excavated soil.

compared to the large tracts of habitat further south. With small, patchy habitats and concomitant large home ranges, in addition to the lack of an important prey species (northern pocket gopher) the ability of northern badgers to build fat reserves sufficient to permit extended bouts of torpor may be compromised. As such, the animals may be forced to forage more regularly, yet the efficiencies and costs of doing this during extreme winter conditions may be significant.

As previously described, the North American badger possesses a suite of characteristics unlike other mustelids, suggesting the animals will cope with winter using notably different strategies. In fact, North American badgers living near the extreme northern limits of their range may be facing an ecological conundrum, forage above-ground through winter or limit activities, undergoing extended torpor bouts. Intuitively, the northern continental winters will present challenging conditions for *Taxidea*, a mid-sized, solitary carnivore that hunts fossorial prey. Winters (involving lower temperatures, higher snow cover, frozen ground, and short periods of daylight; Figure 1.3) will place added energetic constraints on the animal.

Winter and the Conservation of Badgers in British Columbia

Three subspecies of badgers are formally recognized in Canada and all are listed as species at risk (COSEWIC 2012). The *jeffersonii* subspecies (*T. t. jeffersonii*) ranges northward into western Canada, inhabiting British Columbia's southern interior grassland matrix (Figure 1.2, Figure 1.4). Currently, this animal is listed in this province as endangered/threatened (*i.e.*, "red listed" and nationally in Canada as "endangered"; BC Conservation Data Center 2008, COSEWIC 2012). Recent estimates of the population place the number of individuals between 230 and 340 (*jeffersonii* Badger Recovery Team 2008). The primary threats to this population are mortality from vehicle collisions and habitat loss (Weir *et al.* 2004). Given the status of this species, there has been considerable research into its summer and breeding ecology, yet a focused winter ecology study has been notably lacking. Understanding the winter ecology of this species thus becomes vital for crafting effective management plans for this animal. Prior to this study, cursory observations made on badgers near their northern limit suggested activity levels may be higher than anticipated, and burrows used during winter may differ in construction than those used in the summer (Klafki *unpubl.*). These observations prompted this

detailed, focused winter study of these animals as a means to provide relevant data on their relationship to the northern environment.

Objectives and Thesis Organization

To investigate the winter ecology of the North American badger, I took advantage of the groundwork laid by a recent study of badger ecology (Klafki *in progress*) occurring in the Cariboo region of central British Columbia. Location data collected between May 2007 and August 2009 by this previous project was used to supplement the data collected during my more focused field work over the winters of 2009/2010 and 2010/2011. In this way, data across four winters could be analyzed to investigate the activities, movements, home range, and fine-scale habitat of North American badgers during winter near the northern limit of their range. This work is presented in Chapters 2 and 3 of this thesis.

In Chapter 2, I specifically examine activity of badgers during winter. To do this, I compare home range sizes and longer movements (burrow to burrow) shown by the animals in winter to those seen in summer. I also present baseline data on the relationship of the animals to their winter burrows, including the length of time spent in the burrows (and incidences of torpor), frequency of emergence, and length of winter forays. In Chapter 3, I compare the fine-scale habitat features of winter burrows to those used in summer, to examine whether the animals are selecting specific sites to deal with winter conditions. In addition, I examine the characteristics that differentiate winter (and natal) burrows from summer burrows to determine if they can be effectively discriminated from one another, which would enable managers to identify which burrows are critically important. My final Chapter (4) presents a summary of my study and provides suggestions for future research as well as recommendations for managing badgers in the Cariboo region of B.C.

Details of Study Area

The study area was located at the northern extent of the range of North American badgers in the Cariboo Region of central interior British Columbia (Figure 1.2, 1.4, and 1.5; Rahme *et al.* 1995). Specifically, field work was roughly centred near 100 Mile House, British Columbia (10U 618054 E 5722832 N; WGS84). The landscape here is composed of a matrix of forested and grassland communities (Figure 1.4). Forests consist primarily of Douglas-fir (*Pseudotsuga menziesii*), falling within the designated Interior Douglas Fir (IDF) biogeoclimatic (BEC) zone



Figure 1-5. Location of the Study Area (red outline) in the Cariboo Region near 100 Mile House, British Columbia.

of the province (Meidinger and Pojar 1991). Grasslands are commonly intermixed with forested stands due to the fire history and dry nature of the ecosystem. However, they primarily occur along highways near valley bottoms or in esker terrain surrounding wetland complexes in the south of the study area. Many of the grasslands in the study area have been altered due to grazing or agriculture. Trembling aspen (*Populus tremuloides*) copses occur frequently in grasslands and pastures. Secondary BEC zones, Sub-Boreal Spruce (SBS) and Sub-Boreal Pine-Spruce (SBPS) zones occur at slightly higher elevations and cover moderate to very limited areas, respectively (Meidinger and Pojar 1991, Steen and Coupé 1997). These zones are dominated by coniferous stands of hybrid white spruce (*Picea engelmannii* × *glauca*) or lodgepole pine (Meidinger and Pojar 1991).

Forestry is a major industry in the Cariboo, where timber harvesting frequently occurs on Crown land (Ministry of Natural Resource Operations 2005). This has converted forested land to a mosaic of open and early-seral habitats. More recently, salvage harvesting has occurred throughout the study area in response to the impact of the mountain pine beetle (*Dendroctonus ponderosae*) on stands of lodgepole pine (*Pinus contorta* var. *latifolia*). Agriculture is another major industry in the region, including a large ranching industry (Ministry of Natural Resource Operations 2005). This in turn has resulted in timothy (*Phleum pratense*) and alfalfa (*Medicago sativa*) being commonly grown in pastures.

Soils in the study area are dominantly Gray Luvisols as well as Eutric and Dystric Brunosols (Valentine *et al.* 1986). Parent materials are largely lacustrine silts and clays and alluvial silts and fine sands in the valley bottoms and glacial-till at higher elevations on the plateau (Valentine *et al.* 1986).

Climate in the IDF is continental, with warm, dry summers and cool winters, whereas the SBS and SBPS are characterized by severe snowy winters and warm, moist, short summers (Meidinger and Pojar 1991). Over the course of the year, the daily average temperature in the town of 100 Mile House is 4.4°C. Daily minimums in January average -13.5°C with daily maximum temperatures averaging -3.2°C; temperature lows as extreme as -48°C have been recorded (26 December 1996) (Environment Canada 2011). Average snowfall in January is 34.8 cm and averages 159 cm throughout the year (Environment Canada 2011; Figure 1.3 and 1.6). The

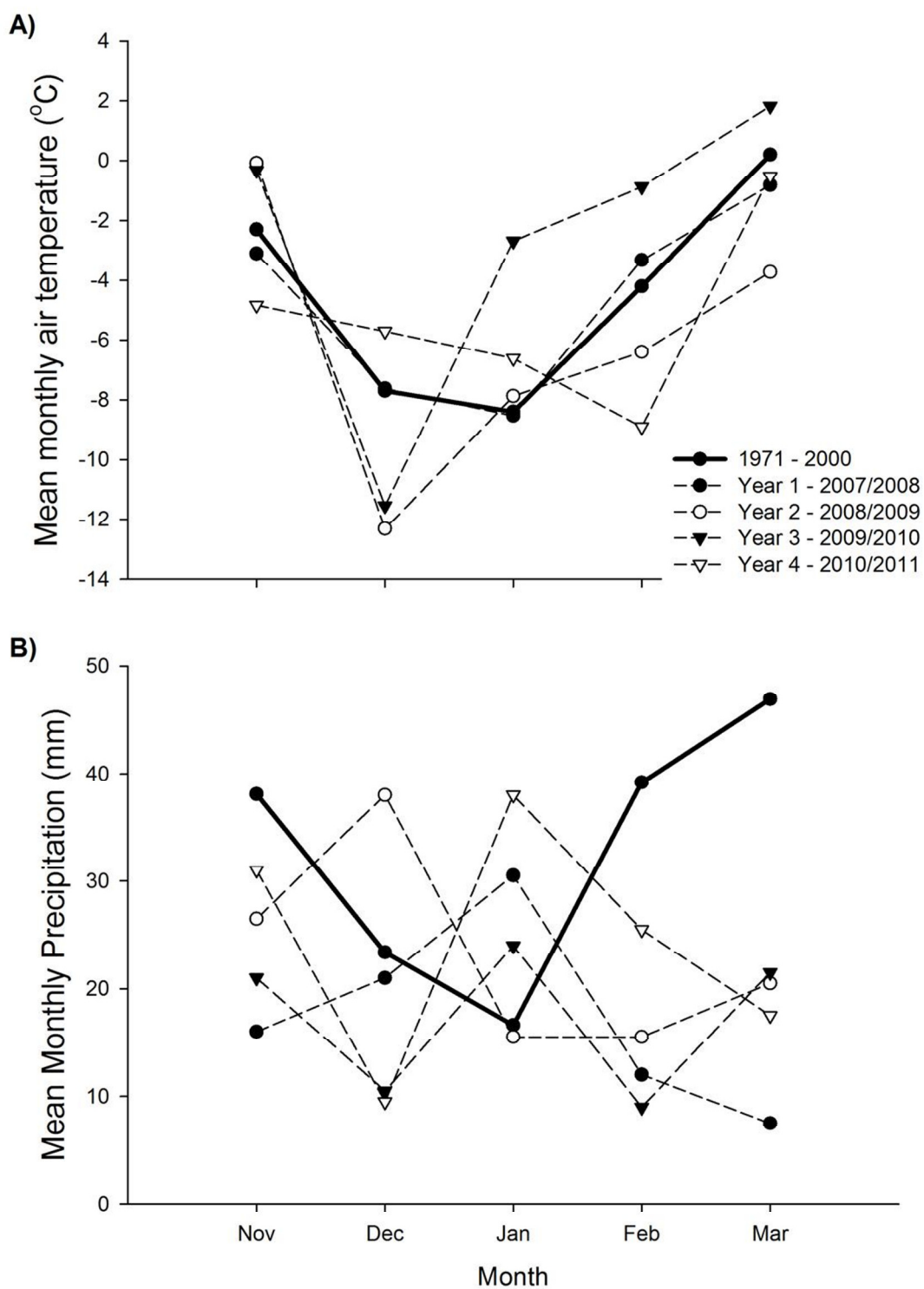


Figure 1-6. Comparison of recent climatic norms in temperature (A) and precipitation (B) for the study area (data from 1971-2000 – Environment Canada website.) with the monthly averages experienced during the course of this study.

median start date of snow-cover onset³ is between November 1 -and 15th; the median end date of snow-cover⁴ is between April 1 and 15th (Natural Resources Canada 2011).

Species of mammals in the area that are known to be potential prey items for badgers include Columbian ground squirrel, yellow-bellied marmot, muskrat (*Ondatra zibethicus*), red squirrel (*Tamiasciurus hudsonicus*), snowshoe hare (*Lepus americanus*), and various mice and voles (Families: Microtinae, Cricetinae, and Heteromyidae; Packham and Hoodicoff 2004, Hoodicoff 2006). Chipmunks (*Tamias* spp.) occur in the study area, and although they are not a reported prey animal for badgers in BC, they do occur frequently in the diet of Ontario badgers (Sayers *Pers. Comm.*). Other small mammal species occurring in the study region that could serve as prey include common porcupine (*Erethizon dorsatum*), northern flying squirrel (*Glaucomys sabrinus*), shrews (*Sorex* spp.), and bushy-tailed woodrat (*Neotoma cinerea*).

Investigation of badgers in the Cariboo has been ongoing since 2003, when the estimated population size was extremely low (13 individuals = minimum number known to be alive; Packham and Hoodicoff 2004). From 2007 – 2009 a summer road ecology study refined the population estimate based on mark and recapture methods (Klafki *in progress*). This work suggested that the population had increased to approximately 72 animals by 2008 (95% CI 67-83 including kits; Klafki *in progress*). This study also demonstrated that road mortality was the largest threat to this population, primarily due to a major highway (Highway 97) bisecting the generally linear nature of the habitat. The apparent increase in the size of the population seen in the last several years is thought to be due to improved human tolerance of the animals (through outreach activities by government, consultants and academia) and increased open habitat resulting from beetle-killed pine, rather than a decrease in road mortality.

³ **Median start date of snow-cover onset** is defined as the first date with 14 consecutive days of snow cover greater than 2 centimetres in depth).

⁴ **Median end date of snow-cover** is defined as the last date with 14 consecutive days of snow cover greater than 2 centimetres in depth).

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Chapter 2. Winter Activity Patterns of the North American Badger (*Taxidea taxus jeffersonii*) at the Northern Extent of its Range.

Introduction

Winter is a critical time for wildlife inhabiting temperate regions (Pruitt 1960, Campbell *et al.* 2005). Here, wildlife must cope with the high costs of thermoregulation, compounded by scarce food resources, cold temperatures, and restricted mobility due to snow cover (Formozov 1946, Pruitt 1957, Pruitt 1960, Telfer and Kelsall 1984, Buskirk and Harlow 1989, Marchand 1996). To cope with the high costs of winter, many mammals reduce or limit their activity to periods when conditions are favourable (Storm 1972, Thompson and Colgan 1994, Tanaka 2006, Kowalczyk *et al.* 2009, Zub *et al.* 2009), escape to refuges with warmer, stable temperatures (McCafferty *et al.* 2003, Moore and Roper 2003, Hwang 2005, Sidorchuk and Rozhnov 2008), or enter torpor to reduce thermoregulatory costs. Although the latter strategy appears to be a response to climate, ultimately it may be an adaptation to cope with scarce resources (Aleksiuk and Stewart 1977, Landry-Cuerrier *et al.* 2008, Kowalczyk *et al.* 2009).

Various strategies for remaining active during winter are demonstrated by mammals occupying colder habitats. Large fat reserves are often stored prior to the onset of winter to reduce thermoregulatory costs and offset scarce resources (Folk *et al.* 1972, Young 1976, Fowler and Racey 1988, Buskirk and Harlow 1989, Prestrud and Nilssen 1992, Hwang 2005, Tanaka 2006, Kowalczyk *et al.* 2009). This may or may not be accompanied by bouts of torpor. Although some mammals employ a strategy of deep torpor (hibernation) and do not emerge during winter, utilizing shallow torpor may allow individuals to take advantage of favourable conditions to forage for food (Newman *et al.* 2011), by essentially “sleeping though” periods of less favourable conditions. Hock (1960) termed a type of shallow torpor among carnivores as ‘carnivorean lethargy’, a phenomenon exhibited among several mesocarnivores (raccoons: *Procyon lotor* and striped skunks: *Mephitis mephitis*). The ability to employ this tactic may be compromised in colder climates where mammals may be unable to store sufficient fat reserves prior to the onset of winter, thus necessitating the need for periodic foraging during winter (Landry-Cuerrier *et al.* 2008).

The behavioural and physiological adaptations used by the North American badger (*Taxidea taxus*) to cope with winter have not been well-studied despite the fact the animal ranges

considerably northward into Canada, where winters are relatively harsh. In particular, surprisingly little research has been conducted on the winter activity patterns of the animal, including time spent in burrows (which might suggest carnivorean lethargy: Hock 1960) *versus* time spent active on the surface. Attempts have been made to radio-track badgers during the winter, but sample sizes have been low ($n=1$; Sargeant and Warner 1972) or the animals were tracked for only a portion of the winter due to mortality or lost transmitters (Lindzey 1978, Lampe and Sovada 1981, Messick and Hornocker 1981). Harlow (1979a, 1979b, 1981) also studied the winter activities and physiological adaptations of badgers; however, only females were used, and they were housed in outdoor enclosures. These limited data suggest that North American badgers not only reduce their activity during winter, but also enter torpor during winter months (Harlow 1979a, Harlow 1979b, Harlow 1981, Messick and Hornocker 1981, Paulson 2007). Badgers also have been observed outside of burrows during winter (Lindzey 1971, Sargeant and Warner 1972, Warner and Versteeg 1995), although the extent and purpose of these winter forays remain unclear.

It seems logical that during winter, badgers must balance the energetic demands for food against the energetic costs of foraging above-ground during cold weather. Moreover, although badgers are normally nocturnal (Lindzey 1971, Goodrich 1994), cold temperatures at night may require the animals to adjust their activities so that they occur during periods of more favorable foraging conditions (*i.e.*, during the day), as seen in other mustelids (marten: *Martes americana*, Thompson and Colgan 1994; least weasel: *Mustela nivalis*, Zub *et al.* 2009). For example, nocturnal activities during winter may not be required given that the normally-diurnal prey of the badger (*e.g.*, Columbian ground squirrels: *Urocitellus columbianus*) will be hibernating during winter. The extreme winters faced by the North American badger at their northern range limit may thus present a suite of environmental conditions that force the animal to balance the energetic savings from torpor/lethargy against the need to forage over the extremely long and harsh winter. Additionally, there may be greater pressure in the north to select burrow sites that provide thermal insulation. Whereas badgers in more milder, southern climes may be able to use less discretion in choosing burrow locations, badgers in the far north may show higher fidelity to specific burrows over the course of the winter.

Badgers in the north portion of their range may also have to deal with other energetic constraints brought on by the fact that they reside in an environment of small, patches of habitat

compared to that encountered by conspecifics living further south. In British Columbia, Canada, badgers utilize more atypical vegetation communities such as clearcuts, forests, alpine, and wetlands (Rahme *et al.* 1995, Weir *et al.* 2003, *jeffersonii* Badger Recovery Team 2008) and have home ranges considerably larger (2x the largest male home ranges reported in the United States) than their southern conspecifics (Newhouse and Kinley 2000, Hoodicoff *et al.* 2009). This increase in home range size is likely due to a combination of low population density (*i.e.*, lack of females on the land base), a lack of suitable or small, patchy habitat, and a reduced prey base (Minta 1993). Indeed, pocket gophers, which are an important and primary prey source of southern badgers (Todd 1980, Lampe 1982, Sovada *et al.* 1999), are absent at the extreme northwest limits of the species (Cariboo Region; Johnstone 1954). Large home ranges and low population density likely lead to more energy and time spent searching for mates in late summer which could therefore result in less development of fat reserves prior to winter. During relatively long and severe winters, badgers might require more above-ground, foraging activity (than seen in badgers near the core of their range) to compensate for depleted fat reserves. The energetic demands of maintaining these large home ranges (and seeking widely-scattered mates), coupled with shorter summers, may mean that the animals must allocate more time to foraging over the winter period. Thus, the animals may be facing an ecological conundrum near their northern limits: short summers and large home ranges may require more frequent foraging, yet colder, snowy winters raise the cost of such activities.

The overarching objective of this study was to examine the winter ecology of *Taxidea* during winter, near their northern range limit. Using radio-telemetry, I examined (i) whether badgers reduce movements and home range during winter, (ii) the frequency of torpor events, (iii) the extent that badgers rely on a particular burrow through winter, in particular the frequency and length of burrow emergence and how this relates to environmental conditions, and finally (iv) whether activities of the animals shift from a nocturnal to diurnal pattern during winter.

Methods

Study Area

The study area (6,377 km²) was located at the northern extent of North American badger range, within the Cariboo Region of central interior British Columbia near the town of 100 Mile House (See Chapter 1 Figures 1 and 2; Rahme *et al.* 1995). The study area is composed of a

matrix of coniferous forest, aspen copses, and grassland (Meidinger and Pojar 1991), much of which has been altered for human use (made into pastures, *etc.*; MNRO 2005).

Climate is continental, with warm dry summers and cool winters (Meidinger and Pojar 1991). Snow cover lasts from between the beginning of November to the middle of April (NRC 2011). Mean total snowfall and ambient air temperature during winter is 165.9 cm and -4.5°C respectively (Environment Canada 2011). During the coldest month (January) the daily temperature averages -8.4°C (± 4.3), but can reach as low as -48°C (mean number of days $< -20^{\circ}\text{C} = 18.6$ days/year; Environment Canada 2011). A more detailed description of the study area can be found in Chapter 1.

Field – Capture

The telemetered badgers used in this study were originally part of a summer road-ecology study that took place between 2007 and 2009 (Klafki, *in progress*). All badgers (except three orphaned kits – see below) were live-trapped using off-set, padded “soft-catch” foothold traps (Victor 1 ½ coil spring) anchored into the ground. Traps were covered with soil and located in proximity to active badger burrows. Once captured, badgers were restrained using a handling pole. A visual estimate of body mass was used to administer an appropriate dosage of 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol). Radio-tags were surgically implanted off-site by a veterinarian in either 100 Mile House or Williams Lake, BC, depending on distance to capture site. Each badger was fitted with an intraperitoneal VHF transmitter (IMP400L Telonics, Mesa, AZ). Badgers recovered from anesthesia in a transfer container (modified plastic 205 L barrel) where they were wrapped in a blanket to prevent hypothermia. The animals were released at their burrow once fully recovered, and thereafter were checked frequently during the following 48 hours to ensure normal activity.

Three orphaned animals were added to the study after their mother was killed by a vehicle. These kits were live-trapped at the natal burrow in mid-May 2010 and reared at the BC Wildlife Park near Kamloops, BC. To monitor their re-introduction to the wild, prior to release these animals were implanted with transmitters after gaining sufficient weight. After seven days of post-surgery monitoring, the animals were transferred to a soft-release enclosure in the Cariboo region (July 19th 2010). After one week, the animals started exiting and returning to the enclosure using a hole in the fence they created. By August 21st all three animals had dispersed

and began displaying typical badger activities and movements (Klafki and Packham *unpubl.*). One of these animals (♂) was killed shortly thereafter by a vehicle. The remaining two (1♂, 1♀) were subsequently incorporated into this winter study. These two animals, along with two late-captured animals (1♂, 1♀) were fitted with transmitters equipped with temperature-sensitive pulse rates (IMP400L with Opt. MS4 Temperature Sensor Telonics, Mesa, AZ) allowing me to also monitor their body temperatures.

Field – Radio-telemetry

The sample of telemetered badgers that provided winter data consisted of 14 badgers live-trapped in the wild (11 ♀♀ + 3 ♂♂) along with two (1 ♀ + 1 ♂) released orphans for a total of 16 badgers (12♀ + 4 ♂). The strong sex-bias in the live-trapped sample was a product of the high road-kill mortality experienced by adult males in B.C. populations during the breeding season (Newhouse and Kinley 2000, Hoodicoff *et al.* 2009, Klafki *in progress*).

Telemetered badgers were located a minimum of once per week in the first three winters (2007/2008, 2008/2009, 2009/2010) and approximately once every other day in the fourth winter (2010/2011). I defined winter as the snow season from November through March and summer as the snow-free season from April through October. Once located, Universal Transverse Mercator (UTM) coordinates were recorded using a handheld GPS (Garmin GPSmap76x, Olathe, KS.). All locations were collected during the day. For those badgers that had temperature sensitive transmitters (n=4), beats-per-minute (BPM) were recorded once using a stopwatch (for a full 60 seconds), and then body temperature was calculated using the linear function provided by the manufacturer. I considered these measurements to be sufficiently accurate, as a difference of 1 BPM (the maximum difference between consecutive measurements) translated into only a 0.72° C difference in body temperature. Although temperatures estimated in this manual fashion are less precise than through an automated system, the body temperatures I measured were similar to those measured by Harlow (1981) and the resolution sufficient to detect torpor events (defined as when body temperature (T_b) dropped below 28° C; Harlow 1981).

Other data collected at badger locations included weather conditions such as cloud cover, precipitation, wind speed (Beaufort scale), temperature, and days since snowfall. In the fourth winter of the study (November 2010 – March 2011), I recorded whether each animal was active

and whether fresh badger tracks or a soil fan (indicating recent digging) were present above the snow.

Camera placement at Winter Burrows

I defined a ‘winter burrow’ as any burrow used for more than seven consecutive days between November 1st and March 15th. I felt that using seven days as the criteria for ‘winter burrow’ was reasonable given that burrows were rarely re-used for longer than four days (Figure 2.1). Therefore, burrows used consecutively for longer than four days may indicate these burrows were unique. Further, the frequency of re-locating badgers (~7 days) during the first three winters (2007/2008, 2008/2009, and 2009/2010) was the minimum length of burrow use that could be detected in those years.

Burrows used after March 15th were not considered, as this corresponded to the period when females moved into natal burrows (*pers. obs.*). To monitor emergence from winter burrows, and to gather baseline information on badger activities, I placed passive infrared remote cameras outside of occupied winter burrows (RC55 Rapidfire RECONYX, Holmen, WI) in the third and fourth winters (2009/2010 and 2010/2011). All cameras were placed in either lockable, beige-coloured, metal cases or attached to a nearby tree, and positioned approximately one metre above the ground to capture images of badger emergence. Settings on the cameras included high sensitivity, three photos per trigger, rapidfire picture interval, and no delay. Cameras recorded date, time, and temperature (°C), on the digital photographs. In the third winter (2009/2010), several cameras were inadvertently set with delays ranging from 3 to 15 seconds.

Data Preparation - Home Range and Movements

As badgers tended to remain in the same burrow during the winter, I only used unique burrow locations (*i.e.*, “location” = an event during which a badger was found or located). Re-locations were spaced at a minimum of 24 hours apart to calculate home range. As such, all locations were spatially and temporally independent (Worton 1987, Swihart and Slade 1985). This however, reduced the number of locations available to calculate home range, preventing me from using 95% fixed kernel home range calculations (Worton 1989, Worton 1995, Seaman and Powell 1996, Seaman *et al.* 1999). As an alternative, I used Geographical Information System software to calculate 100% minimum convex polygons (100% MCP, Mohr 1947) to represent

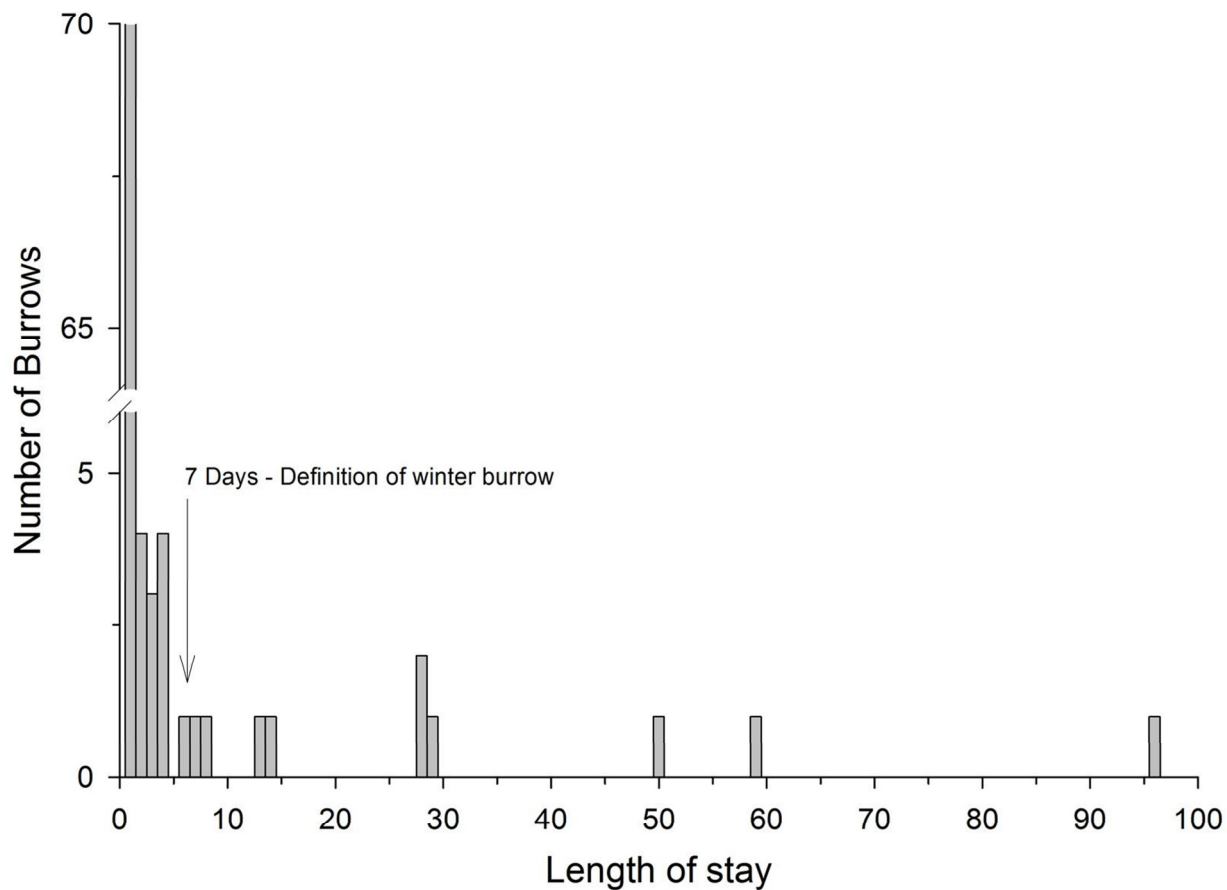


Figure 2-1. Histogram showing the number of re-used burrows (in the fourth winter - 2010/2011) and their associated length of stay by North American badgers (*Taxidea taxus jeffersonii*) in the Cariboo Region of British Columbia, Canada. Burrows identified as having been used for ≥ 7 days were defined as 'winter burrows'

seasonal home ranges for each individual (Animal Movement extension 2.0, USGS Alaska Science Center, along with ArcView 3.2, ESRI Redlands, CA). Although values likely represent a conservative estimate of home range size given that badgers used the area surrounding burrows for foraging, they allowed me to compare home ranges to those reported by other studies.

I estimated daily movements of badgers by measuring the Euclidean distance between successive telemetry radio-locations. The number of days differed between each sequential location, therefore I standardized by dividing the distance moved by the number of days between each radio-location.

Data Preparation - Torpor, Activity, and Burrow Use

After plotting body temperatures on a graph, I estimated the number of torpor ‘events’. Torpor was defined when an individual badger’s temperature dropped to 28° C over a 29 hour cycle (Harlow 1981). Although continuous body temperatures were not measured, torpor events could still be detected, as decreasing body temperatures that were still above 29° C were considered an indication that the individual was entering or emerging from torpor. Euthermic temperature appeared to be 36.4° C in the badgers that I sampled; a minimum drop of 2° C below this temperature was considered an indication of a torpor event. As torpor cycles in badgers last 29 hours, I assumed a separate torpor event had occurred, if body temperatures on the subsequent visit (>24 hours later) remained unchanged. As subsequent visits were often 48 hours apart, I do not believe this overestimated the number of torpor events.

To examine the level of activity, length of foraging bouts, relationship between emergence and environmental conditions, and to determine whether badgers exhibited a more diurnal foraging strategy during winter, I used photos taken by the remote cameras to identify emergence and entrance times of badgers during winter activity. Only the first photo and corresponding time for each new activity (burrow ingress and egress) were used. On occasion, a badger would return to the entrance of a burrow after completing a foray, but leave to conduct a second foray without actually re-entering the burrow. I counted these events as two separate forays.

For the relationship between emergence and environmental conditions, I obtained temperature and snow depth data from a nearby government weather station (100 Mile House, British Columbia; Environment Canada 2012). I also counted the Julian day (a continuous count of days) for each emergence event; however, as the winter spans across the end of one year and

the beginning of a second, I used December 1st as the first day of the count, and ended at the day of emergence. To compare emergence events with non-emergence events, I randomly selected an equal number of days within the camera monitoring period when individuals did not emerge from winter burrows and collected the same data (temperature, snow depth, and Julian day).

I calculated the number of burrows used during the winter, the number of winter burrows used, the mean residence length in winter burrows, and the mean total residence length of all winter burrows used. The residence length in winter burrows was defined as the date of first detection in the burrow until the last date that a badger used the burrow continuously (that point when the animals chose to overnight elsewhere than the focal winter burrow). In some cases, individuals left winter burrows for more than one night, but then returned; these were treated as separate stays.

Data Analysis

I used R Statistical Software Version 2.15.2 (R Development Core Team, Vienna, Austria) for all data analysis. I conducted exploratory analysis and checked assumptions by plotting data and residuals in histograms, boxplots, quantile-quantile plots, *etc.* before testing for normality and equal variances using the Kolmogorov-Smirnov and Fligner-Killeen tests (Quinn and Keough 2009, Zar 2010). I made Log + 1 or Root transformations when required (Quinn and Keough 2009).

I used linear mixed effects models (LME) to test for differences in fixed variables (home range, movements, activity, and burrow use) between sex and season (summer: April to October *versus* winter: November to March) or year (Winter 1, Winter 2, *etc.*) while taking into account random effects caused by individual badgers. Models were built with function *lme* (package *nlme*, R Version 2.15., <http://www.r-project.org>) using Restricted Maximum Likelihood Estimation (REML).

To examine the relationship between badger emergence and environmental conditions (temperature, snow depth, and Julian day) I used generalized linear mixed effect models (GLMM) to build a univariate model for each variable using function *glmer* (package *lme4*). Models were compared by an information criteria approach using Akaike's second-order information Criterion (AIC_c) for small samples (Burnham and Anderson 2002, Johnson and Omland 2004).

LME and GLMM modeling is analogous to multi-level (nested) / repeated measures analysis of variance (ANOVA) and logistic regression, respectively. Mixed models are able to control variation in the model due to differences between individuals (random effects) (Pinheiro 1994, Zuur *et al.* 2009). Moreover, LME and GLMM models handle unbalanced designs well (Pinheiro 1994, Zurr *et al.* 2009). As badgers in this study were typically tracked for more than one year, I had multiple seasonal home range estimates for some individuals. However, not all badgers were tracked in the same year, nor for the same length of time. Additionally, as mentioned, my sample size for males was lower than for females and consequently my design was unbalanced.

As time data are circular in nature, I used a Rayleigh's test to determine whether the times of events were uniformly distributed (Zar 2010). Watson's Two-Sample Test of Homogeneity was used to compare activity events between years (Zar 2010).

Results

Home Range and Movements

Radio-telemetry yielded a total of 1448 locations between July 30th 2007 and March 28th 2011. Five hundred and forty-eight locations (548) were collected during the winter period. On average, sixteen individual badgers were tracked over 123 (SD=31) days to 18.8 (SD=10.9) radio-locations each winter.

When modeled with mixed effects, 100% MCP home ranges significantly differed by sex ($F_{1, 16} = 11.1, n = 57, P < 0.01$), season ($F_{1, 37} = 86.4, n = 57, P < 0.0001$), and an interaction between the two factors ($F_{1, 37} = 17.5, n = 57, P = <0.001$). Mean female 100% MCP home range was smaller in winter than summer, representing a reduction of 83% (Figure 2.2). Similarly, male home ranges reduced by 97% during winter. Male summer home ranges were larger than those of females; however, male winter home ranges were similar to females (Figure 2.2). Despite being smaller than in summer, the largest winter home range was 11.9 km² and 8.3 km² for females and males respectively.

Movements in winter also were significantly reduced in size compared to summer for both females and males (Figure 2.3). Movements differed significantly between sex ($F_{1, 18} = 31.5, n = 1368, P < 0.0001$), season ($F_{1, 1346} = 346.1, n = 1368, P < 0.0001$) and an interaction between both factors ($F_{7, 1336} = 25.0, n = 1368, P < 0.0001$). Although male and female summer

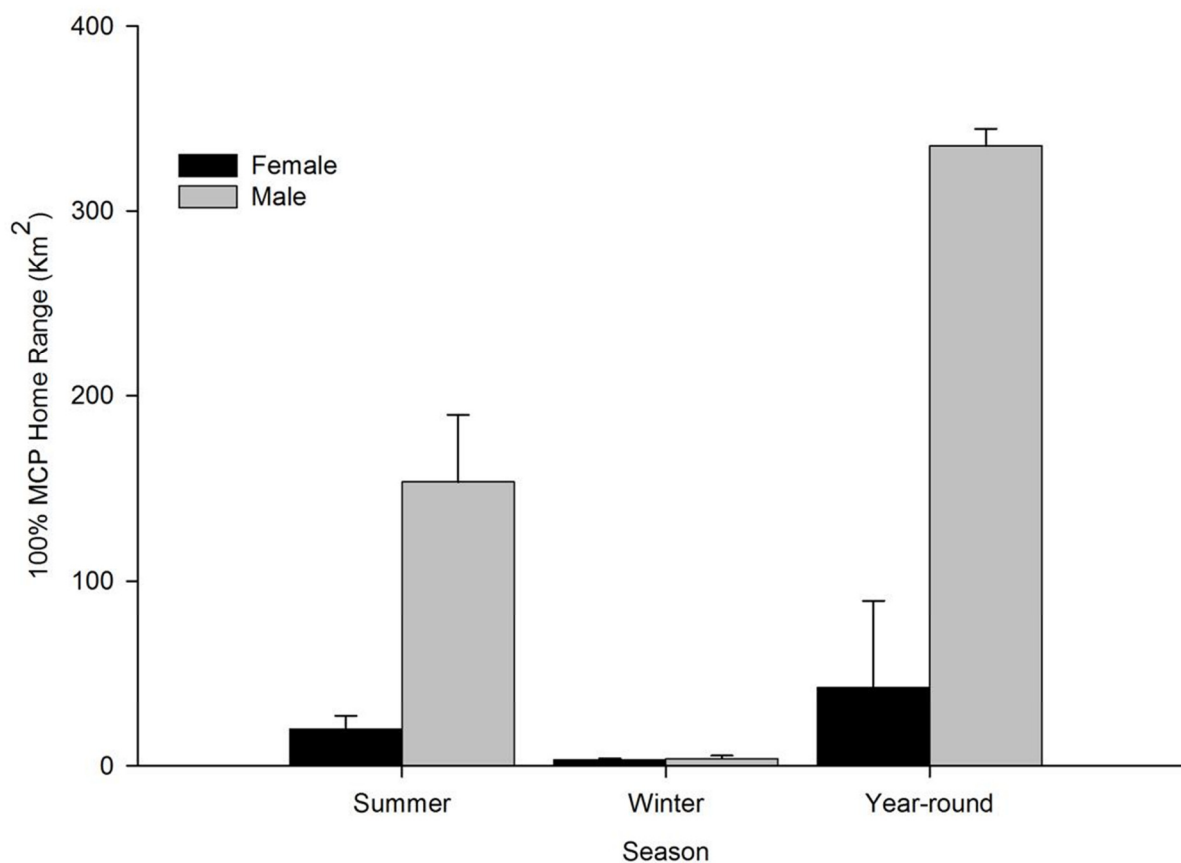


Figure 2-2. Mean ($\pm$ SE) 100% MCP home range for male ($n = 8$) and female ($n = 12$) North American badgers (*Taxidea taxus jeffersonii*) in winter (November to March), summer (April to October), and year-round* in the Cariboo Region of British Columbia, Canada between 2007 and 2011. Year-round MCP only includes those individuals that were tracked for longer than one year (both winter and summer seasons; male ($n = 2$) and female ($n = 9$)).

movements differed, winter movements did not differ according to gender (Figure 2.3). Mean female movements were 80% shorter in winter than summer, whereas mean male movements were 94% shorter in winter than summer. Although the majority of time badgers did not move (*i.e.*, 0 m/day), the maximum distances I recorded during winter by badgers were 2,815 m/day and 4,243 m/day for males and females, respectively. These maximum winter movements were 1.5 and 7.5 times the average summer movement respectively (Figure 2.3).

Torpor

Radio-locations from badgers implanted with temperature sensitive VHF transmitters produced 171 temperature readings from four badgers (two ♀♀, two ♂♂ - Figure 2.4a-d). All badger body temperatures were approximately 37° C at the beginning of monitoring in November.

Initial torpor events were generally detected within the first week of January. In total, I detected 54 torpor events (mean 13.5 ± 5.7 events per badger, range: 6 to 20; Figure 2.4). The minimum recorded body temperature was 25.6° C. A lack of continuous body temperature data from the badgers prevented me from testing for a direct relationship between torpor events and changing outside environmental conditions. However, the onset of torpor did not appear to be related to temperature or snow cover, for at the end of November 2010, the mean daily temperature dropped below -20° C (Figure 2.4a-d) and snow cover was present by the end of October, yet during this period, no torpor events were detected. Furthermore, temperatures in the month of December remained cold and were relatively similar to temperatures in January and February (Figure 2.4a-d), yet torpor events were not detected until early January. Cold temperatures and snow also persisted to the end of March, well after the final torpor events. One of the study animals (♀2, Fig. 2.4d) was first detected in torpor on December 16th and her final such event occurred much earlier (January 26th 2011) than the other animals, showing torpor initiation and termination of torpor to be variable between individuals. During the period when torpor was frequently occurring in the population (January to March), remote cameras still regularly captured individual badgers emerging from winter burrows (Figure 2.4a-d)

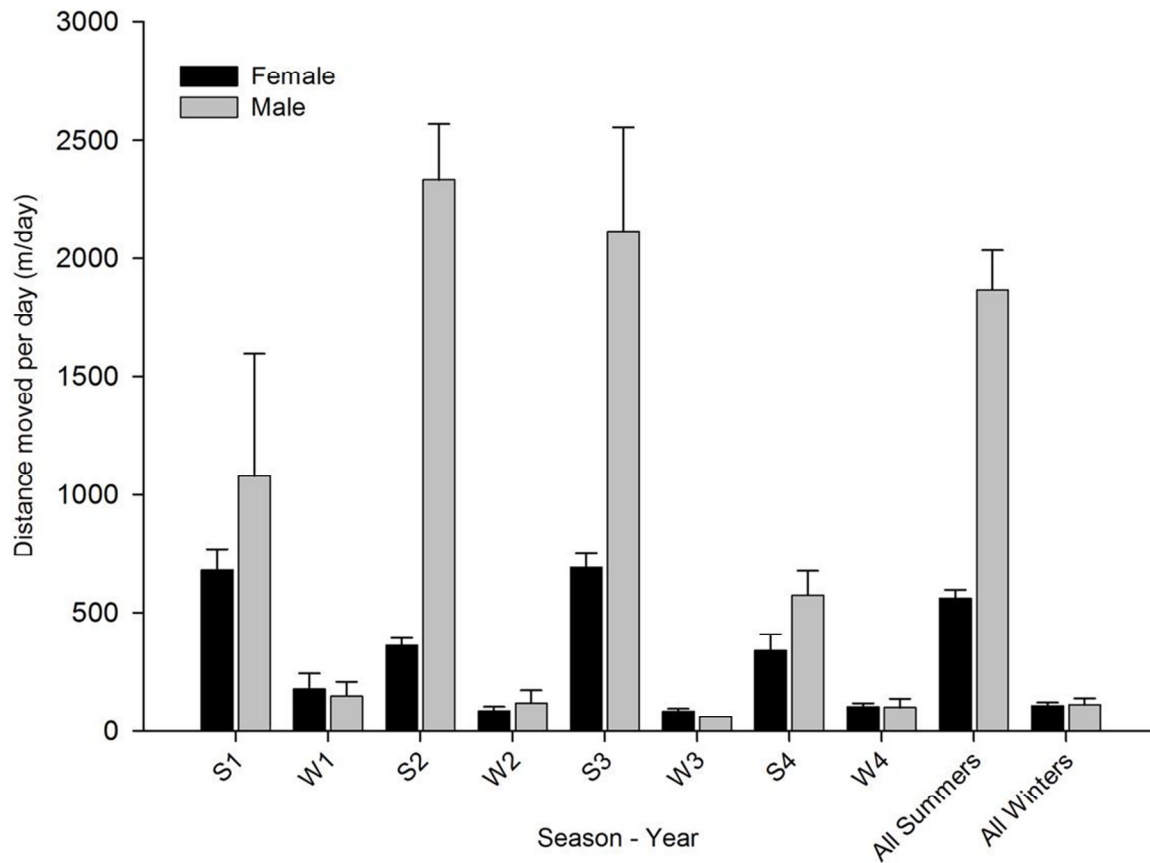


Figure 2-3. Mean distance moved between burrows for each field season (Summer 1:S1, Winter 1:W1, etc.) and all summers and winters combined, standardized by the number of days between successive locations for male ($n = 8$) and female ($n = 12$) North American badgers (*Taxidea taxus jeffersonii*) in the Cariboo Region of British Columbia, Canada between 2007 and 2011. Summer was defined as between April and October, winter was defined as between November and March.

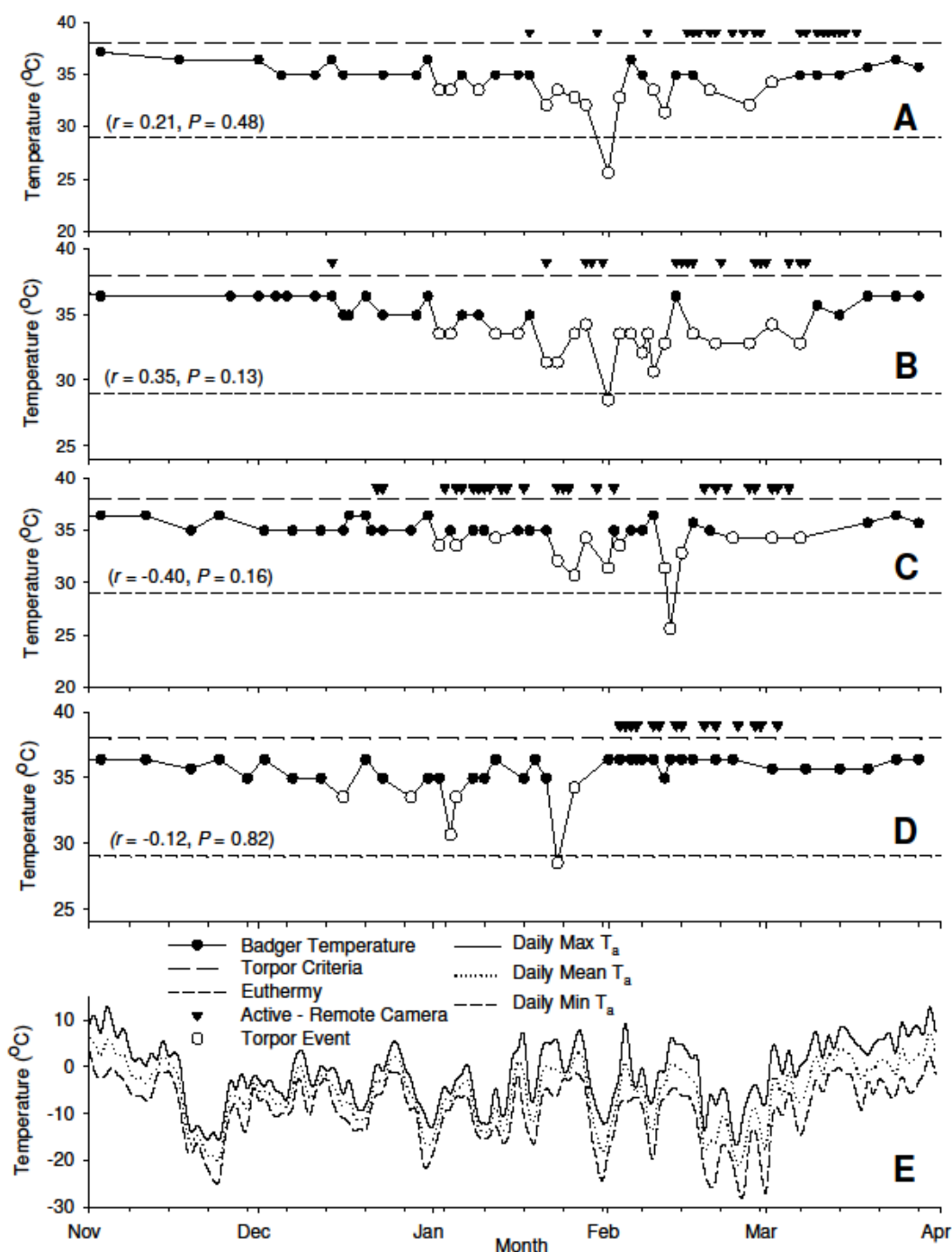


Figure 2-4. Body temperature of a sample of North American badgers as recorded through telemetry during the winter of 2010/2011, along with ambient temperatures for comparison. **Top Plot A** shows data for ♀1, for reference, dashed lines extend across each graph at 29° C and 38° C, the temperature criterion for torpor and euthermia, respectively. Circular points represent temperature measurements; white circles indicate estimated torpor events. Triangles along euthermia line indicate days in which camera monitoring detected the badger being active (Jan 16th – Mar 14th). **Plots B** ♂1 (Dec 14-16th, Jan 2nd- Feb 5th and Feb 8th – Mar 10th), **C** ♂2 (Dec 21-23rd and Dec 31st – Mar 7th), and **D** ♀2 (Jan 16th – Mar 14th), are analogous. **Plot E** shows the daily mean, minimum, and maximum ambient air temperatures obtained for 100 Mile House, B.C during winter (November 2010 to March 2011) through environment Canada (www.climate.weatheroffice.ec.gc.ca).

Winter Burrow Residence

The number of burrows and winter burrows used by radio-tagged badgers, the mean residence time per winter burrow, and the mean total winter residence time, all did not differ between sex, year or the interaction between sex and year (Table 2.1). These data reveal that the animals used an average of 10.6 (SD = 6.0) different burrows over the course of a winter, but on average, only 1.3 (SD = 0.8) burrows matched my criteria for being classified as a ‘winter burrow’ (>7 days of continuous use).

The majority of badgers used a maximum of two winter burrows (following my criteria); however, two females (one in 2008/2009 and another in 2010/2011) each used three winter burrows. On average, the date that a badgers first used a ‘winter burrow’ was December 31st (range: November 20th - February 8th), which also coincided with the first detection of torpor. The mean residence time in each winter burrow was 24.8 (SD = 20.5, range: 8 - 46, $n = 41$) days. Often, more than one winter burrow was used by an individual animal; the mean last date of use for the first winter burrow was January 30th, and the mean starting date for use of a second winter burrow was February 5th (average interim time 12 days, SD = 8.6, $n = 12$). The mean distance between winter burrows for each animal was 503 m (SD = 729.8, $n = 13$). The total time spent in winter burrows used by the animals was on average 34.4 days (SD = 25.0, $n = 29$). On average, the last day badgers appeared associated with a winter burrow was February 16th, but this ranged from December 20th to March 15th.

Activity Patterns

Using remote cameras, I captured 0.14 photos / functioning camera-hour in 2009/2010 and 0.17 photos / functioning camera-hour in 2010/2011. The cameras were successful at detecting badgers emerging from their winter burrows; however, the frequency at which badgers emerged varied considerably among individuals, with some emerging frequently and others rarely (Figure 2.5 a-b). As only two individuals had emergence data for both years, I pooled data from both years for further testing. There was no significant difference in the number of emergence events/camera-night between years after pooling data ($t = -0.76$, $d.f. = 12$, $P = 0.46$) and mean emergence was 0.3 events/camera-night (SD = 0.27, $n = 14$).

Table 2-1. Results of linear mixed-effects model ANOVA comparing difference in North American badger (*Taxidea taxus jeffersonii*) burrow-use variables between sex and year (winter 2007/2008, winter 2008/2009, winter 2009/2010, and winter 2010/2011) in the Cariboo region of British Columbia, Canada.

Variable	<i>n</i>	Sex			Year		
		<i>F</i>	<i>d.f.</i>	<i>P</i>	<i>F</i>	<i>d.f.</i>	<i>P</i>
# Burrows Used	28	0.01	1,14	0.9	2.8	3, 9	0.1
# Winter Burrows Used	28	1.4	1,14	0.3	0.6	3, 9	0.6
Residence Time / Winter Burrow (days)	28	0.3	1,14	0.6	0.9	3, 9	0.5
Total Winter Residence (days)	28	2	1,14	0.2	1.9	3, 9	0.2
Distance (m) Between Winter Burrows	15	0.8	1,8	0.4	2.3	3, 2	0.3

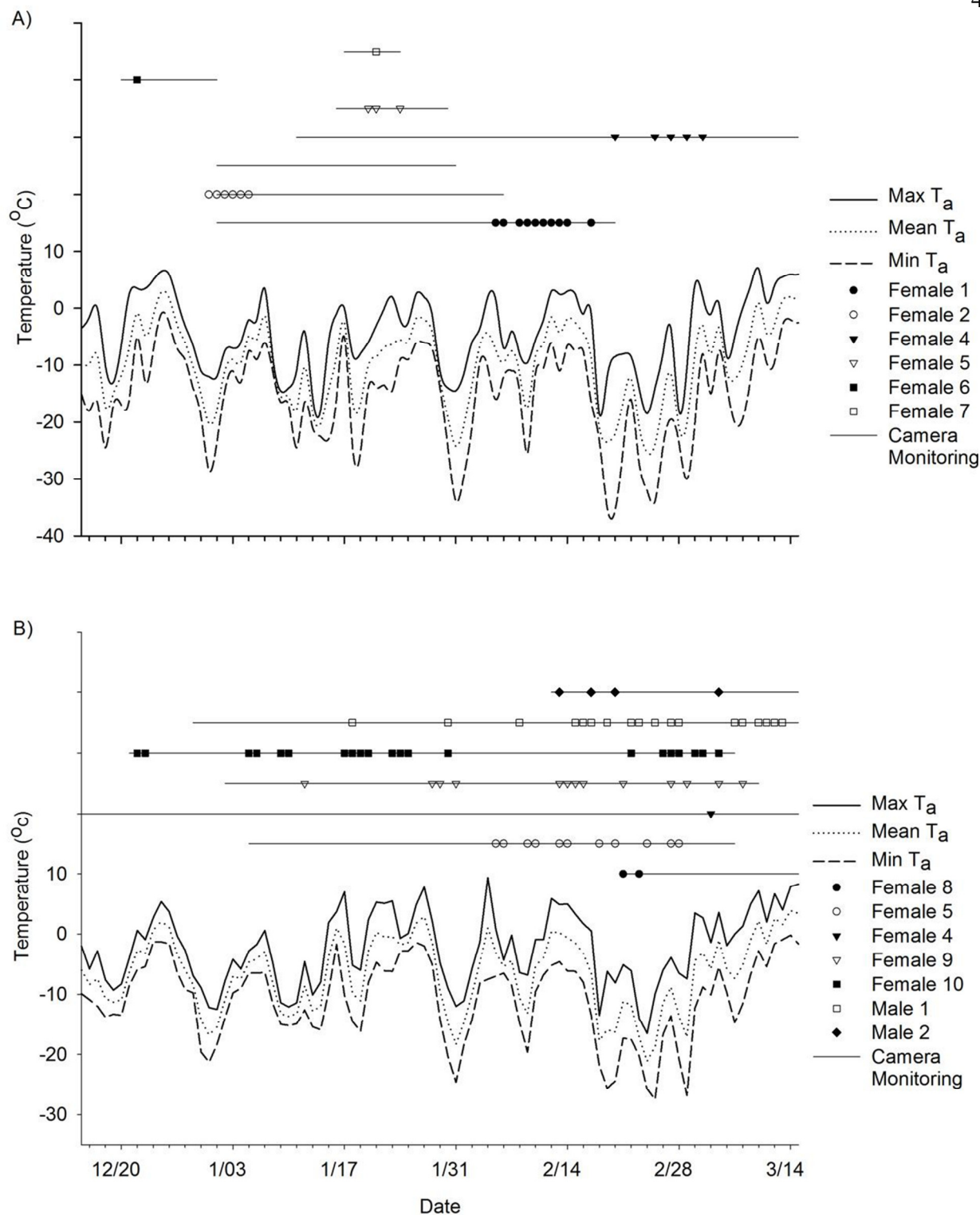


Figure 2-5. Winter burrow emergence events of 12 (10♀♀, 2♂♂) North American badgers (*Taxidea taxus jeffersonii*) captured by remote cameras during **A)** winter 2009/2010 and **B)** winter 2010/2011 in the Cariboo Region of British Columbia, Canada. Points indicate dates when individuals emerged from their winter burrows, corresponding lines indicate the duration of remote camera monitoring. Also included are the ambient temperatures (daily mean, minimum, and maximum air temperature) obtained through Environment Canada (www.climate.weatheroffice.ec.gc.ca).

Temperatures at emergence in both years ranged from +18°C to -31°C. Mean temperature at emergence was mild in 2009/2010 ($-1.0 \pm 4.7^\circ\text{C}$, $n = 69$), but ranged from -0.2°C to -13.8°C. In 2010/2011, mean emergence temperature was significantly colder ($-8.6 \pm 8.9^\circ\text{C}$, $n = 177$) than in 2009/2010 ($F_{1, 235} = 14.53$, $P < 0.001$). However, the 2009/2010 winter was slightly milder than in 2010/2011 (See Chapter 1, Figure 1.6). There was no difference between the sexes with respect to the temperature at which they emerged ($F_{1, 8} = 3.24$, $P = 0.11$).

When date of emergence was plotted against ambient temperatures, there was no obvious relationship as badgers emerged over a wide range of temperatures, including severe cold (Figure 2.5 a-b). The GLMM analysis showed that Julian day best explained badger emergence from burrows, whereas snow depth and temperature performed poorly (Table 2.2). A confusion matrix of the top model (Julian day) showed an overall correct prediction of 76% (Emerged: 72%; Not Emerged: 81%). Even prior to the deployment of remote cameras, badgers were moving to new burrows (mean days between re-locations = 3.5 days) in November, despite ambient temperatures ranging between -18°C to -24°C, further evidence to the lack of a relationship between activity and temperature.

Badgers remained largely nocturnal during winter (Figure 2.6). Mean emergence time in winter 2009/2010 was 20:04 ($n = 69$) while in winter 2010/2011 it was 01:36 ($n = 177$). Despite this, badgers emerged at all times of the day (Figure 2.6). However, it appeared that most activity in the fourth winter (2010/2011) was centred on the very early hours of the morning (midnight to 6am); whereas in the third winter (2009/2010), activity was much more even throughout the day, albeit with the highest proportion of emergence events occurring in the late afternoon (Figure 2.6). Emergence times for both years were tested for uniformity and both were found to be randomly distributed (Year 3: $z = 0.25$, $P = 0.01$; Year 4: $z = 0.5$, $P = 0$).

In both years, emergence and entrance events indicated foraging activity and, in three cases, a badger was detected bringing unidentified prey back to burrow. Further, back-tracking of badger trails in the snow revealed foraging behaviours (Symes, *in prep*). Total foraging time (standardized by length of camera monitoring) did not significantly differ between sex ($F_{1, 7} = 1.69$, $n = 65$, $P = 0.23$) or year ($F_{1, 55} = 3.46$, $n = 65$, $P = 0.07$) and ranged between 3 minutes to 5 hours 22 minutes (mean: 46.70 ± 65.44 minutes). There was no relationship between the length of foraging bout and ambient temperature ($r^2 = -0.015$, $n = 63$, $P = 0.78$; Figure 2.7) or between length of bout and snow depth ($r^2 = -0.015$, $n = 63$, $P = 0.88$; Figure 2.7) during emergence.

Table 2-2. Univariate generalized linear mixed models predicting the emergence of 12 (10♀♀, 2♂♂) North American badgers (*Taxidea taxus jeffersonii*) from winter burrows in the Cariboo Region of British Columbia, Canada (2010/2011). ‘Julian day’ is a continuous count of days since December 1st before an individual emerged. ‘Null’ indicates an intercept-only model without any additional explanatory variables. ‘Snow Depth’ (cm) was measured within 5 m of the burrow on the day of emergence. ‘Temperature’ was the air temperature (°C) at the time of emergence taken from Environment Canada (www.climate.weatheroffice.ec.gc.ca) at the 100 Mile House, B.C. station.

Fixed Effect	Random Effects (Badger) σ^2 ($\pm$ SE)	Coefficient Value	SE	K	LL	AIC _c	Δ AIC _c	ω_i
Julian day	1.1 $\pm$ 1.1	0.02	0.008	3	-117.5	241.2	0	0.92
Null	1.0 $\pm$ 1.0	-	-	2	-121.6	247.2	6	0.05
Snow Depth	0.8 $\pm$ 0.9	0.01	0.01	3	-121.3	248.7	7.5	0.02
Temperature	1.1 $\pm$ 1.0	0.01	0.02	3	-121.6	249.2	8	0.02

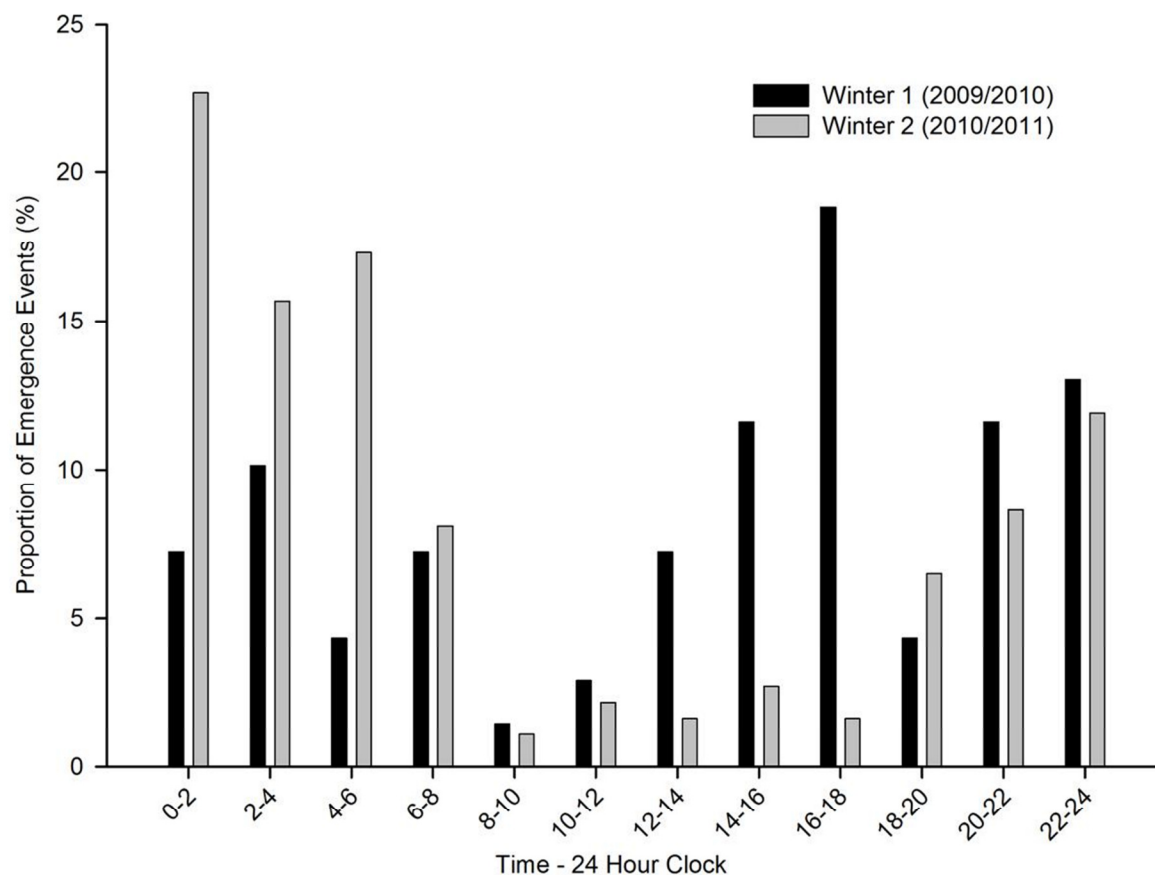


Figure 2-6. Winter activity patterns of 12 (10♀♀, 2♂♂) North American badgers (*Taxidea taxus jeffersonii*) captured by remote cameras. Activity based on emergence from burrows expressed as a proportion of total emergence events in third winter (November 2009 to March 2010) and fourth winter (November 2010 to March 2011) in the Cariboo Region of British Columbia, Canada.

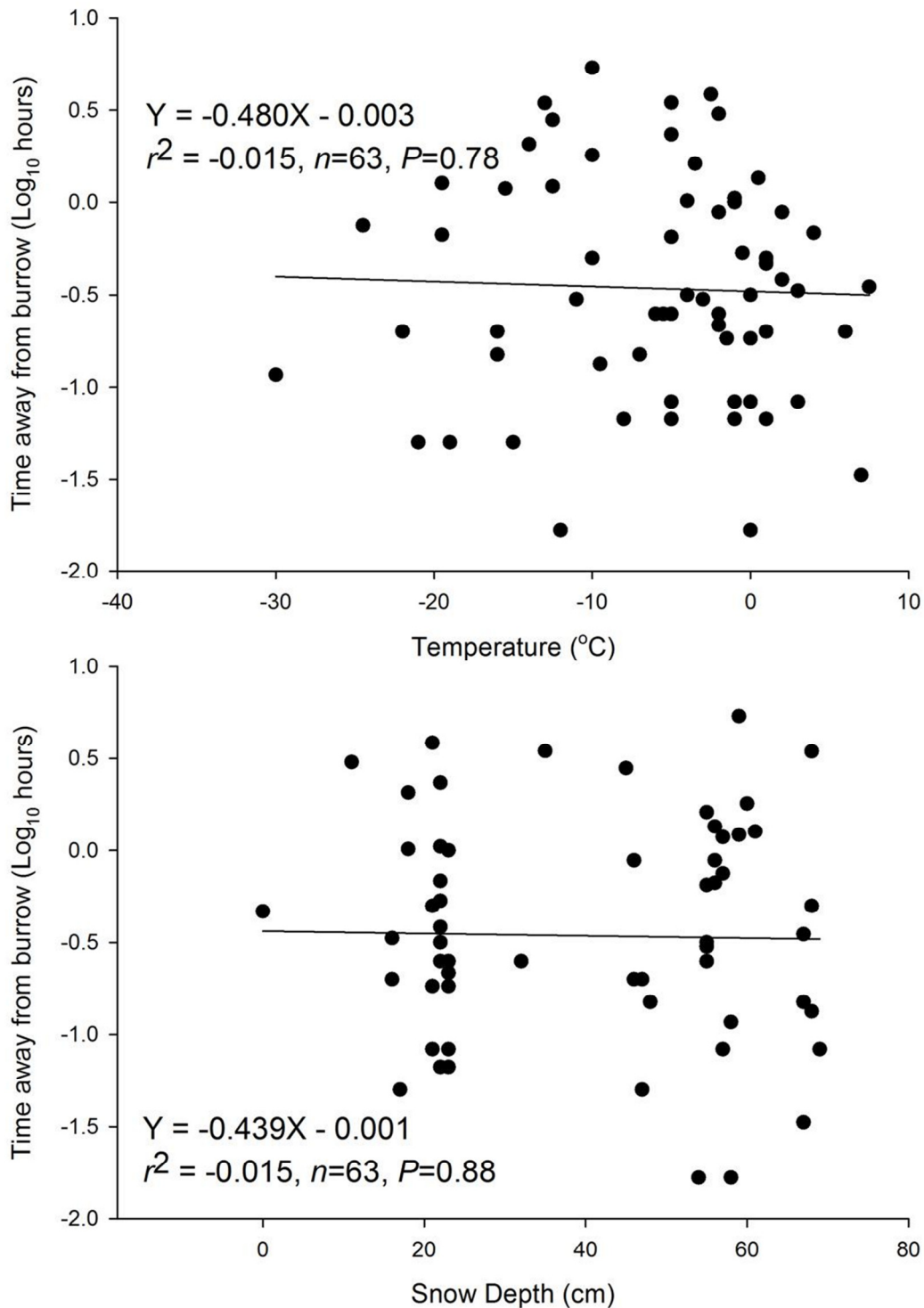


Figure 2-7 (A) Relationship between time away from burrow (log transformed) and ambient air temperature and (B) relationship between time away from burrow (log transformed) and snow depth for 12 (10♀♀, 2♂♂) North American badgers (*Taxidea taxus jeffersonii*) emerging from winter burrows during winters 2009/2010 and 2010/2011 in the Cariboo Region of British Columbia, Canada. Air temperature measurements were obtained through environment Canada for 100 Mile House, B.C. (www.climate.weatheroffice.ec.gc.ca)

Discussion

Despite the fact that my results are generally similar to those of previous studies, badgers in the Cariboo appear to be more active than reported elsewhere. There are two possible explanations for this difference. First, badgers at the northern limit may be unable to store enough fat reserves prior to winter due to a combination of small and patchy habitat, fewer or inaccessible suitable prey, large home ranges and increased energetic costs during mating season, or extreme conditions found at their northern range limit; therefore they must forage relatively often throughout the winter. Alternatively, the authors of these previous studies did not locate badgers frequently enough during winter to assess movement and activity levels.

Movements and Home Range

The study animals reduced their home range size, movements, and surface activities over winter while also employing torpor (Sargeant and Warner 1972, Lindzey 1978, Messick and Hornocker 1981, Minta 1993, Warneer and Ver Steeg 1995, Hoodicoff 2003, Paulson 2007, Quinn 2007, Duquette 2008, Hoodicoff *et al.* 2009). Given that the low stature of badgers may make travelling in deep snow difficult (Telfer and Kelsall 1984), and that they have the ability to store fat reserves and enter torpor (Harlow 1979a, Harlow 1979b, Harlow 1981), these results are not unexpected and are consistent with the generalized winter strategy indicated in the literature (*e.g.*, storage of fat reserves, intensive burrow-use to escape cold, and entrance into torpor to decrease metabolic costs).

The reduction in home range and movements, in addition to the onset of torpor, all coincided with the intensive use of winter burrow(s). In contrast, badgers rarely re-use the same burrow over consecutive days in summer (Lindzey 1971, Sargeant and Warner 1972, Lindzey 1978, Lampe and Sovada 1981, Paulson 2007), but they travel from burrow to burrow as they forage (Lindzey 1971). Settling into one or two burrows over winter likely represents a trade-off between travelling to more productive foraging areas *versus* reducing costly movements through deep snow and cold temperatures. Consequently, smaller home ranges and shorter movements conceivably represent an energy-conservation strategy. Although these winter burrows provide a refuge from unfavourable conditions, they may also provide a central location from which to mount short hunting forays, similar to the

movements witnessed by Lindzey (1971), Sargeant and Warner (1972), and Symes (*in prep.*). These hunting trips could then be made as required during favourable environmental conditions, thus reducing the need to travel large distances.

Despite the seasonal reduction in home range size and movements seen in my study, these metrics were still large in comparison to the little data available for conspecifics further south, but similar to those reported at the eastern range limit of the species (Illinois - Warner and Ver Steeg 1995; Table 2.3). The exception to this (data from Utah - Lindzey 1978) included fall locations (September and October) when badgers were still relatively active (Lindzey 1971, Hoff 1998, Paulson 2007), possibly accounting for the difference. Not only were home ranges in the Cariboo large (compared to badgers in the south), but winter movements were as well. It is unclear what drove these large movements. Perhaps an exhaustion of food resources surrounding winter burrows induces travel. All told, the home range size and movements reported here reflect the amount of area required to sustain animals through the winter in the Cariboo.

Winter burrow residency

The majority of badgers in my study switched to a sedentary lifestyle during winter, where one or two burrows were intensively used, but it is unclear why these particular burrows were chosen. Eurasian badger burrows have been found to consistently buffer fluctuating ambient air temperature (Roper and Kemenes 1997, Moore and Roper 2003, Sidorchuk and Rozhnov 2008). Moreover, it is well known from studies of other animals that occupying underground refugia insulated by snow will help conserve heat and mitigate cold temperatures (Pruitt 1960, Vose and Dunlap 1968, Stephen 1969, Brocke 1970). Thus, it is possible that the winter burrows used in my study have characteristics that make them especially favourable to buffer cold temperatures. Alternatively, these burrows may be situated such that they are near predictable, dependable or easily accessible food resources. I explore this scenario further in Chapter 3.

Torpor

Despite a small sample size of animals carrying temperature-sensitive transmitters, some interesting patterns emerged from my examination of their torpor events. For instance, the first and last detected torpor events coincided with the initial use of winter burrows;

Table 2-3. Mean ($\pm$ SE) estimated North American badgers (*Taxidea taxus jeffersonii*) winter home range (km^2) from previous studies throughout North America. Home range sizes are 100% minimum convex polygon (100% MCP) unless otherwise noted.

Study	Sample Size (<i>n</i>)		Location	Time Period	Male	Female
	Female	Male				
This study (2013)	12	8	British Columbia	Nov 1 – Feb 28	$3.93 \pm 3.65 \text{ km}^2$	$3.40 \pm 2.88 \text{ km}^2$
Sargeant and Warner (1972)	1	0	Minnesota	Dec 2 – Jan 9	-	0.02 km^2
Lindzey (1978)	5	2	Utah	Male: Mid Sept – Mid Dec	5.83 km^2	0.09 km^2
				Female: Jan 19 – Mar 17		
Warner and Ver Steeg (1995)	11	13	Illinois	Nov 1 – Feb 28	$2.95 \pm 3.64 \text{ km}^2$	$3.65 \pm 1.94 \text{ km}^2$
Paulson (2007) ¹	3	5	Washington	Dec 1 – Feb 28	$0.54 \pm 0.13 \text{ km}^2$	$0.58 \pm 0.16 \text{ km}^2$
Duquette (2008)	0	2	Ohio	Nov 1 – Feb 28	$0.77 \pm 0.05 \text{ km}^2$	-
	9	3	Illinois	Nov 1 – Feb 28	$12.51 \pm 15.69 \text{ km}^2$	$5.36 \pm 3.55 \text{ km}^2$

¹Buffered each location with 300m (maximum movement in winter Sargeant and Warner 1972, overlapping areas merged and home range was calculated as the total area of overlapping buffers).

however, the trigger for torpor initiation is unclear. It is difficult to compare my torpor data to that of Harlow (1981) because of a lack of continuous data, however, body temperatures recorded in this study were on par with those he collected. Harlow showed that when faced with a lack of food during winter, North American badgers reduce body temperature by 1.7°C , presumably to reduce metabolic expenditures and energy requirements (Harlow 1981b). Badgers in the present study also showed a slight drop in body temperature through the fall and early winter, which may reflect a similar response to periods of lower food availability.

I believe the relatively low number of torpor events detected in this study (*cf.* Harlow 1981) is an accurate representation of winter activity patterns in these animals, rather than an artifact of discontinuous monitoring. Given that a badger's torpor cycle lasts 29 hours (Harlow 1981), and I re-located and measured badger temperature approximately every 48 hours, the only time I would have failed to detect a torpor event was if it had been initiated immediately after I located the individual, and then ended prior to the next relocation. Outside of this 29 hour window, I would at the very least have detected the entrance and exit of the cycle. Therefore, I am confident that at the very least, my estimate is not greatly under-representative of the use of torpor by badgers in the Cariboo.

Some simple energetic calculations support the notion that badgers in the study area may not be able to rely heavily on torpor to conserve energy overwinter. Harlow's (1981) torpor events were characterized by a 9°C reduction in body temperature (T_b) to 29°C from 38°C and a 50% reduction in heart rate from 55 to 25 beats/min (Harlow 1981). In contrast, basal metabolic rate for a 9.0 Kg badger was reported as 311 Kcal / day for the same study. The total torpor cycle for a badger from initiation to return to basal metabolic rate and temperature lasts 29 hours (Harlow 1981). It is estimated that a total energy saving of 81 Kcal/torpor cycle (or 27%) could be achieved by entering into torpor (Harlow 1981). Using these numbers and the average number of torpor bouts shown by my study animals, I estimate that at a minimum, badgers in my study area would realize a minimum energy savings of 1073 Kcal (range 486 Kcal to 1782 Kcal) over the course of a winter. If a Columbian ground squirrel is estimated to provide 2846 Kcal based on average weight (555 grams) prior to hibernation (Boag and Murie 1981) and a caloric energy value of 5.1 Kcal/g (Jense 1968), then the energetic savings experienced by a badger using torpor in my study site would be on average roughly equivalent to less than one ground squirrel. Thus, these savings may not be enough to see badgers in my study area through the

winter, and they may be required to engage in more winter foraging activity than individuals in more southern environments. Indeed, between torpor bouts, badgers in my study regularly emerged from the burrows, rather than remaining in them.

Although further data will be required to specifically test the relationship between torpor and environmental factors, the patterns seen in this study suggest that rather than temperature alone, some other factor(s) may drive the initiation of torpor. Indeed, a lack of food resources has been suggested to be the case for torpor use in European badgers (Kowalczyk *et al.* 2009).

Overall, the badgers in my study used winter strategies (torpor, T_b below euthermia) similar to those employed by badgers studied previously (Harlow 1981; Harlow 1981b). However, it appears that animals in the extreme north may not utilize these measures to the same extent as in the south. Instead, they appear to be supplementing physiological mechanisms with active foraging to buffer increased energetic costs.

Activity Patterns

My results suggest badgers in the north are considerably more active than those at the core of their range (Sargeant and Warner 1972, Lindzey 1978, Harlow 1979a, Harlow 1979b, Lampe and Sovada 1981, Messick and Hornocker 1981, Paulson 2007). However, the limited data available for comparison makes these conclusions tentative at best. Nearly all previous studies that examined badger ecology have been largely focused on what happens during summer, with most information regarding badger activity during winter being somewhat anecdotal. In Minnesota, Sargeant and Warner (1972) found that a female badger only emerged four times between December 2nd and January 9th (38 days). In Idaho, one female emerged only once after 72 days (at day 38) (Messick and Hornocker 1981). In his study, Harlow (1981) observed a 92% reduction in activity from November through February. Although Paulson (2007) did not specifically study emergence patterns, he did not detect any movements during winter. Although these previous studies have noted only the rare emergence of badgers from winter burrows, it is unclear whether a lack of continuous monitoring data in these studies has resulted in a biased estimate of winter activity, or whether badgers in my study area are indeed more active than those in the south.

Although badgers realize metabolic advantages by occupying burrows and entering torpor, frequent emergence from winter burrows suggests a need to forage. The emergence

events detected in my study were often characterized by signs of foraging behaviour in which other burrows and subnivean sites were investigated or excavated (Symes *in prep.*). Hence, these activities outside of burrows during winter presumably represent hunting forays. Although it might seem reasonable to assume badgers would make use of optimal (warmer) conditions for foraging, emergence and foray from burrows did not appear to be related to air temperature or snow depth; rather, the model that best predicted badger emergence in my study was Julian day (*i.e.*, as winter progressed activity increased). In fact, I detected badgers leaving burrows on winter forays at temperatures well below that suggested by Harlow (critical threshold of -17°C , Harlow 1979b). However, Sargeant and Warner (1972) also observed a female badger in Minnesota (near eastern range limit) to emerge when temperatures ranged from -18°C to -29°C . These conditions hardly seem optimal, yet circumstances and local conditions at range limits may require individuals to risk exposure to cold temperatures or deep snow to forage for food. It may be that hunger (as a result of local conditions) necessitates badger emergence from winter burrows, which in turn may explain the general lack of pattern in badger emergence (in relation to any environmental variables) seen in this study.

Not only did badgers in my study emerge at extremely cold temperatures, but they remained primarily nocturnal. North American badgers are primarily a nocturnal species (Lindzey 1971, Goodrich 1994) and elsewhere it has been shown that they become less nocturnal as winter progresses, particularly during January and February (Harlow 1979b). This switch to more diurnal activity is presumably a combination of more optimal foraging conditions (*i.e.*, warmer temperatures) and a reduction in the need to hunt their primarily diurnal prey at night (because of hibernation). It is unclear why badgers in my study did not switch their above ground forays into the warmest part of the day. Badgers do not appear to be well adapted for travelling in snow (*sensu* Telfer and Kelsall 1984, *sensu* Murray and Boutin 1991). However, as snow cover becomes more supportive at colder temperature (*i.e.*, night; Tusima 1975), remaining nocturnal may reduce the costs of travelling through warmer, softer snow during the day. In the third winter (2009/2010), snow had disappeared from much of the study area by Mid-February, and temperatures at times remained cold. However, by that time, badgers no longer remained in winter burrows and remote cameras were only deployed on one individual. As such I was unable to determine at what time of day (or night) they moved. Further research in a low (or no) snow year with cold temperatures may help shed further light on this issue.

Also of interest was the fact that the winter forays I detected were longer than previously reported (Harlow 1979b), possibly another indication of the cost associated with living in the patchy habitat of the Cariboo. In Harlow's (1979b) study in Wyoming, the duration of nocturnal activity dropped to less than 0.4 hours in February, nearly half the length of bouts seen in my study. This longer foraging time may indicate the need to travel further to acquire food. If this is the case, it may be a reflection of patchy and atypical habitat.

The pattern of an increase in activity for northern badgers, in contrast to what occurs in the south, as suggested by my study, is the opposite observed for Eurasian badgers in the Palaearctic (Western Europe to Central Siberia; Kowalczyk *et al.* 2009). Food resources and energy costs may be higher for the carnivorous and solitary North American badger, compared to the omnivorous and gregarious Eurasian species. This may support the notion that large home range size and longer movements during the breeding season (which would result in higher energy expenditures), in concert with small and patchy habitat, may reduce the ability of the North American badger to acquire sufficient resources in the fall to forego frequent foraging in the winter, even with the occasional bout of torpor.

The considerable variation in activity levels seen among individuals in this study is striking and may indicate differing strategies based on variation in accumulated fat reserves or local conditions within their home range. Some individuals rarely exhibited extended stays in burrows, whereas others did not emerge the entire winter period. This variability has also been seen in other studies (Messick and Hornocker 1981, Newhouse 1997). Although the majority of badgers in my study emerged relatively frequently compared to what has been observed in previous studies, I did detect prolonged stays in a particular burrow through the entire winter period. Descriptions of extended stays of several weeks, even up to 98 days, are not uncommon in the literature (Lindzey 1978, Harlow 1979a, Harlow 1979b, Messick and Hornocker 1981, Newhouse 1997). In fact, I detected prolonged stays that lasted the entire winter. It could be that some individuals employ a strategy relying exclusively on torpor, remaining inactive through nearly the entire winter (as bears, skunks, and raccoons do; Lindzey *et al.* 1976, Mutch and Aleksyuk 1977, Pitt *et al.* 2008.). Alternatively, these individuals may be utilizing larders as badgers have been known to cache food in other seasons (Michener 2000). In contrast, other individuals might remain active, foraging for food as needed (as is the case of other mustelids). A continuum likely exists between the two different strategies. Interestingly, within the sample

of females in this study, a range of winter behaviour patterns were demonstrated, yet all of these animals were able to produce kits the following spring (Symes and Klafki *unpubl.*).

Overall, my study suggests badgers at the northern periphery of their range may be more active than is reported for conspecifics farther south, but further, more detailed study of other populations (both in the north and south) will be required to address whether this pattern holds. It seems plausible that the animals at this location must deal with constraints imposed by the northern environment, where short summers coupled with long, severe winters impose limitations on the use of torpor as an energy-saving tactic. This in turn requires the animals to rely more heavily on winter foraging as a means to counter these demands, and the design of badgers for pursuing fossorial prey may further complicate this balancing act when faced with snowpacks and frozen ground. Experimental manipulations (*i.e.*, food addition) may be a possible avenue for examining whether these constraints drive winter activity and, moreover, place limitations on the animal at its extreme northern range limit.

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Chapter 3. Are all burrows created equally? Variation in burrows of North American badger (*Taxidea taxus jeffersonii*) across seasons

Introduction

The identification of ‘critical habitat’ has recently become a focus of conservation planning for species at risk. For endangered species in North America, federal legislation in both the USA (*Endangered Species Act* - 1973) and Canada (*Species at Risk Act* - 2002) provides legal protection for critical habitat that, in Canada, is defined as “habitat necessary for the survival or recovery of a listed wildlife species...” (*Species at Risk Act* 2002). However, identification of critical habitat can be difficult for species whose requirements change both temporally and spatially, or for those species with large ranges and shifting habitat requirements on the landscape.

One approach to defining critical habitat is to focus on places of ‘residence’ (*e.g.*, dens, nests, *etc.*) that are occupied during important periods in a species life-history (*Species at Risk Act* 2002). Identification of some residences may be relatively straightforward. For example, traditional hibernacula of temperate-zone animals are an obvious starting point for conservation (*e.g.*, snake dens and bat caves), or nests and dens used during the natal period. However, for some animals, particularly wide-ranging or nomadic species, pinpointing a ‘residence’ may be more problematic.

The concepts of critical habitat and residence are not easily applied to the management of endangered badger populations in Canada (jBRT 2008, OABRT 2009, COSEWIC 2012). The subspecies of badger in western Canada, *Taxidea taxus jeffersonii* has extremely large home ranges (Newhouse and Kinley 2003, Hoodicoff *et al.* 2009; Klafki *in progress*, Chapter 2 this thesis) and uses a variety of atypical vegetation communities such as forests and alpine areas (Rahme *et al.* 1995, Newhouse and Kinley 2000a, Apps *et al.* 2002, Hoodicoff 2003, Weir *et al.* 2003). Moreover, much of the grassland habitat has been impacted by anthropogenic disturbance (Hoodicoff 2003, MNRO 2005, jBRT 2008). Consequently, identification of critical habitat is difficult because these animals apparently use a diverse range of habitats, indeed even quality of habitats, across their large home ranges. Identification of badger ‘residences’ is also problematic. Burrows occupied during long periods in the winter (Sargeant and Warner 1972, Lindzey 1978, Harlow 1979a, Harlow 1979b, Harlow 1981, Messick and Hornocker 1981,

Chapter 2 this thesis) and during spring natal periods (Lindzey 1976, Messick and Hornocker 1981, Klafki *in progress*) are undoubtedly ‘residences’. However, it is difficult to determine whether burrows used outside of these seasons constitute ‘residences’, as the badgers in summer rarely extend their stay in a specific burrow for longer than one day (Sargeant and Warner 1972, Lampe and Sovada 1981, Messick and Hornocker 1981, Paulson 2007). For the majority of the year, badgers are relatively nomadic in nature, hunting nightly, traveling from burrow to burrow (Lindzey 1971). Thus, considering these summer burrows as being ‘occupied’ is debatable. Moreover, the availability of burrows does not appear to be limited if given proper soil conditions (Lay 2008), as badgers are able to quickly dig new burrows when needed (Symes *per. obs.*). All told, the issues confounding the definition of residences could unnecessarily stall or impede development and conservation efforts, for although burrows are often easily detected, there is currently no way to rapidly assess their relative importance. Any tool or process that would make this feasible will greatly aid in decisions surrounding land use.

The factors (if any) that characterize different types of burrows has not been well studied. There has been some previous investigation into badger burrow characteristics (Lindzey 1976, Hoodicoff 2003, Collins 2004, Paulson 2007, Quinn 2007, Huck 2010), and some studies have shown that burrows often are re-used (Lindzey 1978, Messick and Hornocker 1981, Newhouse and Kinley 2000b, Paulson 2007). However, a key question that remains is whether burrows used at different times of the year (*e.g.*, winter or natal burrows) have characteristics that differentiate them from one another. Discovering these differences will not only improve our knowledge of badger ecology, but help in the assignment of different levels of protection to different burrows.

If discrimination among burrow types by badgers does occur, it should be particularly accentuated near their northern range limit. Intuitively, badgers living in northern environments may be more constrained in burrow availability due to the small, patchy nature of the habitat *versus* the ubiquitous habitat in the south. In Canada, badgers are at their northern range limit. Here, they experience winter conditions that are more extreme than conspecifics further south (See Figure 1.3, Chapter 1 this thesis). As winter is a critical time period for northern mammals (Formozov 1946, Pruitt 1957, Pruitt 1960, Marchand 1996), burrows used during this time presumably should have characteristics that increase insulation, as reported for other mammalian species (Vroom *et al* 1980, Burger *et al.* 1988, Davis 1996, Hwang *et al.* 1997, Ross *et al.* 2010).

Features such as higher shrub and snow cover may create warmer burrow temperatures (Liston *et al.* 2002). Conversely, during the natal period (spring), when temperatures are warmer but young are vulnerable to predators, the emphasis could switch to burrows that have characteristics that aid in predator avoidance, such as is seen in other species (Bleich *et al.* 1996, Magoun and Copeland 1998, Fernández and Palomares 2000, Arjo *et al.* 2003, Hayes *et al.* 2007, Hwang *et al.* 1997, Organ *et al.* 2008, Ross *et al.* 2010). In short, the burrows used during the winter and natal periods may be more specific than those used at other times of the year. To date, there has been no in-depth investigation of fine-scale habitat features of badger winter burrows.

Furthermore, although a few ($n = 4$) natal burrows have been excavated, mapped, and described (Lindzey 1976, Weir *et al.* 2003), there is very little description of external features that might aid in their rapid assessment or identification

The ultimate goal of this research is to develop a model that would allow wildlife professionals to rapidly assess burrows as to their relative importance for badger conservation. To accomplish this, I examined whether different types burrows could be differentiated. Specifically, I investigated whether (1) winter burrows had characteristics (*such as* shrub cover or snow depths) that increase insulation and reduce thermal stress, resulting in higher subterranean temperatures than other burrows, (2) natal burrows had characteristics (*including* high horizontal cover) that may increase predator avoidance and protection to young, and (3) whether these metrics (thermal condition and features relative to predator avoidance) in tandem with other, easily-measured variables such as construction (infrastructure), location (habitat and topography), and burrow dimensions (entrance and soil fan size), could be used in a multivariate model to discriminate among natal, winter, and summer burrow types.

Methods

Study Area

The study area (6,377 km²) was located at the northern extent of North American badger range, situated in the Cariboo Region of central interior British Columbia near the town of 100 Mile House (See Chapter 1 Figures 1 and 2). The study area is composed of a matrix of coniferous forest, aspen copses, and grassland (Meidinger and Pojar 1991), much of which has been altered for human use (*e.g.*, pastures, *etc.*; MNRO 2005).

Climate is continental, with warm dry summers and cool winters (Meidinger and Pojar 1991). Snow cover lasts from the beginning of November to the middle of April (NRC 2011). As such, I defined two seasons based on snow cover, namely summer (April to October) and winter (November to March). Mean total snowfall during winter is 165.9 cm (range 99.0 to 245.4) and mean temperature is -4.5°C (range -1.0° to -6.9° ; Environment Canada 2011). During the coldest month (January), the daily temperature averages -8.4°C (± 4.3) but can reach as low as -48°C (mean number of days $< -20^{\circ}\text{C}$ = 18.6 days/year; Environment Canada 2011). A more detailed description of the study area can be found in Chapter 1.

Capture and Radio-telemetry

The telemetered badgers used in this study were originally live-trapped as part of a summer road-ecology study that took place between 2007 and 2009 (Klafki, *in progress*). All badgers (except three orphaned kits – see below) were live-trapped using off-set, padded “soft-catch” foothold traps (Victor 1 ½ coil spring) anchored into the ground. Traps were covered with soil and located in proximity to active badger burrows. Once captured, badgers were restrained using a handling pole. A visual estimate of body mass was used to administer an appropriate dosage of 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol). Radio-tags were surgically implanted off-site by a veterinarian in either 100 Mile House or Williams Lake, BC, depending on distance to capture site. Each badger was fitted with an intraperitoneal VHF transmitter (IMP400L Telonics, Mesa, AZ). Badgers recovered from anesthesia in a transfer container (modified plastic 205 L barrel) where they were wrapped in a blanket to prevent hypothermia. The animals were released at their burrow once fully recovered, and thereafter were checked frequently during the following 48 hours to ascertain if they were behaving normally.

Three orphaned animals were added to the study after their mother was killed by a vehicle. These kits were live-trapped in mid-May 2010 and reared at the BC Wildlife Park near Kamloops, BC. To monitor their re-introduction to the wild, these animals were implanted with transmitters after sufficient growth and weight gain. After seven days of post-surgery monitoring, the animals were transferred to a soft-release enclosure in the Cariboo region (July 19th 2010). After one week, the animals started exiting and returning to the enclosure using a tunnel they had created. By August 21st, all three animals had dispersed and began displaying

typical badger activities and movements (Klafki and Packham *unpubl.*). One of these released badgers (♂) was killed shortly thereafter by a vehicle. The remaining two were subsequently incorporated into this study.

The sample of telemetered badgers that provided burrow data consisted of a total of 16 animals, including 14 live-trapped adults (11 ♀♀, 3 ♂♂) and two (1 ♀, 1 ♂) rehabilitated orphans. The strong sex-bias in the live-trapped sample likely is a product of the high road-kill mortality experienced by adult males in B.C. populations during the breeding season (Newhouse and Kinley 2000, Hoodicoff *et al.* 2009, Klafki *in progress*).

Badgers were re-located in resting burrows during daylight hours using a 3-element Yagi antenna and R1000 receiver (Communications Specialists Inc., Orange, CA. Badgers were located at a minimum of once per week during winter in the first three winters (2007-08, 2008-09, 2009-10) and approximately once every other day in the fourth winter (2010-11). Badgers were re-located regularly during the first three summers (approximately every 5 days; Klafki *in progress*). Once located, Universal Transverse Mercator (UTM) coordinates were recorded using a handheld GPS (Garmin GPSmap76x).

Burrow Selection

I defined five categories of burrows:

1. **Single-use summer (SUS)** burrows detected being used only once between May and October;
2. **Re-used summer (RUS)** burrows detected being used on either two or three occasions between May and October;
3. **Heavily-used summer (HUS)** burrows used on four or more occasions between May and October;
4. **Winter (WB)** burrows (or dens) used consecutively for longer than one week between November and March 15th; and finally,
5. **Natal (NB)** burrows (or dens) used exclusively by females, continually through March and April. These burrows were confirmed as natal by the presence of kits or by the female's display of natal-like behaviour (single burrow used for long periods between March and April).

The criteria of my burrow-use categories (SUS, RUS, and HUS) were justified by a *post hoc* examination of burrow re-use. Badgers re-used on average 15.3% (SD = 4.8, $n = 1086$) of summer burrows, after excluding WB and NB (which are used extensively). These burrows were re-used for an average of 2.6 (SD = 0.4, $n = 164$) occasions. Therefore, using my protocol, those

burrows showing average or less than average ‘re-use’ were assigned to the RUS categories, whereas burrows used more than average (≥ 4 times) were placed in the heavily-used (HUS) category

From a total of 1448 badger locations (collected between July 30th 2007 and March 28th 2011), I identified WB used each winter (November-March), NB used each spring (March-April) and SUS, RUS, and HUS used each summer (May-October). In situations where sufficient data existed, I paired the WB used by an individual badger with randomly selected burrows in each of the SUS and RUS categories (from the same badger), resulting in a randomized block design. Often, because badgers were tracked for multiple years, several WB were identified for each badger. To maximize sample size, I included these additional WB and matched to SUS and RUS as above. Natal burrows (NB; used only by females) and HUS were less common and were matched to the appropriate block (*i.e.*, individual badger) if detected, resulting in an unbalanced data set. All told, the final dataset consisted of 139 burrows (HUS: $n = 18$, RUS: $n = 36$, SUS: $n = 36$, NB: $n = 13$, WB: $n = 36$) from 16 badgers (12 ♀♀, 4 ♂♂).

Insulative and Thermal Characteristics (Snow depth and Temperature)

As a proxy for measuring insulative differences among burrow types, I measured snow depth three times throughout the winter (December 18th 2010 to March 12th 2011) at a subset ($n = 98$) of the burrows selected for fine-scale measurements. The number of burrows sampled here was lower because it did not include the WB (and matched SUS, RUS, HUS, and NB) detected in the final winter (2010/2011), during which snow depth sampling occurred. Snow depth was averaged to the nearest 0.5 cm at three locations in proximity (approximately 5 m) to the burrow. Care was taken not to disturb the snow around the burrow preventing bias in subsequent measurements from compacted snow.

In addition to measuring snow depth, I measured air, subnivean, and burrow temperatures from a random selection of winter and summer burrows drawn from the full ($n = 1448$) data set of badger locations. I randomly selected seven WB from seven badgers (2 ♂♂, 5 ♀♀) and paired them with seven summer burrows (*i.e.*, any burrow used between May and October) used by the same individual. Temperatures were measured using IButton® thermochron temperature data loggers (DS1921G-FS; operating range: -40°C to $+85^{\circ}\text{C}$ ($\pm 1^{\circ}\text{C}$)) and IButton® Temperature/Humidity data loggers (DS1923; operating range: -20°C to $+85^{\circ}\text{C}$

($\pm 0.5^{\circ}\text{C}$); Maxim Integrated Products Inc., Sunnyvale, CA, USA) between November 2010 and March 2011.

With the use of snake-handling tongs, three data loggers were placed in each burrow as far as I could reach ($\sim 1.5\text{ m}$). Similarly, the same number of data loggers was used to measure temperature at subnivean and air sites, giving a total of nine data loggers at each burrow location (three in the burrow, three subnivean, and three air). For the subnivean measurements, data loggers were placed outside of burrows within 1 metre of the burrow entrance prior to snowfall, and allowed to be subsequently covered by snow such that they rested in the subnivean. Air measurements were made by attaching data loggers $\sim 1.5\text{ m}$ above the ground to a nearby object such as a fence or tree, within a 5 m radius of the burrow. As air measurements can be affected by radiative heating from direct sunlight and reflection from snow (Georges and Kaser 2002; Hubbart *et al.* 2005), all ambient data loggers were protected by radiation shields fashioned after the double-cone design of Tarara and Hoheisel (2007). To reduce the risk of solar radiation impacting the data logger due to specular reflectance of the cone material, the inside of the stacked cones were painted white (Tarara and Hoheisel 2007). Burrow data loggers were placed in 35 mm film containers while subnivean and air data loggers were placed in a small resealable storage bag. Data loggers were anchored to a central point near the burrow entrance using twine or fishing line (burrow and subnivean) or to the radiation shield (air).

Predator Avoidance Characteristics

Data on the physical structure of burrows were collected from the 139 burrows selected from the full dataset in the ensuing summers, (July 22 -27 2010, and June 26 -July 13, 2011) when the burrows were unoccupied.

I measured visual obscurity (*i.e.*, horizontal cover) using a vegetation profile board (Nudds 1977). This board measured 1 m tall by 8.9 cm wide and was divided into four 0.25 m segments alternating in black and tan colour. I averaged the estimated horizontal cover (percentage $\pm 5\%$) at 0 to 0.5 metres and 0.5 to 1.0 metres at a distance of 15 metres from the main burrow entrance in each of the four cardinal directions and from a height of 1 metre (Nudds 1977). In addition to assessing the predator avoidance features of a burrow, I took the same measurements from a height of 27 cm (the approximate height of a ground squirrel - Karels and Boonstra 1999) to estimate the visibility of the burrow by potential prey.

Other Metrics for Burrow differentiation (Construction, Location, and Dimensions)

Badger burrows are primarily subterranean, but I also described any additional infrastructure of the burrow, namely roots, stumps, coarse woody debris, road cuts, boulders, and woody debris piles (hereafter referred to as residue piles). I also noted surrounding vegetation community (coniferous, deciduous, mixed-wood, pasture/agricultural, grassland, right-of-way/road cut, burn, or riparian) and classified the topographic position of the burrow (crest, upper, mid, lower, toe, depression or level). I measured slope and aspect using a clinometer and compass respectively. I measured additional vegetation cover surrounding the burrow in a 2 m radius (12.5 m²) plot. I estimated the percent cover ($\pm 5\%$) of canopy, shrub, bare ground, coarse woody debris (>10 cm in diameter), and litter. I recorded the number of trees <7 cm diameter and >7 cm diameter in a 5.64 metre radius (100 m²) plot centered on the main burrow entrance; however, I later combined these into a single count.

The opening showing the most apparent use was designated the main entrance to each burrow. For example, main entrances were typified by larger soil fan, lack of vegetation growing in the soil fan, tracks present, or entrance tunnel free of debris and soil. I measured the width and height of the main entrance at the narrowest point of the tunnel, in addition to the maximum width and length of any associated soil fan (*i.e.*, soil that has been excavated from the burrow with a characteristic fan shaped appearance). I estimated the number of additional entrances (secondary entrances) based on the distance and direction to the main entrance and probable chamber location. I measured the distance of each secondary opening to the main entrance. I measured similar dimensions (entrance, soil fan) at secondary entrances. From the main burrow entrance, soil samples were collected and soil textures classified based on the proportions of clay, sand, and silt (ACECSS 1987, USDA 1999).

To quantify the abundance of prey around the burrows (particularly at different times of the year) would have been an enormous undertaking, well beyond the scope and resources of this study. However, I did conduct a cursory assay of potential prey by counting prey sign (ground squirrel, mice, vole and marmot burrows, as well as mice and vole runs; Elbroch 2003) along a 2 x 100 metre transect radiating from the main burrow entrance at a random bearing. This transect length was chosen based on the maximum distance I recorded for a badger foray (leaving and returning to the same burrow) over the winter of 2009/10. Although counts of burrows do not indicate actual abundance or density of prey species (Van Horne *et al* 1997), they do allow rapid

assessment of presence and availability. I included these data as a means to test a proposed method of evaluating wildlife habitat areas for badgers in B.C. (Paige and Darling, 2010).

Landscape variables were calculated using GIS software ArcMap 10.0 (Redlands, CA). I obtained this information for the study area from the Vegetation Resource Inventory (VRI) data set in British Columbia (GeoBC 2012), measuring the distance of each burrow to the nearest forest cover (0 m if burrow occurred inside a forested stand) and edge. I calculated the distance to the nearest road using the Digital Road Atlas spatial data (GeoBC 2012). Finally, I calculated the distance to water after combining streams, rivers, lakes, wetlands, and man-made water body layers from the freshwater atlas of B.C (GeoBC 2012). Distance measurements were obtained by using the ‘Near’ function in the proximity analysis toolset (ArcMap 10, ESRI Redlands, CA).

Data Analysis

Univariate Analysis – Linear Mixed Effects Models

To examine whether differences existed in insulation, thermal environment, and predator avoidance characteristics among burrows, I used linear mixed effects models (LME). Fixed effects variables (% shrub cover, snow depth, temperature, and horizontal cover) were compared among burrow types while taking into account random effects caused by individual badgers. Models were built using function *lme* (package *nlme*, R Version 2.15., <http://www.r-project.org>) using Restricted Maximum Likelihood Estimation (REML). Modeling with LME is analogous to a randomized block or repeated measures analysis of variance (ANOVA) and is able to control variation in the model due to differences between individuals (*i.e.*, random effects) and can handle unbalanced designs well (Pinheiro 1994, Zuur et al. 2009).

Similar to above, other metrics (construction, location, and dimensions) that could be used to differentiate burrow types were analyzed to refine a list of variables for use in multivariate analysis. Categorical data (habitat, soil texture, infrastructure, and topographic position) were analyzed using Log-likelihood ratio tests of independence (G-test) without correction (Zar 2010). To increase expected frequencies for habitat and infrastructure, I created two new variables at a coarser scale (habitat: wooded, open, road/industrial; infrastructure: present, absent).

Multivariate Analysis – Linear Discriminant Analysis

After identifying potential candidate variables through the univariate process, I attempted to differentiate among burrow types by using linear discriminate analysis (LDA). This is a classification technique that takes data from a set of response variables (discriminating variables) in multivariate space, and creates a new linear combination of variables that maximizes the probability of differentiating between the dependent variable (*i.e.*, the pre-defined categories in question; McGarigal *et al.* 2000; Quinn and Keough 2009). In short, LDA is functionally equivalent to Multivariate Analysis of Variance (MANOVA) in that it maximizes among-group while minimizing within-group variation (McGarigal *et al.* 2000; Quinn and Keough 2009). The resultant model can then be used for prediction by assigning new observations into one of the pre-defined categories (Quinn and Keough 2009).

Due to the high dimensionality of the dataset, I limited my candidate variables for multivariate analysis to those that were continuous, not categorical (McGarigal *et al.* 2000; Quinn and Keough 2009). Variables used in this analysis were those shown to be significant discriminators based on univariate tests or those that were easy to measure or considered ecologically relevant (*e.g.*, prey sign). The linear discriminant model was built in a forward selection process, where Wilk's λ identified variables contributing most to overall group selection.

Univariate analyses of both continuous and categorical data revealed little difference between HUS, RUS, and SUS burrows; therefore, I combined these burrow types into a new category termed Summer Burrow (SB). Eight of the sampled burrows contained a missing value (missing values were from different variables). To maximize the sample size for multivariate analysis, I substituted missing values with the mean of that particular variable (Quinn and Keough 2009). I considered this method acceptable given that there were only a small number of missing values, compared to the loss of valuable information if a more conservative approach was taken (such as completely removing the data for a burrow with missing data; Quinn and Keough 2009).

In a typical rapid assessment of a burrow, wildlife professionals would be unaware of the gender of the badger that constructed or used the burrow of interest. Therefore, I pooled male and female burrows together and did not test for differences between genders, being interested only in whether seasonal burrow types could be differentiated.

I used R Statistical Software Version 2.13.2 (R Development Core Team, Vienna, Austria) for data analysis. All data were first examined for departures from univariate and multivariate normality, equal variance, and multicollinearity, using exploratory plots of both residuals and raw data (histograms, boxplots and quantile-quantile) and tests (Kolmogorov Smirnov and Fligner Killeen) (Quinn and Keough 2009, Zar 2010). Variables not fitting normal distributions were transformed when possible using arcsine, root, or log transformations (Quinn and Keough 2009). All univariate assumptions were met; however, an energy test (mvnorm.etest; package *energy*) did not detect multivariate normality. However, LDA is robust to violations of multivariate normality (McGarigal *et al.* 2000, Quinn and Keough 2009) and therefore I proceeded cautiously. Subsequent examination of the resultant discriminant scores revealed no departures from normality. I assessed overall correct classification rate using a re-substitution method and jackknife leave-one-out cross validation; the performance of the classification was then estimated by using Cohen's Kappa (McGarigal *et al.* 2000). Cohen's Kappa provides an estimate of classification performance by correcting for chance. For example, a value of 0 indicates the classification was no better than chance; alternatively, a value of 1 indicates perfect classification.

Results

Insulation and Thermal Environment – Shrub cover, Snow Depth and Temperature

There was a significant difference in shrub cover among burrow types ($F_{4, 121} = 3.05$, $n = 139$, $P = 0.02$); winter burrows had roughly twice as much shrub cover ($16.2 \pm 2.8\%$) as RUS and SUS (mean RUS: $7.8 \pm 1.8\%$; SUS: $8.56 \pm 1.8\%$; $P < 0.05$) and HUS ($6.8 \pm 2.2\%$; $P < 0.1$). Natal burrows did not differ from WB and were found to have a moderate amount of shrub cover (mean: $12.1 \pm 3.2\%$).

Snow depths at WB did not differ from any other burrow type (mean WB: $28.4 \pm 1.8\text{cm}$; HUS: $27.5 \pm 2.3\text{ cm}$; RUS: $29.15 \pm 1.8\text{ cm}$; SUS: $26.70 \pm 1.8\text{ cm}$); however, NB had significantly less snow (mean: $21.87 \pm 2.2\text{cm}$) than other burrows ($F_{4, 270} = 3.7$, $n = 139$, $P < 0.01$).

During winter, subnivean and burrow temperatures at both winter and summer burrows provided a relatively warm and stable thermal environment compared to ambient air temperature (Figure 3.1). Unexpectedly however, there was a significant difference in the subnivean

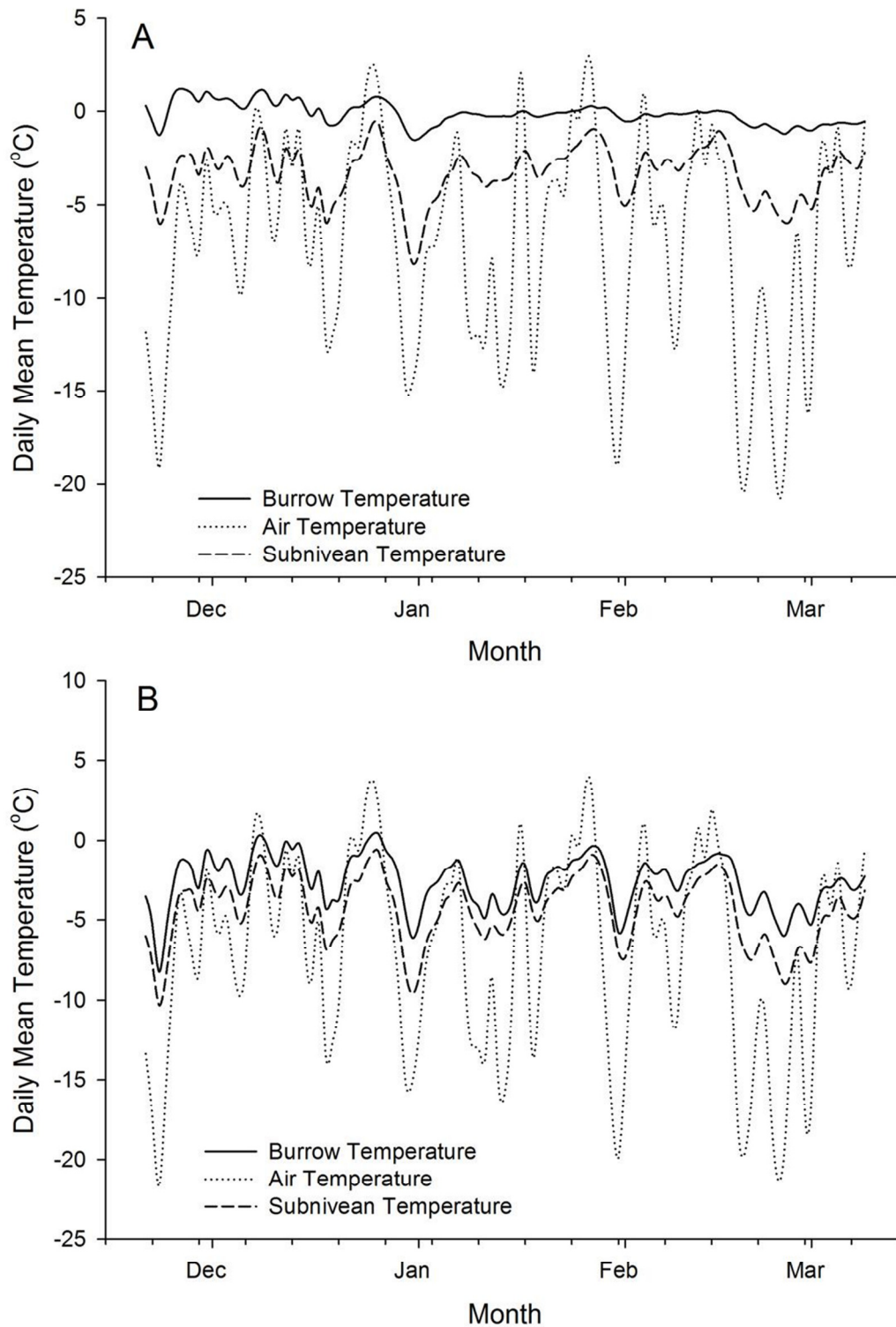


Figure 3-1. Daily mean temperatures at burrow, subnivean, and air sites at (A) summer ($n = 7$) and (B) winter burrows ($n = 7$) of the North American badger (*Taxidea taxus jeffersonii*) in the Cariboo Region of British Columbia, Canada between November 2010 and March 2011. Note burrow and subnivean temperatures are more stable (*i.e.*, less variable) at summer burrows (A) than winter (B).

temperature (winter mean: $-4.3 \pm 0.1^{\circ}\text{C}$, summer mean: $-3.3 \pm 0.1^{\circ}\text{C}$; $F_{1, 1378} = 34.9$, $n = 14$, $P < 0.0001$) and burrow temperatures (winter mean: -2.1 ± 0.1 , summer mean: -0.2 ± 0.1 ; $F_{1, 1181} = 593.3$, $n = 14$, $P < 0.0001$) between summer and winter burrow types. Although winter burrows were buffered against cold, fluctuating ambient air, temperatures in winter burrow and subnivean sites were less stable than those at corresponding summer sites (Figure 3.1).

Predator Avoidance Characteristic (Horizontal Cover)

Horizontal cover (0.5 – 1 m height) was significantly higher at NB and WB (mean: $53.7 \pm 7.6\%$) than other burrow types (mean: $33.1 \pm 2.9\%$; $F_{4, 119} = 5.4$, $n = 139$, $P < 0.001$) when taken from a reading of 1m. Horizontal cover at the 0 – 0.5m height was nearly significant ($F_{4, 119} = 2.3$, $n = 139$, $P = 0.06$). When measured from the height of a ground squirrel, horizontal cover was not significantly different among burrow types (0 - 0.5m: $F_{4, 119} = 0.6$, $n = 139$, $P = 0.7$; 0.5 - 1m: $F_{4, 119} = 1.4$, $n = 139$, $P = 0.2$).

Other Burrow Metrics (Locations, Construction, and Dimensions)

I found a significant difference in vegetative communities (when data were combined into broader categories: wooded, open, or road/industrial), among burrow types ($G = 15.8$, $d.f. = 8$, $n = 139$, $P < 0.05$ - Figure 3.2). Burrow types SUS, RUS, and HUS were primarily in open communities (Figure 3.2). Conversely, WB and NB burrows were found in similar proportions in open and wooded communities, but were found more often in the latter than other burrow types (Figure 3.2).

Nearly 36% of burrows were found with additional infrastructure ranging from under boulders, coarse woody debris, residue piles, roots of live trees and dead stumps. Moreover, four burrows (1NB, 3WB) showed evidence of previous use by bears. Of those with additional infrastructure, burrows under roots were the most common, followed by residue piles and coarse woody debris, stumps and finally, under boulders. Data were combined into two categories (presence and absence of additional infrastructure) to increase expected frequencies for analysis. WB and NB were found most often constructed with additional infrastructure, whereas other burrow types were found more often without additional infrastructure ($G = 33.4$, $d.f. = 24$, $n = 139$, $P < 0.001$ – see Figure 3.3).

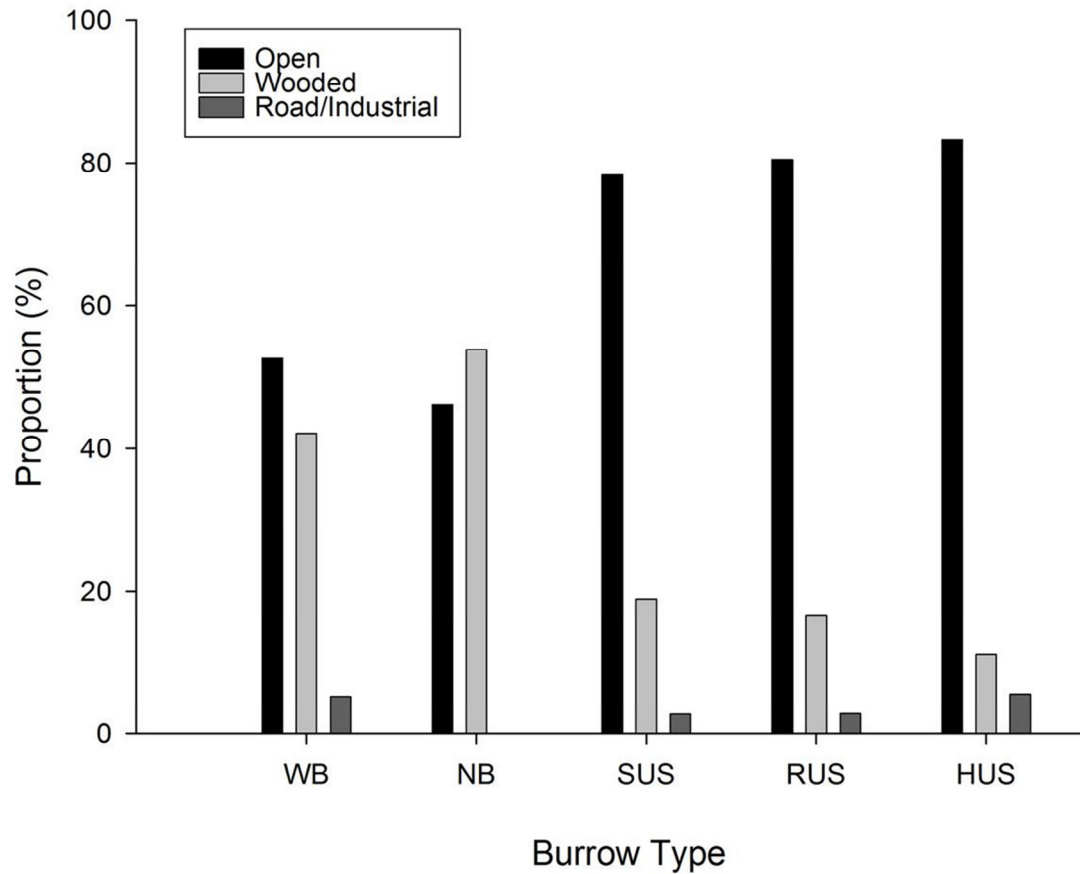


Figure 3-2. Proportion of coarse habitat types (open, wooded, and road/industrial) found at 139 seasonal burrow types (Winter (WB): $n = 36$, Natal (NB): $n = 13$, Single-use summer (SUS): $n = 36$, Re-used summer (RUS): $n = 36$, and Heavily-used summer (HUS): $n = 18$) of North American badgers (*Taxidea taxus jeffersonii*) in the Cariboo Region of British Columbia, Canada, between 2009 and 2011.

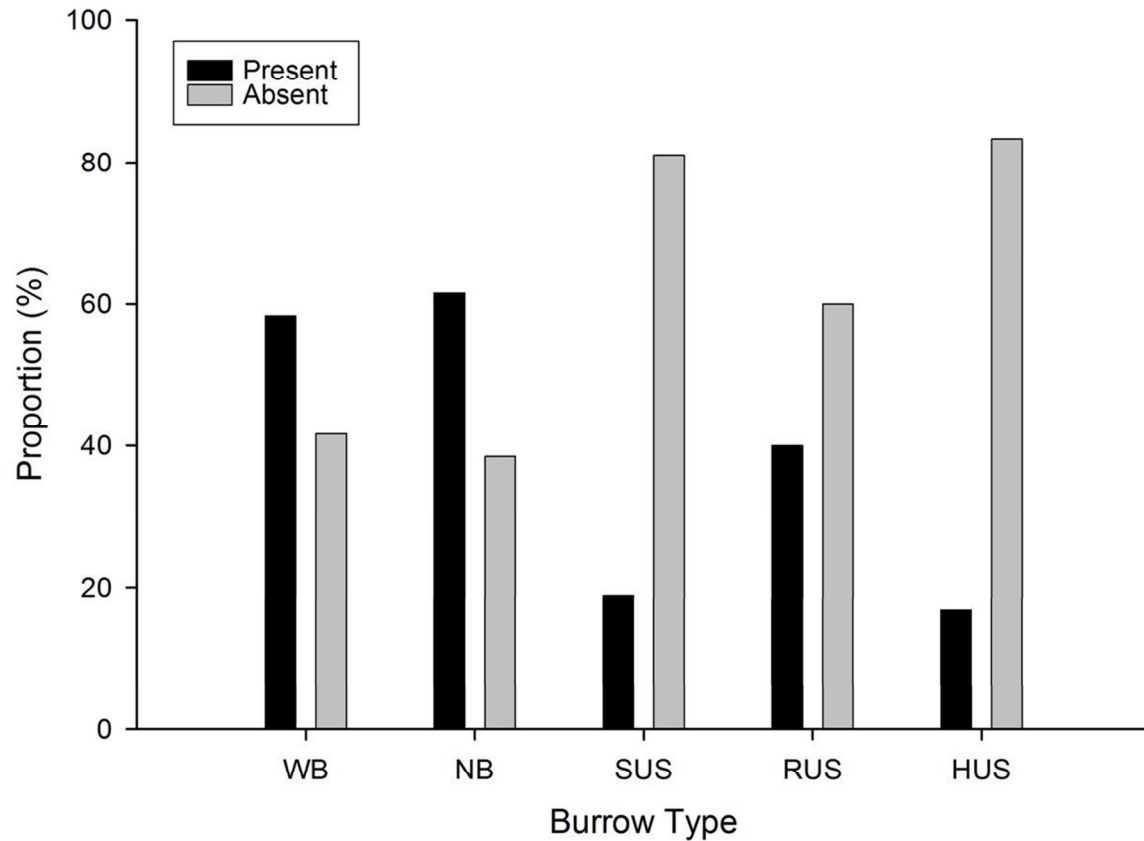


Figure 3-3. Proportion of North American badger (*Taxidea taxus jeffersonii*) seasonal burrow types (Winter (WB): $n = 36$, Natal (NB): $n = 13$, Single-use summer (SUS): $n = 36$, Re-used summer (RUS): $n = 36$, and Heavily-used summer (HUS): $n = 18$) with and without additional infrastructure (*i.e.*, roots, stumps, coarse woody debris, woody residue piles, *etc.*) in the Cariboo Region of British Columbia, Canada, between 2009 and 2011.

Burrows were found on slopes with varying aspects that ranged across all cardinal directions. However, I found that only HUS burrows had aspects that deviated from expected ($\bar{R} = 0.5, n = 18, P < 0.01$); mean aspect was $\bar{x} = 171^\circ$. Aspects of SUS ($\bar{R} = 0.09, n = 36, P = 0.75$), RUS ($\bar{R} = 0.02, n = 36, P = 0.99$), WB ($\bar{R} = 0.1, n = 36, P = 0.6$), and NB ($\bar{R} = 0.3, n = 13, P = 0.40$) were not significantly different from expected.

Badger burrows occurred on a variety of slopes ranging from 0° to 42° , however, on average they were found on $13.0 \pm 8.2^\circ$ slopes. There was no difference in slopes among burrow types ($F_{4,119} = 0.74, n = 139, P = 0.57$). In terms of topographic positions, the majority of the burrows were found mid-slope (38%) followed by upper slope positions (28%). I found no pattern between topographic position and burrow type ($G = 12.6, d.f. = 16, n = 139, P = 0.7$). Badger burrows occurred in a range of soil textures and burrow type was found to be independent of soil texture ($G = 34.6, d.f. = 36, n = 139, P = 0.5$). When the relationship between burrow type and the number of prey detected during transect searches was tested, no difference was found ($F_{4,119} = 0.04, n = 139, P = 0.99$).

I found significant differences among burrow categories for several burrow metrics (Table 3.1). Specifically, differences were found in the number of entrances and the size of the soil fans. Burrows in NB (and to some extent WB) categories had the largest soil fans. Moreover, NB and HUS had significantly more entrances than SUS and RUS. There was no difference among burrow types in the height for main entrances (mean: 18.5 ± 0.6 cm) or width (main mean: 25.7 ± 0.5 cm; secondary mean: 23.5 ± 0.9 cm) of main and secondary entrances.

I also found several other habitat characteristics that significantly differed among burrow types (Table 3.1). In general, WB had higher vegetative cover, specifically for features that are typically found in wooded communities (*i.e.*, # trees, canopy, CWD, litter, *etc.*). The opposite pattern was found for RUS and SUS.

There was no difference in landscape cover variables (distance to forest: 80.1 ± 9.1 m $F_{4,119} = 0.2, n = 139, P = 0.94$; edge: 95.5 ± 8.7 m, $F_{4,119} = 0.5, n = 139, P = 0.74$; water: 227.1 ± 16.9 m, $F_{4,119} = 0.82, n = 139, P = 0.51$; or road: 116.2 ± 9.1 m, $F_{4,119} = 0.05, n = 139, P = 0.99$) among burrow types.

Table 3-1. Mean ($\pm$ SE) values for significant burrow measurements used to examine multivariate differences among seasonal burrow types (WB –winter burrow, NB-natal burrow, HUS-heavily-used summer, RUS-re-used summer, and SUS-single-use summer) of North American badgers (*Taxidea taxus jeffersonii*) in the Cariboo Region of British Columbia, Canada between 2009 and 2011. Different superscript letters denote significant differences among burrow types.

Variable	WB (n = 36)	NB (n = 13)	HUS (n = 18)	RUS (n = 36)	SUS (n = 36)	d.f.	F	P
# of entrances	2.2 $\pm$ 0.3 ^{b,c}	4.4 $\pm$ 0.6 ^a	3.2 $\pm$ 0.5 ^{a,b}	1.8 $\pm$ 0.2 ^c	2.0 $\pm$ 0.2 ^c	4,119	8.2	<0.001
Max soil fan length – main entrance (cm)	167.8 $\pm$ 10.5 ^{a,b}	211.0 $\pm$ 19.5 ^a	133.9 $\pm$ 12.9 ^{b,c}	119.9 $\pm$ 7.5 ^c	116.2 $\pm$ 10.7 ^c	4,119	7.5	<0.001
Max soil fan width – main entrance (cm)	152.3 $\pm$ 9.8 ^{a,b}	202.0 $\pm$ 20.1 ^a	147.6 $\pm$ 17.5 ^{b,c}	122.2 $\pm$ 8.1 ^b	106.5 $\pm$ 10.4 ^c	4,119	5.9	<0.001
Max height – secondary entrance (cm)	19.2 $\pm$ 0.9 ^a	17.7 $\pm$ 2.1 ^{a,b}	16.2 $\pm$ 1.1 ^{a,b}	15.1 $\pm$ 1.1 ^b	21.4 $\pm$ 3.1 ^{a,b}	4,56	3.4	0.02
No. of trees	7.1 $\pm$ 1.7 ^a	6.9 $\pm$ 2.2 ^{a,b}	3.8 $\pm$ 2.1 ^{a,b}	2.6 $\pm$ 1.0 ^b	2.4 $\pm$ 0.7 ^b	4,119	3.9	<0.01
% Canopy Cover	19.2 $\pm$ 4.7 ^a	24.5 $\pm$ 7.2 ^{a,b}	5.0 $\pm$ 3.6 ^b	5.2 $\pm$ 2.4 ^b	10.3 $\pm$ 3.6 ^b	4,119	4.1	<0.01
% CWD	23.4 $\pm$ 5.4 ^a	10.6 $\pm$ 8.2 ^{a,b}	2.3 $\pm$ 1.8 ^b	7.1 $\pm$ 3.1 ^b	2.8 $\pm$ 0.9 ^b	4,119	4.2	<0.01
% Litter cover	20.2 $\pm$ 3.4 ^a	13.6 $\pm$ 4.6 ^{a,b}	17.6 $\pm$ 5.1 ^{a,b}	12.9 $\pm$ 2.4 ^{a,b}	8.9 $\pm$ 1.6 ^b	4,119	2.7	0.04 [†]

Linear Discriminant Analysis

After combining the HUS, RUS, and SUS categories into one ‘summer’ burrow type, then randomly re-selecting replacement samples, a total of 84 burrows were used in the multivariate analysis. Eleven variables were selected as candidates for multivariate testing based on univariate tests and ecological considerations (Table 3.2).

The linear discriminant analysis resulted in two discriminant functions, with the first (LD1) explaining 77% of the total between-group variation, and the second (LD2) explaining 23% (Table 3.2). Squared canonical correlation which is the ratio of among-group *versus* pooled within-group variation (*i.e.* the amount of canonical variation due to group differences) was 0.48 for LD1 and 0.22 for LD2; although relatively low, both linear discriminants were significant (LD1: $F_{2,81} = 37.8$, $n = 84$, $P < 0.001$; LD2: $F_{2,81} = 11.6$, $n = 84$, $P < 0.001$).

Plotted discriminant scores appeared to show moderate success in differentiating burrow types (Figure 3.4). Structure coefficients, which are standardized and take into account multicollinearity, allow the comparison of variables that contribute most to the discriminant functions (*i.e.* the higher the structure coefficient, the more that variable contributes to discrimination among groups). In LD1, structure coefficients indicated that maximum fan length, horizontal cover, percent canopy cover, and number of entrances contributed most to the first discriminant function (Table 3.2). The largest contributors of LD2 were number of entrances, percent coarse woody debris, and percent litter (Table 3.2).

The overall correct classification rate when using a re-substitution method showed reasonable success with 73% of the burrow types correctly identified (Table 3.3). When a jackknife leave-one-out cross-validation (LooCV) method was used (McGarigal *et al.* 2000), overall correct classification was lower at 63%, but retained relatively moderate success (Table 3.3). Cohen’s Kappa scores for both performance classifications showed moderate agreement for the re-substitution method (Cohen’s Kappa: 0.56 [95% CI: 0.41- 0.71] and only fair to moderate success for the LooCV method (Cohen’s Kappa: 0.40 [95% CI: 0.23 – 0.57]. The ‘summer’ burrow type was classified correctly (Re-substitution: 81%; LooCV 75%) more often than WB (Re-substitution: 67%; LooCV(58%) or NB (Re-substitution: 67%; LooCV (42%) (Table 3.3). In fact, in the LooCV method, NB burrows were misclassified as WB as often as they were correctly classified (50% misclassification, 42% correct classification); whereas they were only misclassified as SB 8% of the time.

Table 3-2. Structure coefficients showing the correlation between two linear discriminant functions (LD1 and LD2) and ten variables used to measure differences among 84 seasonal burrow types (Natal: $n = 12$, Winter: $n = 36$, Summer: $n = 36$) of the North American badger (*Taxidea taxus jeffersonii*) in the Cariboo Region of British Columbia, Canada. Variables with larger coefficients indicate variables that contribute more to the discriminatory power of the function. Bold coefficients are those that were significant at $P < 0.05$.

Variable	LD1	T	P value	LD2	T	P value
	Structure Coefficient	statistic		Structure Coefficient	statistic	
Slope*	-0.267	-2.51	0.01	-0.135	-1.23	0.22
% Litter	-0.277	-2.61	0.01	0.451	4.58	<0.001
% Bare Ground	-0.038	-0.35	0.73	-0.327	-3.14	<0.01
% Horiz. cover [†]	-0.622	-7.20	<0.001	0.093	0.85	0.40
Max Soil Fan*	-0.708	-9.08	<0.001	-0.043	-0.39	0.70
% Canopy	-0.532	-5.68	<0.001	0.092	0.84	0.41
% CWD	-0.324	-3.10	<0.01	0.522	5.55	<0.001
# Entrances	-0.447	-4.53	<0.001	-0.641	-7.56	<0.001
# Trees	-0.355	-3.44	<0.001	0.198	1.83	0.07
# Prey Sign	-0.016	-0.14	0.89	-0.007	-0.07	0.95
Distance to cover	-0.013	-0.11	0.91	-0.007	-0.06	0.95

[†] Horizontal cover (0.5 to 1m) measured at height of 1 m

*Log transformed.

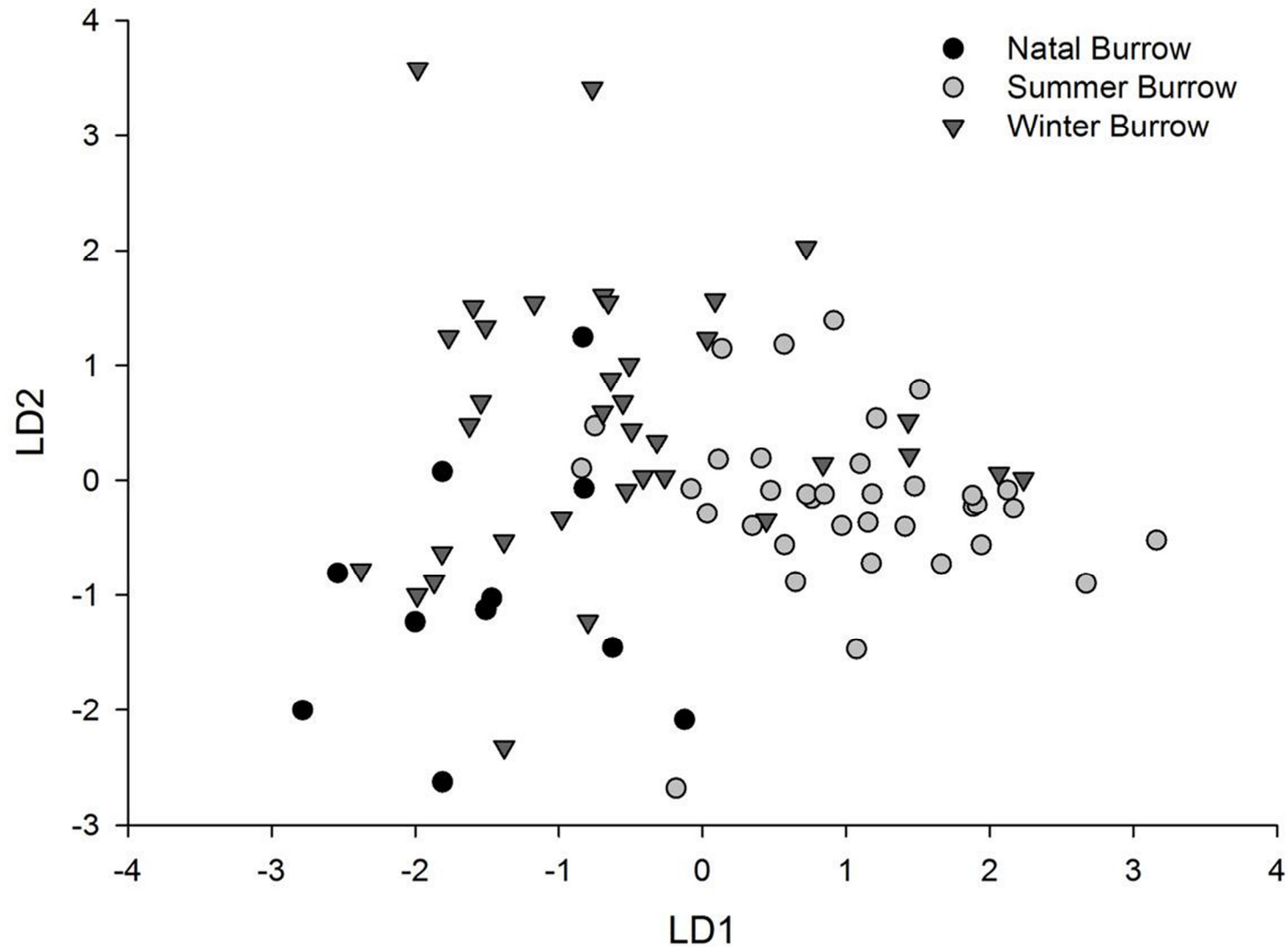


Figure 3-4. Individual scores of linear discriminant functions 1 and 2 (LD1 and LD2) showing differentiation between 84 winter ($n = 36$), natal ($n = 12$), and summer ($n = 36$) burrows of the North American badger (*Taxidea taxus jeffersonii*) in the Cariboo Region of British Columbia, Canada.

Table 3-3. Predicted success of classification using Linear Discriminant Analysis to classify seasonal North American badger (*Taxidea taxus jeffersonii*) burrows using re-substitution (overall success: 73%) and leave one out cross-validation (overall success: 61.4%) methods.

Method	Burrow Type	Predicted	Actual	Success
Re-substitution	Natal	8	12	67%
	Summer	29	36	81%
	Winter	24	36	67%
Leave-one-out Cross-validation	Natal	5	12	42%
	Summer	27	36	75%
	Winter	21	36	58%

Discussion

The results of my study suggest that certain characteristics of natal burrows may help to increase predator avoidance (*e.g.*, horizontal cover), whereas winter burrows, although slightly cooler than summer burrows, displayed some characteristics that may help to improve insulation (*e.g.*, higher shrub cover). However, this may be the result of a spurious correlation of selection for other reasons, such as proximity to food sources. Overall, the results of this study suggest that both winter and natal burrows may be differentiated from summer burrows using broad categories of features: the dimensions and construction of the burrow, and the location and vegetation surrounding the burrow. More specifically, the strongest discriminators of burrow type were the size of the soil fan, the number of entrances, and the horizontal cover. Additional, categorical variables that also appear to aid in the differentiation of burrows include the presence of additional infrastructure and a coarse description of the general habitat.

Winter burrows, insulation and thermal environment

Winter burrows were differentiated from NB and SB in this study; however, the metrics associated with WB did not appear to translate into a more insulative or warmer environment. Snow depth was not significantly deeper, and temperatures were in fact significantly colder than SB, albeit a slight difference (-1.9°C), suggesting they may not be ecologically meaningful. Regardless of the difference, WB in my study still provided a warm, relatively stable refuge from cold, fluctuating ambient air temperatures, similar to that seen in winter setts of Eurasian badgers, (Roper and Kemenes 1997, Moore and Roper 2003, Sidorchuk and Rozhnov 2008). Moreover, at the time of occupation, WB are likely to be several degrees warmer than the temperatures presented in this study due to the contribution of body heat (Moore and Roper 2003).

Although I detected higher amounts of shrub and horizontal cover at the winter burrow sites, these features did not seem to provide any thermal advantages, at least insofar as I was able to measure. Hypothetically, even leafless shrubs could reduce wind chill effects or collect more snow, thereby increasing ground temperature insulation (Buck and Barnes 1999, Liston *et al.* 2002). Conversely, the fact that winter burrows tended to more

often be built in wooded habitats could suggest *lower* snow pack around the burrow sites (as a result of snowfall interception, Golding and Swanson 1986, D'Eon 2004). However, my data did not provide support for either of these arguments, as I failed to detect any significant differences in the depth of snow located around winter burrow sites and that around other summer burrows. It may be that having the winter burrow positioned in the forest provides advantages not associated with the area immediately around the burrow, such as better hunting opportunities. Based on the circuitous, round-trip forays followed during back-tracking during the two winters (2009/2010 and 2010/2011), individuals exhibited hunting behavior in proximity to the burrow (mean track length = 402.8 ± 208.1 m) and within deciduous and coniferous forests (Symes *in prep.*).

Badgers are opportunistic carnivores and show seasonal variation in their diets, often switching to the most available prey, such as small rodents, during fall/winter (Snead and Hendrickson 1942, Jense 1968, Lampe 1982). In the case of Canadian lynx (*Lynx canadensis*), use of habitats with higher horizontal cover during winter reflects a higher abundance of prey in those areas (Squires *et al.* 2010). It is possible badgers have a similar pattern. Thus, badgers may be positioning winter burrows in areas of abundant winter prey, but this would require some sort of habitat assessment on the part of the animal, perhaps even on a yearly basis (given fluctuating resources). Unfortunately, given that the prey sign surveys in my study were conducted outside the winter, and only examined prey availability and not relative abundance, the answer to this question will require further research.

Natal Burrows and Predator Avoidance

In my study, horizontal cover was one of the best indicators differentiating burrow types; for NB, this represents high visual obscurity obstructing the burrow, presumably providing cover and protection for the young. Studies on other species have shown that natal burrows may offer enhanced predator protection (Hwang *et al.* 2007), and in particular, increased horizontal cover (Davis 1996, Pruss, 1999, Martorello and Pelton 2003, Organ *et al.* 2008, Ross *et al.* 2010). Numerous predators of badgers (especially for subadult badgers) occur in my study area, including birds of prey, canids, felids, and ursids. In fact, in our study, bears and coyotes were often photographed investigating natal burrows (Klafki and Symes *unpubl.*). These results contrast sharply with that of Huck (2010), who reported less

visual obstruction at reproductive burrows as compared to random sites. However, only two of the 14 burrows in her study were confirmed natal burrows, and no data was collected on other burrow types. Thus, although horizontal cover appears to be associated with natal burrows in my study, the functional significance of this relationship needs to be further explored.

In addition to horizontal cover, natal burrows also had significantly more entrances than other burrow types, perhaps providing enhanced protection for young badgers. Natal burrows of other species have also been shown to have multiple entrances (Arjo *et al.* 2003; Tannerfeldt *et al.* 2003, Ross *et al.* 2010), possibly because multiple entrances indirectly increase the survival of juveniles by providing multiple points to escape predators (Hayes *et al.* 2007). Here again, my results differed from those seen elsewhere in the literature: both Lindzey (1976) and Weir *et al.* (2003) reported that natal burrows had only a single entrance (Utah/Idaho and southern British Columbia). The entrance counts in these studies are quite reliable, given that the authors actually excavated the natal burrows; however, the combined sample sizes of the two studies was quite low ($n = 4$). It is quite possible that multiple entrances to burrows are a result of repeated, multi-year or lengthy occupations by family groups or even unrelated badgers, rather than planned, deliberate construction on the part of the mother badger. In fact, remote camera photographs monitoring natal burrows as part of a separate study did not indicate deliberate construction of additional entrances by adult females (Symes and Klafki *unpubl.*). Still, the burrowing ability of badgers would suggest that modifications to natal burrows, such as the addition of escape routes, would be relatively easy to establish if so desired. To determine the significance of such burrow features, additional studies are needed over a broader geographic range, using known natal and non-natal burrows.

Other Metrics Differentiating Burrows

Overall, my investigation into burrow dimensions confirms that soil fans are larger in natal than day-use burrows. This identification criterion has been used by others in the literature (Lindzey 1976, Minta and Marsh 1998, Huck 2010), but until now, there has not been an explicit testing of this phenomenon. Larger soil fans, as seen in the NB and WB of my study, may be an indication of the depth, length of stay, frequency of use, or the number

of badgers utilizing the burrow concurrently. For example, large chamber size or regular clearing of waste during long occupations would result in large soil fans. Typically, NB (and to some extent WB) had soil fans over 1.5 times the size of SB. This feature, in addition to the number of entrances, provides a simple measurement for wildlife professionals to identify NB and WB. However, the results presented here are spatially explicit to the Cariboo Region, thus caution is advised when using the soil fan size differential presented here to compare burrows in other regions.

The second broad feature differentiating burrows in this study was the location and the surrounding vegetative characteristics. The higher proportion of WB and NB located in wooded habitats likely explains some of the vegetative and structural differences among burrow types (*i.e.*, number of trees, percent canopy cover, shrub cover, coarse woody debris, litter cover, and presence of additional infrastructure). In British Columbia, it is not uncommon for badgers to utilize forested habitats (Weir *et al.* 2003, Rahme *et al.* 2005, Hogg 2011). In the Thompson-Okanagan Region of B.C., immediately south of our study area, a total of 38% of reliable badger records were from forested habitats, and a further 33% were from open forests (Weir *et al.* 2003). At the eastern range limit, in Minnesota, Oklahoma, Ohio, and Illinois, badgers have also been observed to use and even select for forested habitats (Sargeant and Warner 1972, Tumblison and Bastarache 2007, Duquette 2008). The use of atypical vegetative communities such as forests is likely a product of the small, patchy, and possibly limited habitat at the range extents compared to the ubiquitous habitat at the core of badger range.

The construction of burrows (specifically the presence of additional infrastructure) also aided in the differentiation of burrow types, despite not being entered into the LDA. It is likely that the presence of additional infrastructure is a correlate of burrow location rather than direct selection by the badger for these features. For instance, we can expect features such as roots, stumps, and CWD to be located in wooded habitats. Still, additional infrastructure may provide opportunities to access the soil, helping to alleviate the energetic costs of digging (Vleck 1979). Alternatively, additional infrastructure may add support to burrow construction. Studies of bear burrows have found that roots support burrow ceilings and may reinforce soil cohesion (Vroom *et al.* 1980, McLoughlin *et al.* 2002). Regardless of

the reasons for the presence of additional infrastructure, this too is an easy feature for wildlife professionals to identify seasonal burrows.

One interesting observation to emerge from this study was that badgers in this area often utilize WB and NB that are associated with woody residue piles (including those anthropogenic in origin). These structures may aid in predator avoidance, alternatively they may increase foraging opportunities and prey availability. Other species of mustelids have been observed to utilize residue piles as winter resting sites (Storm 1972, Wilson and Carey 1996, Lisgo *et al.* 2002, Sullivan and Sullivan 2012). During winter, small mammals have been found to be more abundant (and weasels more active) in sites with residue piles (Sullivan and Sullivan 2012). It is plausible that selection for WB and NB is also related to the presence or abundance of prey. Circuitous hunting forays, in which hunting behavior was exhibited by badgers in this study were rarely longer than 500 m (median = 363.37 m, Symes *et al. in prep.*). Therefore, the relative abundance of prey in proximity to burrow types should be further investigated.

Linear Discriminant Analysis Success

In general, the discriminant analysis was reasonably successful at differentiating SB from NB and WB. However, WB and NB shared many characteristics, causing these burrow types to be often misclassified as each other. Regardless, these burrows are jointly considered to be targets for protection; thus the ability to differentiate them from SB is important. Moreover, despite the model performing well when classifying the combined summer burrows (SUS, RUS, and HUS), some (in particular HUS) burrows appeared to be intermediate in nature. This is not surprising, given that there is likely a continuum of differences among burrow types (and, as mentioned above, badgers can modify existing burrows). Burrows that have regular or heavy re-use may have important conservation value. Consequently, wildlife professionals should err on the side of caution and consider burrows with intermediate characteristics as important.

Measurements of Previously-used Burrows (ghosts of badgers past....)

It is important to realize that the characteristics recorded for a badger burrow (and including the surrounding area) at any one time may not necessarily reflect the characteristics

present when the burrow was first established (quite possibly by badgers past). During the history of the burrow, entrances may have filled in, soil fans decreased and settled, and vegetation cover altered through succession or other mechanisms. Moreover, burrows may be used differently by various individuals or used in multiple seasons (winter, natal, or summer), and so burrow types may not be mutually exclusive. This is the typical situation likely to be encountered by wildlife professionals during a rapid assessment in which burrows are identified without a complete or even partial knowledge of their previous usage. Another point to consider is that badgers have the ability to significantly modify the characteristics of their environment, so that the current structure of the burrow may represent the activities of the current occupant. Thus, we caution against an overarching assumption that badgers necessarily ‘select’ burrows for a particular suite of characteristics. This may be true for some features, at some scales, but the ability of badgers to reconfigure the burrow as a resource needs to be appreciated. The characteristics identified in this study provide managers with a tool to discriminate burrows: they do not necessarily predict where the animals are likely to occur.

Management Implications

This investigation demonstrates that burrows used for different life-history stages of badgers can be differentiated reasonably well. However, care should be taken in extrapolating the results of this study to elsewhere. My study area was primarily a matrix of patchy grassland and forested habitats, and areas to the south have increasingly open forests or grassland habitat that is likely more suitable for badgers. Some of the patterns in my study (*e.g.*, additional infrastructure, use of forested habitats) may only apply to areas in the extreme northern portion of the badger’s range, whereas other characteristics (*e.g.*, large soil fans and numerous entrances) may be common throughout the species’ distribution. Still, the results of this study provide a potential template for managers to work from, here and elsewhere, while allowing local assessments and decisions on levels of protection assigned to burrows. In this region, large soil fans, multiple entrances, additional infrastructure, high horizontal cover and wooded habitat appear to typify winter and natal burrow types. Protection of these sites is important given the fact the study population is at the periphery of the species’ range, and is therefore likely experiencing the effects of strong limiting factors.

Further, their lengthy occupations in winter and natal burrows may leave them vulnerable to disturbance. Habitat requirements for badgers include suitable soil for digging and sufficient prey base (Rahme *et al.* 1995). Therefore, it is essential that these elements remain on the landscape. Thus, it is recommended that a precautionary principle is evoked to conserve summer burrows, given that these burrows represent previously utilized foraging habitat. In this way, the cumulative effects of removing habitats that supports valuable prey and burrow construction do not impact the population.

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Chapter 4. Conclusions and Management Implications

Summary

This study has addressed the winter ecology of North American badgers at the northern edge of their range. For this species, I have detailed the home range size, movements, burrow and torpor use, activity patterns, and fine-scale habitat of burrows. Until now, this information has been in scant supply. To effectively manage this endangered species, an understanding of the ecology of badgers across all seasons is required. Based on the results of my study, it appears as though badgers at their northern limit are more active in winter than previously reported, may have individual winter strategies based on local conditions, and use burrows during winter and natal seasons that can be differentiated from other burrows. These results have implications for the management of this species. Accordingly, wildlife managers should focus on:

- protecting and improving the quality of badger foraging habitat, including ensuring a sufficient prey base (a habitat requirement for badgers, Rahme *et al.* 1995); and
- identifying and protecting winter and natal burrows (with setback and buffers) with the caveat that foraging areas (as indicated by summer burrows) must also be retained on the landscape.

Although badger habitats throughout British Columbia have been disturbed by human development (JBRT 2008), efforts on the part of wildlife managers to improve grassland habitats, including the quality of foraging habitat and associated prey base may help to increase badger populations. In her report, Hoodicoff (2005) reviewed the literature on prey habitat, providing a base for outlying measures for enhancing badger foraging habitat in the Cariboo Region. She recommended:

1. increasing habitat and vegetation cover for small mammals, while maintaining a variety of grassland successional stages;
2. decreasing livestock grazing and use of riparian habitats to maintain vegetation cover and soil integrity; and

3. increasing grassland and open forests by reducing forest encroachment and in-growth.

Ensuring there is sufficient healthy grassland habitat in a variety of successional stages, allows for the maintenance of small mammals dependent on vegetation cover and litter (mice and voles), as well as early-successional species such as sciurids and heteromyids (Hoodicoff 2005). Maintaining habitat for a variety of species is particularly important, as badgers rely on a range of prey species as their diet undergoes seasonal shifts (Errington 1937, Snead and Hendrickson 1942, Jense 1968, Messick and Hornocker 1981, Lampe 1982). Hoodicoff (2005) also recommended protecting riparian habitats for muskrats (and other species), which may play an important role in badger diet in the Cariboo (Packham pers. comm.). Finally, increasing grassland area by reducing forest in-growth and encroachment will also benefit badgers by increasing habitat for badger prey (Hoodicoff 2005).

In addition to prey-enhancement activities, it is important that wildlife managers identify and protect important burrows. Through my research, I have been able to determine characteristics that best differentiate seasonal burrows. In general, the size of the soil fan, the number of entrances, and the amount of horizontal cover best differentiate winter, natal, and summer burrows. Additionally, categorical variables that also appear to aid in the differentiation of burrows include the presence of additional infrastructure and a coarse description of the general habitat. In my study, winter and natal burrows had larger soil fans, higher horizontal cover, and were more often found with additional infrastructure (such as under roots, stumps, coarse woody debris, *etc.*) in wooded habitats (Table 4.1). Further, in my study, natal burrows were also typified by numerous entrances (Table 4.1). Summer burrows on the other hand, often had single entrances, smaller soil fans, low horizontal cover and were typically located without additional infrastructure in open habitats (such as grasslands and pastures; Table 4.1). Below is a table outlining the mean ($\pm$ SE and range) values for important variables that differentiate seasonal burrows. Given that variables for burrows of all types show a range in values that occasionally overlap, it is not possible to determine thresholds.

Table 4-1. Mean $\pm$ SE (and range) values for important discriminating variables that differentiate seasonal (Winter, Natal, and Summer) burrows of the North American Badgers (*Taxidea taxus jeffersonii*) in the Cariboo Region of British Columbia, Canada.

Variable	Winter Burrows	Natal Burrows	Summer Burrows
# of entrances	2.2 $\pm$ 0.3 (1 – 8)	4.4 $\pm$ 0.6 (1 - 8)	2.1 $\pm$ 0.1 (1 – 7)
Max soil fan length – main entrance (cm)	169.1 $\pm$ 10.7 (48-296)	211 $\pm$ 19.5 (0-282)	121.0 $\pm$ 5.8 (94-332)
Max soil fan width – main entrance (cm)	152.4 $\pm$ 10.0 (3 -282)	202.0 $\pm$ 20.1 (109-360)	120.6 $\pm$ 6.4 (0-324)
No. of trees	6.8 $\pm$ 1.7 (0-37)	6.9 $\pm$ 2.2 (0-33)	2.7 $\pm$ 0.6 (0-25)
% Canopy Cover	17.7 $\pm$ 4.5 (0-90)	25.5 $\pm$ 7.2 (0-80)	7.3 $\pm$ 1.9 (0-60)
% CWD	22.7 $\pm$ 5.5 (0-100)	10.6 $\pm$ 8.2 (0-100)	4.4 $\pm$ 1.4 (0-100)
% Litter cover	19.1 $\pm$ 3.3 (0-75)	13.6 $\pm$ 4.6 (0-75)	12.2 $\pm$ 1.5 (0-60)
Habitats	44% wooded, 56% open	58% wooded, 42% open	21% wooded; 79% open
Additional Infrastructure	61% with; 39% without	67% with; 33% without	19% with; 81% without

The ability to identify burrows used during critical periods when energy demands are high and resources are low (Pruitt 1960, Bronson 1985, Campbell *et al.* 2005, Persson 2005) is extremely valuable. Badger winter and natal burrows are occupied for relatively long periods of time, which may make badgers particularly susceptible to disturbance during these periods, as seen in other species (Eurasian badger: Lindsay and Macdonald 1985, Wolverine: Magoun and Copeland 1998, Bears: Linnell *et al.* 2000). In fact, domestic dogs were often seen harassing badgers in both winter and natal seasons (Symes *per obs.*). Disturbance to badgers can be reduced in the Cariboo if critical burrows can be identified, protected, and buffered throughout sensitive seasons. To ensure badgers are not disturbed during these important periods, landowners should be targeted for a public outreach campaign to ensure dogs are not harassing badgers at these times (January to family breakup in July). Further, winter and natal burrows were occasionally found in woody residue piles. Landowners should be encouraged to retain these on the landscape. If removal is required, woody residue piles should not be burned between mid-winter and late spring when badger use is long-term.

Burrows that are regularly re-used (particularly those that have heavy-use) may have important conservation value. In my study, heavily-used were intermediate in nature and often shared characteristics similar to winter, natal and summer burrows. Consequently, wildlife professionals should err on the side of caution and consider burrows with intermediate characteristics as important.

Although summer burrows do not appear to be limited on the landbase, the cumulative effects of removing habitat that supports valuable prey and burrow construction will be detrimental to the population. Therefore, it is essential not to neglect protecting foraging habitat (which is indicated by summer burrows). All told, when setting aside habitat for protection, it is essential that it contain characteristics that are suitable for over-wintering, rearing of young, and foraging.

Future Research Needs

Overall, the results of this thesis point to five issues and questions that need to be addressed.

- 1) **Are badgers really more active in the north?** The results of this study suggest that despite a reduction of home range and movements, the incidence of torpor, and an intensive use of winter burrow(s), badgers in my study area are more active in winter than reported elsewhere. What is not clear is whether this difference truly exists or whether it is due to previous studies having to cope with low sample sizes (Sargeant and Warner 1972), loss of study animal(s) or transmitter failure (Lindzey 1978, Lampe and Sovada 1981, Messick and Hornocker 1981), and infrequent monitoring (Paulson 2008, Hoodicoff *et al.* 2009), all of which may have resulted in missed opportunities to document movements and activity levels. Despite the activity levels seen in this study, further research will be required to determine whether northern badgers are truly more active than those in the south and if so, why this might be true. I suggest that more investigation into winter ecology is needed in the core of this species range. Knowing whether badgers that live at the range limits are more active than those in the core of their range may shed some light on whether quality of habitat affects winter activity patterns, and will help improve our knowledge about winter strategies in general.
- 2) **What is the relationship between torpor, environmental conditions, and availability of food?** In this study, North American badgers were found to enter torpor during winter; however, I was unable to investigate the mechanism(s) that triggers this behaviour. From the cursory observations made during this study, as well as studies conducted on Eurasian badgers, environmental conditions such as temperature and snow are not what drive torpor in this taxon; rather it seems to be due to a reduction in food resources (Kowalczyk *et al.* 2009). Therefore, an experimental study manipulating food resources may be able to tease apart the relationship between torpor, environmental conditions, and food resources. An earlier attempt to provision badgers with food in the Cariboo was unsuccessful (Hoodicoff and Larsen, *pers. comm.*), perhaps because this took place during the

summer when badgers may be less willing to take supplementary food items. Understanding the relationship between torpor, environmental conditions, and food availability will help elucidate whether habitat quality affects winter strategy decisions. Further, this may help to determine whether food limits population growth.

- 3) **What is the relationship between habitat quality and winter activity:** In this study, individual badger behaviour and activity over winter was highly variable, suggesting activity levels may be related to local conditions (*i.e.*, quality of habitat). My sample of animals showed a continuum in amount of winter activity and foraging: some individuals rarely emerged to forage whereas others rarely (if ever) settled into a winter burrow. Winter activity in my study was best explained by the progression of the winter season (Julian Day), whereas environmental conditions such as snow depth and temperature had little explanatory power. This may indicate that hunger (or fat levels) could be driving badger emergence from burrows and increased above-ground winter activity. Unfortunately, the scope of this research was unable to address the underlying mechanism behind winter activities. As suggested above, a food addition study would be able to test this relationship. Knowing the relationship between activity patterns and habitat quality will help to elucidate whether quality of habitat affects winter strategy decisions and limits population growth.
- 4) **What factors drive the selection of winter burrows?** I was able to identify characteristics unique to winter (and natal) burrows and these could be differentiated from other burrows with reasonable success. Differentiation was largely a product of (i) the dimensions and construction of the burrow and (ii) the location and vegetation surrounding the burrow. Although the results of my linear discriminant analysis may aid wildlife managers in their ability to identify, classify, and protect critical burrows, it does not answer the question of what drives selection of burrow sites. Future research should attempt to identify reasons behind the selection of these habitats. For instance, the results of this study suggest that winter burrows are not specifically selected for added thermal benefits (at least not ones I could detect). Rather, other factors such as proximity to food resources may drive winter burrow selection. A

study investigating the relative abundance of small mammals in proximity to winter and summer burrows may shed some light on this knowledge gap. Knowing what drives winter burrow selection will help managers predict and then protect or enhance overwintering areas.

- 5) **How will climate change impact badgers?** Climate change may actually improve badger habitat (*e.g.*, through increased fire and forest pests leading to increased grasslands). However, climate change predictions for my study area suggest warmer summers and wetter winters (precipitation falling as rain; BC MWLAP 2002, Dawson *et al.* 2008). Although I found that winter burrows were actually colder than summer burrows during winter, they still maintained a relatively warm, stable environment compared to ambient temperatures. Changes to the snowpack may reduce insulation of badger burrows but perhaps more importantly, may be detrimental to subnivean prey. Furthermore, warmer, drier summers may have a negative impact on prey species, or cause badgers to broaden their prey base. Future research should examine potential impacts of climate change on badgers and their associated prey species. Knowing how climate change might impact badgers will allow managers to predict potential outcomes and help to shape management plans for the future.

Limitations of the study

Badgers in my study region are rare and they range widely over large home ranges, making them difficult to capture. Moreover, these animals suffer from high rates of road mortality. All of these factors contributed directly or indirectly to lower sample sizes in my study, particularly in the case of male animals. Furthermore, transmitter implantation in any animal is an invasive procedure, and researchers should always consider, when possible, ways to reduce this impact. To do this, I made use of study animals carrying transmitters from a previous road ecology study (Klafki *in progress*). Unfortunately over time, this led to the loss of study animals through road mortality and transmitter failure through battery depletion, hindering in some cases, my ability to test for differences between genders and years. The latter would have been particularly useful for teasing apart the responses (activity patterns) to varying winter conditions.

The majority of badgers used in this study were originally instrumented for the road ecology study (Klafki *in progress*), and therefore they did not carry temperature-sensitive transmitters. As such, body temperature data could not be a focal part of my research. Although this lack of continuous body temperature data was not ideal, the data collected still provided a cursory glimpse into the use of torpor by badgers in the Cariboo. Despite these limitations, this study was the first to clearly document torpor use in free-ranging North American badgers. Moreover, this study has revealed new questions to be answered and has provided a platform on which to conduct further research.

As mentioned previously in this thesis, regions differ in their habitat configuration and landscape features, so caution should be taken when extrapolating the results of this study to other areas occupied by badgers. Some, but not all of the patterns observed in the Cariboo may be applicable to other areas, even those also at the extent of badger range.

Conclusion

Although there are limitations to this study, this is the first major investigation into the winter ecology of free-ranging North American badgers. The results presented in this thesis have provided the best insight to date of the home range, movement, torpor use, activity, and fine-scale burrow use of badgers during winter. However, as per baseline ecological studies of wildlife, my work offers only a glimpse into the life-history of badgers during this season. Indeed, it has created more questions in need of addressing. Future investigations into the winter ecology of badgers at both the limit and core of badger range are clearly warranted. As stated at the outset of this thesis, I believe it is particularly important to study the winter ecology of badgers (or any temperate or arctic animal for that matter) given the important, critical nature of the winter period in their life-history.

It is my intent that the results of this study will improve our ability to successfully conserve this endangered species, and time will tell if I have been able to make that contribution. Given the somewhat encouraging signs that badger numbers may be stabilizing or even increasing in at least this part of the province, our attempts to complete the recovery of this impressive and iconic animal in Canada should continue to be guided by well-designed field studies.

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