### From habitat to energetics: eastern chipmunk burrow microhabitat selection and

fine-scale variation in winter torpor expression

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degree of Master of Science

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#### ABSTRACT

This thesis evaluates, in free-ranging eastern chipmunks (*Tamias striatus*), burrow site selection, the effect of burrow microhabitat on individual behaviour and winter torpor expression, as well as resource and climate determinants of fine-scale variation in winter torpor expression and energetics. This was accomplished by characterizing burrow microhabitat, performing behavioural observations, and monitoring winter torpor expression. Among several burrow microhabitat variables related to food availability, predation risk, and hibernacula microclimate, availability of woody debris was the best predictor of burrow site use. Anti-predator benefits associated with availability and use of woody debris are potentially more important than those associated with burrow microhabitat features that are either too spatially invariant (soil temperatures) or too spatially and temporally variant (food sources). Abundance of tree-seeds drastically reduced winter torpor, increasing considerably winter energy consumption, and local density of seed-producing trees was responsible for fine-scale spatial variation in torpor expression. The potential range in winter torpor expression and energy consumption was constrained by microclimate, whereas observed patterns of winter torpor and energy consumption were highly variable and determined primarily by local food abundance.

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## RÉSUMÉ

Cette thèse évalue, chez le tamias rayé (Tamias striatus), la sélection du terrier, l'effet du microhabitat du terrier sur le comportement et la torpeur hivernale des individus, ainsi que l'influence des ressources et du climat sur la variation à petite échelle de la torpeur et l'énergétique hivernales. À cet effet, nous avons caractérisé le microhabitat du terrier, fait des observations comportementales et quantifié l'expression hivernale de torpeur. Parmis plusieurs variables reliées à la disponibilité de la nourriture, au risque de prédation, et au microclimat de l'hibernacle, l'abondance de débris ligneux prédisait le mieux l'utilisation d'un microhabitat comme terrier. Les bénéfices anti-prédateurs associés à la disponibilité et l'utilisation de débris ligneux sont potentiellement plus importants que ceux associés avec des caractéristiques soit spatialement trop invariable (température du sol) ou spatialement et temporellement trop variable (sources de nourriture). L'abondance de graines d'arbre a drastiquement réduit la torpeur hivernale, augmentant considérablement la consommation d'énergie hivernale, et la densité locale d'arbre produisant des graines était responsable de la variation spatiale à petite échelle de l'expression de torpeur. L'étendue potentielle de la torpeur et consommation d'énergie hivernales était contrainte par le microclimat, tandis que les patrons de torpeur et de consommation d'énergie observés étaient hautement variables et déterminés principalement par l'abondance locale de nourriture.

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#### **CONTRIBUTION OF AUTHORS**

This thesis consists of two manuscripts prepared for publication, both formatted for intended journals. The candidate contributed to both manuscripts by developing initial research ideas and sampling methodologies, and being responsible for data collection, management, and analysis and for writing up manuscripts.

Chapter 2 is co-authored by Daniel Munro, Don W. Thomas, and Murray M. Humphries. As the field coordinator of the main project in which this thesis was imbedded, DM contributed extensively to field work and data collection and commented on the manuscript. DWT was involved in periodic guidance and support from initial research ideas to the realization of the manuscript. As the thesis supervisor, MMH provided guidance and support during preparation, field work, analysis, interpretation, and writing. Chapter 1 is co-authored by MMH for the same contributions mentioned above.

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Once back in the confined and more intellectual world of analysis and redaction, I was privileged to be part of this so diversified, resourceful, and supportive lab. Thanks to the people of the Wildlife Ecology and Energetics Lab, with who it was always fun to hang around in pack with, especially during the most productive day of the week, but also to the next coffee break, in downtown restaurants under obscure circumstances, or during our inspiring, constructive, and filling lab meetings.

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## Chapter 2

#### **GENERAL INTRODUCTION**

The study of fine-scale habitat selection, at the individual- or microhabitat-level often considers associations of individual presence with small-scale physical and biological features of the habitat. However, environmental features are rarely considered in a multivariate framework, and are not commonly supported by behavioural or physiological observations to establish ecological causes and consequences of different microhabitat use. Microhabitats, especially those with prolonged and intensive use, represent major determinants of individual success through direct and indirect influences on individual reproduction, behaviours, energetics, and survival. This thesis first evaluates burrow site selection and the effect of burrow microhabitat on behaviour and winter torpor expression, and then investigates fine-scale resource and climate determinants of spatial and temporal variation in winter torpor expression and energetics.

#### Literature Review

The distribution and abundance of animals vary in space and time, often with spatial and temporal heterogeneity of habitat components having direct and indirect consequences on an individual's ability to obtain food, avoid predators, thermoregulate, reproduce, and survive (Cody 1985). This has generated a significant body of habitat selection literature concerned with the identification of physical and biological habitat features associated with animal presence at a variety of spatial scales with the common assumption that animals maximize fitness by using higher quality habitats that better satisfy their ecological requirements (Rosenzweig 1981, Manly et al. 1993). However, from an individual's use of space to a species' geographic distribution, habitat selection reveals

different results and interpretations (Morris 1987), with patterns of use at different scales being driven by different habitat components.

Disentangling the relative consequences of different habitat components on individual success is facilitated at the smallest spatial scale or microhabitat-level, where physical and biological habitat features are spatially less auto-correlated and more heterogeneous. Moreover, microhabitat selection is dictated by space use of individual animals, on which reproductive, behavioural, energetics, and survival consequences of different microhabitat use can be measured. In comparison with transiently occupied microhabitats, den, nest, burrow, and other home-sites that are used more intensively and for longer periods have potentially more important influences on individuals ecological success (Hansell 1993).

Eastern chipmunks (*Tamias striatus*) are sedentary forest-floor sciurids that individually-occupy a burrow system year-around (Yahner 1978). The burrow plays a central and multi-functional role in the ecology of the species and is the most intensively used microhabitat within an individual's home-range (Elliot 1978). Since availability of suitable burrow microhabitats is associated with high density and stable populations (Svendsen and Yahner 1979b), burrow microhabitat quality should represent a major determinant of individual fitness. However, the relative importance of different microhabitat features to burrow site selection and consequences of burrow microhabitats on individual success remain to be explored.

The eastern chipmunk inhabits mature deciduous forests and specializes on seeds from mast-producing trees. As central place lard-hoarder, chipmunks spend most of their time in the close vicinity of their burrow where they accumulate a considerable food

hoard, on which they rely to survive winter (Elliot 1978). During the hibernation period, chipmunks are known to express cycles of torpidity (accompanied by reduced body temperatures and metabolic rates) with periodic arousals to euthermy (Panuska 1959, Wang and Hudson 1971a, Scott and Fisher 1972, Pivorun 1976a, French 2000). Even though the expression of deep and prolonged torpor bouts reduces significantly energy requirements (Wang and Hudson 1971a, Pivorun 1976b), there exists a high variability in the duration and depth of torpor bouts among individual chipmunks exposed to similar experimental (Panuska 1959, Wang and Hudson 1971a, Scott and Fisher 1972, Brenner and Lyle 1975, Pivorun 1976a) or environmental (Humphries 2001, Munro 2004) conditions.

In captive eastern chipmunks, low hibernacula temperatures are associated with longer hibernation and torpor bouts and with shorter arousal periods (Panuska 1959, Scott and Fisher 1972, Pivorun 1976a). Relationships between food hoard size and the duration of torpidity were documented in captive eastern chipmunks (Brenner and Lyle 1975, Wrazen and Wrazen 1982, French 2000) and recently confirmed in free-ranging chipmunks. Individuals with artificially enlarged food hoards reduce the total time spent torpid to less than half that of un-supplemented individuals and maintained a body temperature twice as high (Humphries et al. 2003a, Munro et al. 2005b). Therefore, burrow-site microhabitat features related to food acquisition and hibernacula microclimate are likely to have cascading effects on individuals' winter energetics and torpor expression.

This study was conducted on a free-ranging population of eastern chipmunks in the Ruiter Valley Land Trust, near Sutton Mountains in southern Québec, Canada. As

part of the Ruiter Valley Chipmunk Project, the population is regularly trapped and all captured individuals are marked, sexed, and weighed. Burrow site location is determined for most individuals and winter torpor expression is quantified using external temperature-sensitive radio-transmitters or data-loggers. On the study site, soil temperature, density of hardwood trees, and yearly tree-seed production were quantified. This project, on this perfect candidate system, provided the opportunity to evaluate finescale consequences of intense and prolonged microhabitat use on individual behaviour and winter torpor expression and energetics.

More specifically, the objective of the first chapter of this thesis is to evaluate burrow site selection and the effect of burrow microhabitat features on individual behaviour and torpor expression. In that same chapter, we evaluate the relative importance of different microhabitat features, related to food acquisition, predation risk and hibernacula microclimate, as predictors of burrow site selection. We also provide behavioural and physiological evidence of the relative importance of these different burrow microhabitat components. This was accomplished by quantifying microhabitat variables, and comparing their respective ability to explain patterns of burrow site use. We also performed focal observations to evaluate the role of foraging and anti-predator behaviours in burrow site selection. In the second chapter, we investigate fine-scale relationships between resource- and climate-related microhabitat features and individual variation in winter torpor expression and energetics. This was achieved by relating local seed-producing tree density and burrow soil temperatures to individual patterns of winter torpor expression and energy consumption in two years of greatly different tree-seed abundance.

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### **CHAPTER 1**

# WOODY DEBRIS DRIVES BURROW MICROHABITAT USE IN EASTERN CHIPMUNKS

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Running head: Woody debris and burrow microhabitat

Title: Woody debris drives burrow microhabitat use in eastern chipmunks.

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#### Abstract

In habitat selection, disentangling the relative importance of habitat features related to food availability, predation risk, and climatic condition is difficult at large spatial scales, but enhanced at microhabitat scales, where individual variation in physiology, behaviour, and ecology can be related to particular habitat features. We quantified the behaviour and torpor expression of free-ranging eastern chipmunks (Tamias striatus) occupying a range of microhabitats and assessed the influence of burrow microhabitat features on foraging behaviour, anti-predator behaviour and torpor expression. In a multivariate approach, we established the microhabitat determinants of burrow distribution. Behavioural observations revealed that woody debris is extensively used in anti-predator behaviours and that spatial and temporal variations in food availability and foraging behaviour minimize the importance of food-related burrow microhabitat features. Soil temperatures were too spatially invariant to generate individual variation in torpor expression. Therefore, abundance of woody debris was the microhabitat feature most strongly associated with burrow locations. Direct and indirect benefits of reduced predation risk associated with the presence and use of woody debris might outweigh those associated with burrow microhabitat features that are either too spatially invariant (hibernacula microclimate) or too spatially and temporally variable (local food availability).

**Keywords**: anti-predator behaviour, food availability, foraging behaviour, forest-floor rodents, hibernacula microclimate, microhabitat selection, predation risk, Sciuridae, winter energetics

#### Introduction

Animals select and use habitats according to food resources, predators, and abiotic conditions such as climate (Cody 1985). Disentangling the relative importance of these factors as drivers of habitat use is difficult at large spatial scales (e.g., species ranges) due to spatial autocorrelation in biological and physical variables, but greatly enhanced at fine spatial scales (e.g., individual microhabitat use), where habitats become patchy and individual variation in physiology, behaviour, and ecology can be related to particular habitat features.

Microhabitat selection is typically associated with features related to food availability, predation risk, or microclimatic conditions. For example, small mammals have been shown to select habitats offering abundant and accessible food sources (e.g., Stapp 1997), increased visibility improving predation avoidance (e.g., Karels and Boonstra 1999), or microclimates that reduce thermoregulatory requirements and dehydration (e.g., Rhodes and Richmond 1985).

The eastern chipmunk (*Tamias striatus*) is a diurnal, sciurid rodent present in hardwood forests of eastern North America. Adults individually-occupy a burrow system throughout the year. As central place foragers, chipmunks concentrate most above ground activity and foraging effort on the forest floor in a 30 m core area around their burrow. Acquired food items are either consumed near the capture location, scatter hoarded, or transferred to a larder hoard within their burrow on which they rely to survive winter (Elliot 1978). Chipmunks terminate, or at least substantially reduce, above ground activity during winter and, during this hibernation period, conserve energy by expressing repeated bouts of torpor. Individuals of this species are characterized by minimal pre-

hibernation fat accumulation, but instead consume food from their larder hoard during periodic arousals from torpor (Panuska 1959, Wang and Hudson 1971, Scott and Fisher 1972, Pivorun 1976). When active above ground outside of hibernation, eastern chipmunks are predated upon by a diversity of terrestrial (e.g., mustelids, felids, canids) and aerial predators (e.g., hawks, owls) (Snyder 1982). Individuals produce two distinct alarm calls that discriminate between terrestrial (repeated high frequency chips) and aerial predators (repeated low frequency chucks) (Burke Da Silva et al. 1994).

Previous investigations of fine-scale habitat selection by eastern chipmunks have evaluated the correspondence between the distribution of burrow locations and various habitat features. Svendsen and Yahner (1979) documented an association of chipmunk burrows with microhabitats dominated by woody species, with intermediate ground-level vegetation, and well-drained soils, which they interpreted respectively as reflecting an importance of food availability, predator visibility, and soil conditions (Svendsen and Yahner 1979). In contrast, Mahan and Yahner (1996) reported burrows associated with less and smaller overstory trees, with more logs and stumps, and on steeper slopes, and suggested that factors other than food availability, such as predation risk or soil conditions, might be most important to chipmunk burrow microhabitat selection (Mahan and Yahner 1996). However, in these studies, as in most investigations of small mammal habitat selection, multiple potential drivers of microhabitat selection were not considered in an explicit multivariate framework and there were no corroborating behavioural or physiological observations to establish the hypothesized ecological consequences of habitat features.

In the present study, we quantify the behaviour and torpor expression of individual eastern chipmunks occupying a range of microhabitats and use a multivariate approach to establish microhabitat determinants of burrow distribution. Based on previous studies of burrow site selection by chipmunks and microhabitat selection by small mammals in general, we predict that chipmunk burrows will be distributed in microhabitats offering high local abundance of food resources, enhanced predator detection and avoidance, as well as soil conditions suitable for hibernation. We begin by documenting the behaviour and torpor expression of free-ranging chipmunks to assess which microhabitat features are most likely to influence resource availability, predator avoidance, and torpor expression. We then evaluate the degree to which these and other microhabitat features determine the distribution of chipmunk burrows.

#### Methods

Study area.- The study was conducted in 2005 and 2006 in the Ruiter Valley Land Trust near Mansonville, Québec (45°05'N, 72°26'W). The study area covers 25 ha of mature deciduous forest dominated by sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*), with trout lily (*Erythronium americanum*) and spring beauty (*Claytonia caroliniana*) as the most abundant herbaceous species. In the active season, live-trapping was conducted systematically on a 19.6 ha trapping grid using Longworth traps (Longworth Scientific Instruments Ltd, Abingdon, UK). Each captured animal was weighed, sexed and permanently marked with numbered metal ear tags.

*Burrow identification.*- Adult individuals were collared with radio-transmitters (4 g; model PD-2C, Holohil Systems Ltd, Carp, ON) and tracked to their burrow in early

morning or late evening using a hand-held receiver (model R-1000, Communication Specialists Inc., Orange, CA) and a 3-element antenna. Over the course of the study, we located and marked above-ground 128 adult burrow locations. Trapping, handling, and collaring procedures followed American Society of Mammalogists guidelines (Animal Care and Use Committee 2007) and were approved by McGill University Faculty of Agricultural and Environmental Sciences Animal Care Committee (AUP #4728).

Foraging behaviour.- In the active season of 2006, when red maple, beech and sugar maple produced abundant seed crops (see Chapter 2 for seed collection methodology), we performed focal observations on adult chipmunks (11 females and 10 males) equipped with radio-transmitters by regularly tracking individuals, from May 30<sup>th</sup> to November 7<sup>th</sup>, for a total observation time of 119 hours. Focal observations took place between sunrise and sunset and consisted of following a focal individual and documenting continuously, through a digital voice recorder, all observed behaviour to the most detailed level possible. On average, each focal individual was observed on 18 different days and for a total of 5.6 hours. Based on seasonal patterns of food availability and foraging behaviour, we divided the active season into summer (May 30<sup>th</sup> to July 31<sup>st</sup>) and autumn (August 1<sup>st</sup> to November 7<sup>th</sup>) focal period. For each individual, over all focal observations in each focal period, we obtained the average proportion of foraging time (including searching, handling, eating, pouching, and scatter hoarding of known food items) spent on different food items (e.g., tree-seeds from beech, sugar maple, and red maple or tubers from spring beauty), as well as the average proportion of observation time spent foraging and traveling.

*Anti-predator behaviour.-* During focal observations, we documented any predator encounters or predation attempts. During these predatory events, we recorded the individual's microhabitat location (on woody structures *vs.* forest floor) and vocalizations (chucks or chips). For each individual, over all focal observations, we documented perching behaviour by recording the proportion of observation time spent elevated from the forest floor as well as the structure used as perch site (e.g., rock, stump).

*Torpor expression.* We documented chipmunk torpor expression over two different winters (2005-2006 and 2006-2007) using temperature sensitive radiotransmitters and temperature data-loggers (see Chapter 2 for detailed methodology). For each individual torpor bout, we calculated the minimum torpor skin temperature ( $T_{skin-min}$ ) and torpor bout length (*TBL*).

*Microhabitat sampling.-* Of 85 point locations systematically-distributed over the study area, 51 were identified as unused sites because they were at more than 20 m from a known burrow location. Our exhaustive attempts to capture and determine the burrow location of all individuals present on the study site renders it unlikely that active burrows within our study grid went undetected. Microhabitat variables were sampled at these 51 unused sites and at 87 burrow sites. However, not all microhabitat variables were sampled at all burrows and all unused sites (see Table 1 for sample sizes); overall 22 burrows and 20 unused sites were sampled for all microhabitat variables (excluding soil temperature; Appendix 1).

Hardwood vegetation.- In a 10 m radius circular plot centered on the sampling point, all trees higher then breast height were counted, identified by species and classified

into one of two diameter at breast height (DBH) categories: small trees (DBH  $\leq 10$  cm) and large trees (DBH > 10 cm). The DBH of all large trees was measured. This provided, per sampling plot, the following variables of interest: small hardwood tree density, large beech density, large sugar maple density, large red maple (*A. rubrum*) density, and average DBH of large seed-producing trees (i.e., beech, sugar maple, red maple). In 2006, we also sampled the seed-production from large beech and sugar maple trees over the study area using seed collectors (see Chapter 2 for seed collection methodology).

*Herbaceous vegetation.*- In two circular plots (0.62 m<sup>2</sup> each), randomly placed in two predetermined opposite quarters of the larger 10 m radius circular plot, all herbaceous plant stems were counted and identified by species. Since trout lily and spring beauty were most abundant and because they produce bulbs and tubers known to be consumed and hoarded by chipmunks (Elliot 1978), the only herbaceous vegetation variables we extracted were trout lily density and spring beauty density.

*Canopy cover, ground cover and microtopography.*- On two perpendicular 20 m transects, percent canopy cover and percent ground cover were measured using an ocular tube as described in James and Shugart (1970). Percent slope was measured using a clinometer and slope aspect was determined with a compass. Slope aspect was converted to heat load using the formula: heat load index =  $[1 - \cos(\theta - 45)]/2$ , where  $\theta$  is the azimuth in degrees east of north (Beers et al. 1966, Neitlich and McCune 1997). Heat load rescales the slope aspect symmetrically about a northeast-southwest axis and ranges from 0 to 1, with values closer to 0 representing cooler aspect (i.e. northeast orientation) and values closer to 1 representing warmer aspect (i.e. southwest orientation). We considered the following variables: % canopy cover, % leaf litter cover, % green vegetation cover, %

woody debris cover, % bare soil cover, % rock cover, % water cover, % slope, and aspect heat load.

Soil temperature.- During winter 2005-2006 and 2006-2007, from November to April, soil temperature at 80 cm depth, which is similar to reported depths of chipmunk burrows (Panuska and Wade 1956, Elliot 1978), was recorded every 4 hours using temperature data-loggers (iButton model DS1921G, Dallas Semiconductor, Maxim Integrated Products Inc., Sunnyvale, CA). In each year, soil temperature loggers were installed at eight burrows and at 25 systematically-distributed locations (10 of which were identified as unused sites). In 2005-2006, we compared the average winter soil temperature recorded at burrows and unused sites. In both winters, we obtained average burrow soil temperature during each torpor bout and assessed the effect of prevailing soil temperature on torpor bout variables ( $T_{skin-min}$ , *TBL*).

Statistical analyses.- We used non-parametric univariate Wilcoxon-Mann-Whitney tests to first evaluate differences between burrows and unused sites for all microhabitat variables with all available observations. Prior to multivariate analyses with the 22 burrows and 20 unused sites sampled for all variables, we first used a method of variable reduction similar to the one proposed by Green (1979). With this method, variables correlated (r > 0.5) with other variables presumed to be more biologically relevant were eliminated and, of the remaining variables, only those with univariate differences (p < 0.2) between burrows and unused sites were considered in the multivariate analysis. After variable reduction, we performed a stepwise logistic regression to identify, out of all retained variables, good predictors of burrow

microhabitat use. All analyses were performed using SAS version 9.1 (SAS Institute Inc. 2002).

#### Results

Chipmunk behaviour and torpor expression.- In a year of high red maple, sugar maple and beech seed production (2006), the two main food items consumed by chipmunks during summer (67.6  $\pm$  7.5% of foraging time on known food items, n = 15) were red maple seeds  $(37.0 \pm 8.9\%)$  and spring beauty tubers  $(30.6 \pm 8.3\%)$ , whereas during autumn, the two main food items (77.3  $\pm$  5.3%, n = 16) were beech nuts (56.2  $\pm$ 7.7%) and sugar maple seeds  $(21.1 \pm 7.2\%)$ . In each focal period, there was a negative correlation between proportions of foraging time spent on the two main food items (red maple seed vs. tuber foraging: r = -0.62, p = 0.014; beech nut vs. sugar maple seed foraging: r = -0.75, p = 0.001). This likely results from negative relationships in the spatial distribution of red maple and spring beauty (r = -0.20, p = 0.01, n = 163) and of beech and sugar maple trees (r = -0.34, p < 0.001, n = 163). Because alternative food items were negatively correlated, both in terms of spatial distribution and chipmunk exploitation, evaluating whether individual foraging behaviour was influenced by the local abundance of food sources required extracting principal component scores describing foraging behaviour (relation between tree-seed (beech nuts, sugar and red maple seeds) foraging and tuber foraging) and microhabitat food sources (relation between seed-tree density and spring beauty density averaged for all survey points sampled within 30 m of the burrow location). There was a marginally significant positive relationship between an individual's foraging score and its burrow microhabitat food

score (Figure 1;  $r^2 = 0.24$ ,  $F_{1,20} = 6.06$ , p = 0.02, n = 21), with individuals occupying burrows surrounded by less seed-producing trees and more tubers (i.e., high microhabitat food scores) spending less time foraging on tree seeds and more on tubers (i.e., high foraging scores).

During 119 hours of focal observations, we observed one predation attempt and the presence of hawks, owls, and foxes in the vicinity of focal chipmunks. The predation attempt involved an avian predator (hawk) and a focal individual perched on a log. Upon detection of the diving avian predator, the individual instantly found refuge under the log overhang, started chucking, and remained hidden until the end of the focal observation. Chipmunks chucked whenever they detected a bird of prey, whereas individuals chipped in the presence of foxes. Vocalizations were dominated by aerial predator alarm calls (chucks; 81% of vocalizations). During summer and autumn, chipmunks spent on average 16% (5-41%, n = 21) of their above ground active time elevated on woody structures (e.g., stumps, logs, branches). This is a considerable portion of their time, given they spent on average 13% of their time travelling (5-20%, n = 21) and 29% of their time foraging (15-45%, n = 21). There was no relationship between the amount of time an individual spent perched on woody debris and the local abundance of woody debris surrounding its burrow (Figure 2;  $r^2 = 0.0$ ,  $F_{1,19} = 0.001$ , p = 0.975, n = 20).

Across both winters, the depth and duration of torpor bouts varied respectively between 4.9 and 22.0 °C and between 0.2 and 8.1 days. Torpor expression was much reduced in 2006 relative to 2005, but in each year there was a significant relationship between burrow soil temperature during a torpor bout and the depth ( $T_{skin-min}$ ) and duration (*TBL*) of that bout (Figure 3). However, this was largely driven by seasonal

variation in torpor expression and soil temperature, as average or maximum torpor throughout hibernation did not vary according to average local soil temperature (Chapter 2).

Burrow microhabitat associations.- Univariate comparisons revealed that burrow sites were associated with more large beeches, less large sugar maples and more woody debris than unused sites (Table 1). After variable reduction, six microhabitat variables (large beech density, large red maple density, large seed-tree DBH, % green vegetation cover, % woody debris cover, and % slope) were included in the stepwise logistic regression comparing 22 burrows and 20 unused sites. Only % woody debris cover was retained as a good predictor of burrow locations in the final logistic model ( $r^2 = 0.23$ , Wald  $\chi^2 = 6.52$ , p = 0.01). The odds ratio of 1.223 (95% Wald CI = 1.05 – 1.43), indicates that a site with 15% woody debris cover is more then 7.5 times more likely to be used as a burrow than a site with only 5% woody debris cover.

#### Discussion

Chipmunk foraging behaviour varied according to the spatial and temporal availability of the most abundant and commonly consumed food items. Individual foraging efforts focused on spring beauty tubers and red maple seeds in summer, and then switched to beech nuts and sugar maple seeds in early autumn. Because the availability of multiple food sources was negatively correlated in time (e.g., red maple seeds were abundant when beech nuts and sugar maple seeds were absent) and space (e.g., beech was abundant in locations where sugar maple was scarce), it is impossible for chipmunks to select burrow locations that maximize the local abundance of all food sources at all times of the

year. Large beech density, which was the food-related microhabitat variable that most significantly differed between burrows and unused sites (Table 1), could represent a more profitable burrow microhabitat feature because of the higher profitability of beech nuts relative to other food items (Elliot 1978, Landry-Cuerrier unpublished data). Furthermore, unlike sugar and red maple samaras that are much lighter, beech nuts are not wind dispersed and fall more or less directly under the tree canopy, resulting in a more spatially concentrated food source. Successful exploitation of the many food sources that will not be locally abundant around a given burrow location at a given point in time requires traveling to more distant food patches. Although our focal observations were not designed to generate quantitative measures of the space use of individuals, we did frequently observe individuals traveling and foraging at distances greater than 30 m from their burrow.

Even though chipmunk torpor expression was correlated with seasonal variation in soil temperatures (Figure 3), average soil temperature was too invariant across the small spatial scales included in the present study to explain individual variation in torpor expression (Chapter 2). Furthermore, torpor expression by eastern chipmunks is strongly affected by resource availability, such that the extensive variation in local resource availability and foraging behaviour we documented is likely to swamp the impact of finescale spatial variation in soil temperature (Chapter 2). Accordingly, hibernacula microclimate did not emerge as significant predictor of burrow site use.

Abundance of woody debris was the microhabitat feature most strongly associated with burrow locations. There is indirect evidence that woody debris plays an important role in the anti-predator strategies of eastern chipmunks and other small mammals, but

the scarcity of observed predator-prey interactions in the presence and absence of woody debris prevents direct demonstration of this association. When active above ground, chipmunks spent a considerable portion of their time perched on woody structures (comparable to the portion of time they spent traveling or foraging), but were never observed consuming woody debris or food sources located within woody debris (e.g., saproxylic organisms). Most observations of chipmunks on woody debris involved perched and alert animals that were ingesting food retrieved from their cheek pouches, engaging in vigilance, and/or alarm calling. The next most commonly observed use of woody debris involved chipmunks traveling along fallen logs and branches. In chipmunks and other small mammals, these uses of woody debris are speculated to 1) increase prey detection of predators by elevating prey above the visual clutter of vegetative ground cover (Sherman 1985, MacHutchon and Harestad 1990, Hubbs et al. 1996), 2) reduce predator detection of prey by increasing travel speed and reducing the noise generated by prey movement (McMillan and Kaufman 1995, Roche et al. 1999), and 3) increase the probability of prey escaping a predator attack because of an abundance of nearby refuges (e.g., hollows and crevices, brush piles, log overhangs) (Doyle 1987, Loeb 1999). Finally, woody debris increases microhabitat structural complexity, which has been shown to reduce the capture success of avian predators because of slower attack velocity and more physical interferences (Longland and Price 1991). Overall, to small mammals, availability of woody debris lowers predation risk, which not only confers direct survival benefits, but also indirect advantages associated with reduced vigilance requirements and thus more profitable foraging under low predation risks (Morse 1980, Lima and Dill 1990, Sharpe and VanHorne 1998). Therefore, we hypothesize that chipmunks occupying

burrows surrounded by abundant woody debris are in a more complex, less risky microhabitat, with more low risk travel routes, and good quality refuges and perch sites, and should thus have improved survival and fitness, through direct anti-predator benefits and indirect influences on time and energy allocation.

Microhabitat features related to local food availability or to hibernacula microclimate were less important to chipmunk burrow site selection, especially relative to woody debris availability. Chipmunks can travel to food rich microhabitats away from their burrow, but will always be characterized by concentrated activity around the burrow because of the round-trip nature of central place larder hoarding (Elliot 1978). Since chipmunks are likely to be susceptible to predation when repeatedly traveling between a rich food patch and their burrow, predation avoidance benefits of abundant woody debris within 10 m of their burrow may largely exceed the benefits of highly localized access to seed-producing trees or of a more favourable hibernacula microclimate.

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Habitat selection occurs over a continuity of spatial scales and different habitat features best describe patterns of habitat use at different scales (Morris 1987, Litvaitis et al. 1996). The spatial scale at which habitat selection is investigated relative to the spatial scale at which a given habitat feature varies should influence how much that variable contributes to explain observed patterns of habitat occupancy. In fact, at a given spatial scale, habitat features with the most restricted distribution exert the most powerful constraint and can influence patterns of use of more extensively distributed habitat features (Orians and Wittenberger 1991). In this case, burrow microhabitat selection was best explained by woody debris availability likely because woody debris was more spatially heterogeneous than soil microclimate and, unlike seed-tree density, was not
associated with potential spatial and temporal trade-offs, and is thus a more limiting microhabitat component.

Overall, at the finest spatial scale, individual selection of intensively used microhabitats, such as home-site, nest, or burrow, based on predation risk might provide direct and indirect benefits that largely outweigh those of easily accessing food or of favourable microclimate. Advances in quantifying the complex interplay of direct and indirect effects of habitat use on animal reproduction, behaviours, energetics, inter- and intra-specific interactions, and survival should help better understanding mechanisms of habitat selection operating at different ecological scales.

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#### Figure Legends

Figure 1. Relationship between foraging scores and burrow microhabitat food scores for 21 adult chipmunks observed throughout the active season of 2006. Microhabitat food scores were obtained from the extraction of one principal component accounting for 56% of the total variance in the relation between local density of seed-trees (American beech, sugar maple, and red maple) and local density of tuber-producing herbaceous plants (spring beauties) averaged over all surveyed point within 30 m of the 21 burrow locations. Foraging scores were obtained from the extraction of one principal component accounting for 86 % of the variance, among 21 focal individuals, in the relation between the proportion of foraging time (including searching, handling, eating, pouching, and scatter hoarding of known food items) spent on tree-seeds and the proportion of foraging time spent on tubers. Burrows with higher microhabitat food scores had more seed-trees, but less tuber plants, and individuals with higher foraging scores spent more time foraging tree-seeds and less on tubers.

Figure 2. Woody debris availability around an individual's burrow (averaged for all surveyed points within 30 m of the burrow) and the proportion of perched time spent on woody structures (e.g., stumps, logs, branches). There was no significant relationship between local woody debris availability and use of woody structures as perch sites.

Figure 3. Relationships, over two different winters (2005-2006 and 2006-2007), between torpor bout depth ( $T_{skin-min}$ ) and length (*TBL*) and burrow soil temperatures during that

torpor bout. Among all observed torpor bouts in each year,  $T_{skin-min}$  were significantly lower and *TBL* significantly longer when prevailing burrow soil temperatures were low.

## Tables

Table 1. Comparisons (mean  $\pm$  SE) between burrows and unused sites for 17 microhabitat variables. Single asterisks denote variables that were considered in stepwise logistic regression.

	Burrows	Unused sites		
Variable	Mean ± SE	Mean ± SE	p	-
	<i>(n)</i>	( <i>n</i> )		• • •
Hardwood				
Small tree	64.94 ± 4.31	$64.35\pm4.62$	0.853	
density (no./plot)	(53)	(51)		
Large beech	$4.79\pm0.45$	$2.43\pm0.40$	< 0.001*	
density (no./plot)	(53)	(51)		
Large sugar	$4.55\pm0.43$	$7.16 \pm 0.71$	0.010	
maple density	(53)	(51)	`,	
(no./plot)				
Large red maple	$0.42\pm0.17$	$1.00\pm0.32$	0.172*	
density (no./plot)	.(53)	(51)		
		• •		
Large seed-tree	$26.62\pm0.72$	$33.56\pm2.10$	0.117*	
dbh (cm)	(53)	(51)		
Herbaceous				
Trout lily density	$75.47 \pm 6.34$	$72.07\pm9.71$	0.233	

$(no./m^2)$	(76)	(51)	
Spring beauty	$18.94 \pm 3.38$	$34.28\pm6.66$	0.281
density (no./m <sup>2</sup> )	(76)	(51)	•
Canopy cover (%)	$88.69 \pm 1.47$	86.81 ± 2.39	0.787
· · · · ·	(31)	(20)	
Ground cover (%)		. *	
Leaf litter	$60.81 \pm 2.99$	$60.93 \pm 3.98$	0.802
	(31)	(20)	
Green vegetation	$22.04 \pm 3.09$	$27.28 \pm 3.79$	0.127*
	(31)	(20)	
Woody debris	13.81 ± 1.36	$8.12 \pm 0.88$	0.009*
	(31)	(20)	
Bare ground	$1.47 \pm 0.47$	$1.09\pm0.41$	0.954
	(31)	(20)	
Rock	$1.87 \pm 0.42$	$2.25 \pm 0.67$	0.812
· ·	(31)	(20)	
Water	$0.30 \pm 0.21$	$0.22 \pm 0.22$	0.795
	(31)	(20)	
Microtopography			
Slope (%)	$14.29 \pm 0.97$	$13.05 \pm 1.95$	0.164*
	(31)	(20)	
Aspect heat load	$0.52\pm0.04$	$0.47 \pm 0.05$	0.359
	(31)	(20)	

Soil temperature	$\textbf{4.68} \pm 0.14$	$4.36\pm0.06$	0.083
(°C)	(8)	(10)	

## Appendix

Appendix 1. Spatial distribution of all burrows sampled for some microhabitat variables (open circle; n = 87), of burrows sampled for all microhabitat variables (filled circle; n = 22), of all unused sites sampled for some microhabitat variables (open triangle; n = 51), and of unused sites sampled for all microhabitat variables (filled triangle; n = 20).



- All sampled burrows
  - Burrows sampled for all variables
- All sampled unused sites
- Unused sites sampled for all variables

Figures

Figure 1.



Figure 2.



Figure 3.



## **CONNECTING STATEMENT**

Results from the first chapter demonstrate that because of spatial and temporal trade-offs in food availability and foraging behaviour and because hibernacula microclimates was too spatially invariant, woody debris availability was the most important burrow microhabitat feature and played an important role in chipmunk anti-predator behaviour. This provides indirect evidences of the importance of fine-scale relationships between habitat and individual performance in driving spatial distribution of animals in heterogeneous landscapes. The next chapter directly considers fine-scale consequences of local food availability and hibernacula microclimate on temporal and spatial variation in eastern chipmunk winter torpor expression and winter energetics.

## **CHAPTER 2**

# **MICROCLIMATE AND RESOURCE DETERMINANTS OF THE** FUNDAMENTAL AND REALIZED METABOLIC NICHES OF HIBERNATING **CHIPMUNKS**

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Running head: Metabolic niche of hibernating chipmunks

Title: Microclimate and resource determinants of the fundamental and realized metabolic niches of hibernating chipmunks

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#### Abstract

Torpor is a reversible reduction in endotherm body temperature and metabolic rate. Because torpid endotherms can attain lower body temperatures in colder environments, minimum torpor metabolism generally increases with rising air temperature whereas euthermic metabolism generally declines with rising air temperature. As a result, the fundamental metabolic niche of endotherms that express torpor should be driven by climate and should be broadest in colder environments. On the other hand, if torpor serves primarily as an energy conservation strategy and its expression is influenced by energy availability, then the realized metabolic niche should be defined by resources. To evaluate the influence of resource and climate on torpor use and metabolism of hibernating mammals, we monitored the torpor expression of free-ranging eastern chipmunks (Tamias striatus) over two winters of varying resource abundance. In the lowfood year, soil temperature constrained maximum torpor expression, but was too invariant across small spatial scales to explain individual variation in torpor expression. In the high-food year, torpor was drastically reduced and local density of seed-producing trees predicted fine-scale spatial variation in torpor expression. Thus, the fundamental metabolic niche of hibernating chipmunks in cold environments is broad and constrained by climate, whereas the realized metabolic niche is highly variable among individuals and years and is determined primarily by local resource abundance.

Keywords: body temperature, climate, food-storing hibernator, hibernation, individual variability, intra-specific variation, microhabitat, resource, Sciuridae, torpor expression, tree-seed production, winter energetics.

### Introduction

Renewed awareness of the importance of metabolic traits in ecology has generated increased scrutiny of the drivers of metabolic variation. In an attempt to maximize generality, much recent research in metabolic ecology has focused on coarse-grained variation observed across diverse taxa and large spatial scales (Chown et al. 2004, Osovitz and Hofmann 2007). The remarkable ability of simple mechanistic models, based only on body size and temperature, to account for a large proportion of this coarse-grained metabolic variation suggests a degree of universality in the metabolic physiology of organisms (Brown et al. 2004). However, this notion of universality is challenged by extensive fine-scale variation in metabolic traits, for example among different individuals within a species (Speakman et al. 2003) and within the same individual over time (McLean and Speakman 2000), that is unrelated to or only partially explained by either body size or temperature. Thus, an emerging challenge in metabolic ecology is to identify the major drivers of metabolic variation operating at different ecological and evolutionary scales of comparison.

Torpor is a reversible state of depressed body temperature ( $T_b$ ) and metabolic rate used by many endotherm species to survive daily or seasonal periods of energy or water shortage (Lyman et al. 1982, McNab 2002). Continuous monitoring of torpor expression in the field can be achieved with temperature-sensitive radio-transmitters or data-loggers, providing one of the best means for long-term metabolic monitoring of free-ranging endotherms (Cooke et al. 2004). Recent field studies of torpor patterns reveal substantial unexplained variation in the depth and duration of torpor bouts expressed by individuals of the same species (Young 1990, Wassmer and Wollnik 1997, Wilz and Heldmaier

2002, Humphries and Rodgers 2004, Lehmer and Biggins 2005, Lehmer et al. 2006). The extent of this intra-specific variation frequently ranges from no torpor to deep, prolonged torpor bouts, which approaches the inter-specific variation observed across all endotherms used to categorize species as showing no torpor, daily torpor, or prolonged torpor (Geiser and Ruf 1995). Laboratory and field studies on eastern chipmunks (*Tamias striatus*) have demonstrated that experimental supplementation of food hoards in autumn leads to reduced torpor expression during winter (French 2000, Humphries et al. 2003a, Munro et al. 2005), but little is known about the environmental drivers of individual variation in torpor expression among free-ranging, unmanipulated endotherms.

According to the metabolic niche hypothesis, cold environmental temperature ( $T_a$ ) limits diversity by restricting the range of energetically feasible lifestyles (Anderson and Jetz 2005, Clarke and Gaston 2006). In this context, the metabolic niche can be defined as the metabolic space (bounded by minimal and maximal metabolic rates) occupied by a species or group of species in a given environment. Among endotherms, the primary support for the metabolic niche hypothesis is the observation that the inter-specific range of field metabolic rates, measured on free-ranging birds and mammals with the doubly labeled water technique, is much broader at low latitudes than at high latitudes (Anderson and Jetz 2005). Since the doubly labeled water technique has not been used on hibernating endotherms (Speakman 1997, 2000), the contribution of hibernating species to latitudinal trends in metabolic niche breadth remains unconsidered. This is a critical omission, because torpor substantially enlarges the metabolic niche of endotherms and the extent of this expansion should be greatest in cold environments; low  $T_a$  increases euthermic metabolic rate (because more heat production is required to maintain a

constant elevated  $T_b$ ) and decreases torpor metabolic rate (because  $T_b$  can go lower, resulting in reduced metabolism (Geiser 2004)).

The expression of metabolic traits in nature is influenced by both energy demand and energy supply (Thomas et al. 2001, Humphries et al. 2005). Based on ecological approaches to niche definition (Hutchinson 1957, McGill et al. 2006), the metabolic niche can therefore be envisioned as consisting of a fundamental component, representing the full range of metabolic options available to an animal in a given environment, as well as a narrower, realized component, which is influenced by resources, competitors, and predators that are present in that environment. Because cold  $T_a$  reduces torpor metabolism and elevates euthermic metabolism, the fundamental metabolic niche should broaden with decreasing  $T_a$  and climate should be the principal determinant of the location and breadth of that niche. On the other hand, if metabolic traits in nature are also influenced by resource supply (Humphries et al. 2003b), then the location and the breadth of the realized metabolic niche in any given environment should vary according to resources.

Our objective was to evaluate the environmental determinants of the fundamental and realized metabolic niche of a burrowing mammalian hibernator by documenting how torpor expression is influenced by soil temperature and resource availability. We focus on fine-scale metabolic variation observed within a single population of chipmunks monitored over two years of vastly different resource supply. Eastern chipmunks hibernate alone in a burrow and, during periodic arousals, consume a larder hoard consisting primarily of tree-seeds accumulated through central place hoarding and stored inside the burrow (Elliot 1978). An individual's burrow location should influence local

resource availability, and thus the size and composition of the larder hoard available during hibernation, but also the microclimate in which hibernation occurs. We predicted that, within and among years, differences in local resource availability would account for substantial variation in torpor expression, thereby positioning the realized metabolic niche within a broad fundamental niche defined by hibernacula microclimate.

#### Methods

#### *Study site and population*

The study was conducted from 2005 to 2007 in the Ruiter Valley Land Trust near Mansonville, Québec (45°05'N, 72°26'W). The study site covers 25 ha of mature deciduous forest dominated by sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*), with trout lily (*Erythronium americanum*) and spring beauty (*Claytonia caroliniana*) as the most abundant herbaceous plants. In the active season of each year, live trapping is conducted regularly on a 19.6 ha grid using Longworth traps (Longworth Scientific Instruments Ltd, UK). Each captured animal is weighed, sexed, and permanently marked with numbered metal ear tags. We used the last recorded weight before hibernation as an index of autumn body mass. Burrow location is determined for most individuals by attaching radio-transmitters (4 g; model PD-2C, Holohil Systems Ltd, ON), tracking individuals to their burrow locations in early morning or late evening, and marking above ground, as the central location or nest chamber of a burrow-site, where the signal was the strongest.

Torpor expression

Thermoregulatory patterns during hibernation were continuously monitored with neck-mounted temperature-sensitive collars recording skin temperature  $(T_{skin})$  (e.g., Barclay et al. 1996, Munro et al. 2005). In autumn of 2005 and 2006 respectively, 8 (3 adult females, 5 adult males) and 18 (6 adult females, 4 adult males, 3 juvenile females, and 5 juvenile males) chipmunks were fitted with collar-mounted, temperature-sensitive radio-transmitters (4.1 g; model PD-2CT, Holohil Systems Ltd, ON). Transmitters were recalibrated prior to use in the field and were recorded throughout the hibernation period with stationary Yagi antennas and two data-logging radio-receivers (model SRX-400 W-21, Lotek Wireless Inc., ON). To increase our potential sample size of temperaturemonitored individuals, in autumn 2006, we fitted an additional 16 chipmunks with collarmounted, temperature-sensitive data-loggers (2.2 g; recording interval of 37.5 minutes; iBCollar 22L, Alpha Mach Inc, QC). In spring 2007, eight data-loggers were recovered on recaptured individuals and seven were functional (3 adult females, 2 juvenile females, and 2 juvenile males). The spring recovery of data-loggers (8/16) was comparable to the survival into spring of individuals fitted with radio-transmitters (9/18). Thus, in 2006, between radio-telemetry and recovery of functional data-loggers, we successfully monitored torpor patterns of 25 chipmunks (18 with radio-transmitters and 7 with dataloggers).

We seek to evaluate how torpor patterns varied seasonally, but the number of successfully monitored individuals varied over the course of the winter as a result of natural mortality, radio-transmission failures, and occasional gaps in radio-reception. Therefore, we targeted a 20-day window in early winter and late winter that maximized the number of individuals with complete and continuous records during that period in

both winters. Accordingly, in both years and for all individuals, early winter was from November 7 to 26 and late winter from April 3 to 22. In each year, mid-winter was set on an individual-by-individual basis to include the most intense torpor expression, and therefore was defined as the 20-day window between December 17 and March 12 characterized by the longest and deepest torpor bouts.

We defined torpor bouts as events when  $T_{skin}$  remained < 30 °C for more than five consecutive hours including maintenance of a stable  $T_{skin}$  baseline (± 2 °C) for longer than one hour. We recorded torpor bout length (*TBL*; the time between the last  $T_{skin}$ record above and below 30 °C) and minimum  $T_{skin}$  ( $T_{skin-min}$ ) observed for each torpor bout. For each individual, we calculated the percent time spent in torpor (*torpid time*), as well as the average *TBL* and  $T_{skin-min}$  of all torpor bouts expressed during each window, which we then averaged over all individuals in each window. In both years, for each individual monitored during mid-winter, we obtained the  $T_{skin-min}$  of their deepest torpor bout and the *TBL* of their longest torpor bout expressed.

#### Metabolic consequences

We used measurements presented in Wang and Hudson (1971) to estimate the fundamental and realized metabolic niches, expressed as kJ/day assuming 4.8 kcal/L O<sub>2</sub> and therefore 20.0 kJ/L O<sub>2</sub>, of hibernating eastern chipmunks that expressed the least and most torpor in each year. We calculated the lower and upper bounds of the fundamental metabolic niche based on the thermal constraints imposed by soil temperature ( $T_{soil}$ ). The lower bound of the metabolic niche is imposed by the constraint that, above the torpor set-point temperature, minimum torpor  $T_b$  tracks  $T_{soil}$ , with a minimum  $T_b - T_{soil}$  differential of about 1 °C. In eastern chipmunks, minimum observed torpor metabolic rate

 $(MR_T)$  at a  $T_b$  of 4 °C is 5.4 mlO<sub>2</sub>/hr (Wang and Hudson 1971). Thus, assuming  $Q_{10} = 2.5$ , minimum achievable  $MR_T$  varies with  $T_{soil}$  according to  $5.4 \cdot 2.5$   $^{(Tsoil+1-4)/10}$ . The upper bound of the fundamental metabolic niche is defined by the thermoregulatory requirements of euthermy in the hibernaculum, which we modeled as  $183 - (2.7 \cdot T_{soil})$ ; this equation generates the average resting metabolic rate of chipmunks at a lower critical temperature of 27 °C (Wang and Hudson 1971) and includes a thermal conductance concordant with spending most euthermic time inactive in a well-insulated nest (Pauls 1978), but cannot be used to predict euthermic requirements when  $T_{soil}$  exceeds the lower critical temperature.

To estimate the realized metabolic niche of individuals that expressed the least and most torpor in each year, we classified each  $T_{skin}$  record as euthermic, torpid (including entry and baseline), or arousing, based on the previously described definition of a torpor bout as  $T_{skin} < 30$  °C for  $\ge 5$  hr. To accommodate the uncertainty involved in predicting metabolic rate from documented torpor patterns and  $T_{soil}$  exposure, particularly because Wang and Hudson (1971) present a wide range of measured metabolic rates for torpor and euthermic states, we predicted an envelope (rather than a point estimate) of plausible metabolic rates that could arise from different forms of torpor expression. Accordingly, we modeled a minimum and maximum value for each major parameter. Our maximum estimate for euthermic metabolic rate ( $MR_E$ ) was the same used to define the upper bound of the fundamental niche ( $MR_E = 183 - (2.7 \cdot T_{soil})$ ). Our minimum metabolic rate estimate assumed chipmunks are always at rest and thermal neutral when euthermic and thus have a constant  $MR_E$  of 92 mlO<sub>2</sub>/hr (Wang and Hudson 1971). For torpor, we estimated minimum  $MR_T$  as  $5.4 \cdot 2.5$  (Tskin - 4)/10 based on the range of minimum torpor metabolic rates presented by Wang and Hudson (1971). We assumed arousal metabolic rate ( $MR_A$ ) was a minimum of 300 mlO<sub>2</sub>/hr and a maximum of 913 mlO<sub>2</sub>/hr (Wang and Hudson 1971). To predict the upper edge of the envelope for realized metabolic niche, we predicted metabolic rates from observed  $T_{skin}$  and  $T_{soil}$  patterns using the maximum estimates for  $MR_E$ ,  $MR_A$ , and  $MR_T$ . We predicted the lower edge of the envelope in the same manner, but based on the three minimum estimates.

#### $T_{soil}$ , air temperature, and snow depth

In both years from November to April, we used temperature data-loggers (iButton model DS1921L, Dallas Semiconductor, CA; recording interval of 4 hours) to measure  $T_{soil}$  at 80 cm depth, which is similar to reported depths of chipmunk burrows (Panuska and Wade 1956, Elliot 1978). Temperature loggers were inserted underground at 8 burrows and 25 systematic locations evenly distributed over the study area to incorporate the range of topography, soil condition, and vegetative cover present within the study area. Soil temperature loggers were placed at 80 cm depth using a soil corer to excavate a hole, insert the data-logger, then refill the hole with the soil core to minimize soil disturbance. A rope attached to the data-logger was fed through the refilled hole to the surface to permit recovery of the data-logger at the end of the recording period. Similar to Buck and Barnes (1999), burrow temperature loggers were inserted 2 m away from the location of the burrow chamber, as estimated with radio-telemetry, so as to not disturb the integrity of the burrow and avoid chipmunks interfering with the data-logger. For each burrow with an inserted temperature logger and occupied by a monitored individual, we calculated average burrow  $T_{soil}$  over the 20-day mid-winter window (to relate with torpid

*time* calculated over the same 20-day mid-winter window) and average burrow  $T_{soil}$  over the duration of each torpor bout (to relate to the depth and duration of that torpor bout). Air temperature ( $T_{air}$ ) and snow depth data were obtained from the closest meteorological station, which is located 20 km away from our study area (Sutton, Québec, 45°04'N, 72°41'W, Environment Canada; www.weatheroffice.ec.gc.ca). In each year, from November to April, daily, monthly and six-month winter averages in  $T_{soil}$ ,  $T_{air}$ , and snow depth were calculated.

#### Local tree density and seed production

When available, seeds from beech, sugar maple, and red maple (A. rubrum) are extensively consumed and hoarded and represent the major autumn and hibernation food source of chipmunks at our study site (Landry-Cuerrier and Humphries unpublished data). Accordingly, we quantified the density of seed-producing trees (i.e., beech, sugar maple, and red maple) around all chipmunk burrows (n = 47) known to be active at the time of tree sampling and around systematic sampling points that were evenly distributed over the study area (n = 85). At each location, within a 10 m radius circular plot centered on the sampling point, we counted the number of beech, sugar maple, and red maple trees with diameters at breast height (DBH) larger than 10 cm (James and Shugart 1970). To quantify the foraging microhabitat in the local vicinity of each monitored chipmunk's burrow, we used all survey points sampled within 30 m of the burrow (from 1 to 4 survey points) and calculated the average number of seed-producing trees per  $100 \text{ m}^2$ . We selected a 30 m radius because, although chipmunks are known to travel more than 150 m to exploit localized food sources, individuals most intensively use a core area within 30 m of their burrow (Elliot 1978, Landry-Cuerrier and Humphries (unpublished data)).

We sampled annual seed production of beech and sugar maple, which are the two most abundant tree species within the study site. At 30 of the 85 tree density sampling points, selected so that they were evenly distributed across the study site, we placed a seed-collecting bucket  $(0.06 \text{ m}^2)$  under the canopy of the nearest beech and sugar maple tree with DBH > 10 cm. Thus, in total we installed 60 seed-collectors including 30 under sugar maple trees and 30 under beech trees. To deter seed-predator access, buckets were more than 40 cm deep, elevated above-ground with two smooth metal poles, and installed 1 m away from the trunk of the target tree. Buckets were installed in late summer of 2005 and 2006, well before autumn seed fall of both species, and the contents were counted twice between September and November. The fruiting bodies of American beech consist of a spiny husk enclosing two or three seed coats each containing a kernel, whereas the fruiting bodies of sugar maple consist of paired samaras each composed of a flattened wing attached to a seed coat containing a kernel (Burns and Honkala 1990). Because chipmunks consume kernels and discard seed coats from both species, and because both species frequently abort seed coats lacking kernels, we opened all collected seed coats to determine the proportion that contained kernels. For each tree species, we report the average number of seed coats per m<sup>2</sup> as well as the proportion of seed coats containing kernels.

#### Statistical analysis

Within years, we used linear regression to evaluate relationships between autumn body mass and mid-winter *torpid time* and multiple ANOVAs to assess the effects of window and sex and age class on torpor expression variables (*torpid time*, average *TBL and*  $T_{skin-min}$ ). Differences in torpor expression between years, windows, and sex and age

classes were verified using non-parametric Wilcoxon-Mann-Whitney tests. To evaluate the effect of year, window, individual, and burrow  $T_{soil}$  (averaged over the course of each torpor bout) on  $T_{skin-min}$  observed during each torpor bout, we performed mixed model repeated measures analysis. Because there were window-to-window differences in both torpor expression and the number of individuals monitored (due to natural mortality or radio-transmission or reception failures), we limit our analysis of fine-scale environmental determinants of torpor expression to individuals monitored during midwinter. In each year, we used linear regression to assess whether mid-winter *torpid time* (over the 20-day mid-winter window) varied with burrow  $T_{soil}$  (averaged over the same 20-day mid-winter window) or with local seed-producing tree density and whether the lowest  $T_{skin-min}$  and longest *TBL* observed during midwinter varied with burrow  $T_{soil}$ (averaged over the duration of that torpor bout) or with local seed-producing tree density. All statistical analyses were performed using SAS version 9.1 (SAS Institute Inc. 2002).

#### Results

Seed fall under the canopy of target beech and sugar maple trees varied substantially between years. In autumn 2005, we collected  $44 \pm 20$  beech seed coats per m<sup>2</sup>, none of which contained a mature kernel, and  $5 \pm 4$  sugar maple seed coats per m<sup>2</sup>, 22% of which contained a mature kernel. In autumn 2006, we collected  $256 \pm 55$  beech seed coats per m<sup>2</sup>, most of which contained a mature kernel, and  $388 \pm 64$  sugar maple seed coats per m<sup>2</sup>, 79% of which contained a mature kernel. Thus, we collected significantly more beech (t = 3.2, df = 58, p = 0.003) and sugar maple seed coats (t = 2.9, df = 58, p = 0.008) in 2006 than in 2005, and the proportion of seed coats containing kernels was also higher in

2006 than 2005. As a result, the hibernation season 2005-2006 will be referred as the low-food year and 2006-2007 as the high-food year.  $T_{soil}$  was significantly warmer in the low-food year than the high-food year (Fig. 1). Six-month average  $T_{air}$  was warmer and total snow accumulation was less in the low-food year (-1.3 °C; 282 cm) than in the high-food year (-2.2 °C, 320 cm) (Fig. 1).

Winter torpor patterns of eastern chipmunks differed widely between years and among individuals within years (Fig. 2). Generally, the depth and duration of torpor bouts increased from early to mid-winter and decreased from mid- to late winter (Fig. 3). In each 20-day winter window of the low-food year, adult chipmunks spent a majority of time torpid (torpid time: 81-90%; Fig. 3a) and expressed deep (T<sub>skin-min</sub>: 6.0-8.6 °C; Fig. 3c) and prolonged torpor bouts (TBL: 3.6–5.6 days; Fig. 3b). In that year, torpor variables differed between windows (torpid time:  $F_{2,13} = 4.7$ , p = 0.03;  $T_{skin-min}$ :  $F_{2,13} = 10.7$ , p =0.002; TBL:  $F_{2,13} = 7.1$ , p = 0.008), but not among sexes (Appendix A). In each 20-day winter window of the high-food year, adult chipmunks spent much less time torpid (torpid time: 0-31%; Fig. 3a) and expressed shallower (T<sub>skin-min</sub>: 15.1-17.0 °C; Fig. 3c) and shorter torpor bouts (TBL: 0.7-1.1 days; Fig. 3b) than in the low-food year. In the high-food year, only torpid time differed between windows interacting with age and sex classes ( $F_{9,48} = 6.6, p < 0.001$ ), with juvenile males in mid-winter expressing less torpor than juvenile females and adults (Appendix A). Statistical analysis of between-year differences in torpor variables is reported in Fig. 3. Since no individual in late winter of the high-food year expressed torpor, it was only possible to assess, for that window, the between-year difference in *torpid time*. Autumn body mass was marginally higher in the high-food year (98.5  $\pm$  1.5 g; n = 11) than in the low-food year (92.2  $\pm$  3.3 g; n = 5; t =

2.0, df = 14, p = 0.07), but there was no relationship between autumn body mass and mid-winter *torpid time* within the low-food year ( $r^2 0.52$ , p = 0.2, n = 5), the high-food year ( $r^2 0.04$ , p = 0.6, n = 11), or across the two years of study ( $r^2 0.09$ , p = 0.3, n = 16).

Estimation of the metabolic consequences of the observed torpor variation revealed that, in the low-food year, metabolism approached the minimum rate permitted by  $T_{soil}$  throughout winter, whereas in the high-food year, metabolism approached the maximum metabolism defined by  $T_{soil}$  (Fig. 2). Overall, there was a 3.3-fold difference in the total winter metabolism of the individual that expressed the most and the least torpor across the two years of study (2,920 kJ vs. 9,620 kJ over a 200-day winter).

Repeated measures analysis revealed that, in both years of the study, seasonal variation in the  $T_{skin-min}$  of individual chipmunks tracked seasonal variation in their burrow  $T_{soil}$  (averaged over the course of the same torpor bout). However, the relationship between  $T_{skin-min}$  and burrow  $T_{soil}$  differed between years, with a much stronger influence of  $T_{soil}$  in the low-food year ( $r^2 0.52$ , p < 0.001, n = 47) than in the high-food year ( $r^2 0.27$ , p < 0.001, n = 43; Appendix B). Overall,  $T_{skin-min} - T_{soil}$  differentials were much larger in the high-food year (average = 8.1 °C, range = 2.4–18.0 °C) than in the low-food year (average = 1.7 °C, range = -1.22–4.9 °C). Furthermore, individual variation in  $T_{skin-min}$  was significantly higher in the high-food year than in the low-food year (Appendix B).

During mid-winter, individual variation in torpor expression was related to finescale spatial variation in resource availability in the high-food year, but not in the lowfood year (Fig. 4). In the high tree-seed production year, individuals with burrows surrounded by higher densities of seed-producing trees spent less time in torpor (*torpid time*:  $r^2 0.32$ , p = 0.07, n = 11) and expressed shallower ( $T_{skin-min}$ :  $r^2 0.51$ , p = 0.03, n = 9)

and shorter (*TBL*:  $r^2 0.62$ , p = 0.01, n = 9) torpor bouts during the mid-winter window (Fig. 4). In contrast, in the low tree-seed production year, local density of seed-producing trees was not related to torpid time ( $r^2 0.001$ , p = 0.96, n = 5),  $T_{skin-min}$  ( $r^2 0.46$ , p = 0.21, n= 5), or TBL ( $r^2 0.51$ , p = 0.18, n = 5) during the mid-winter window when all individuals spent a majority of time torpid and expressed long and deep torpor with  $T_{skin}$  routinely approaching  $T_{soil}$  ( $T_{skin-min}$  -  $T_{soil}$  = 1.4–2.9 °C; Fig. 4). Mid-winter burrow  $T_{soil}$  (averaged over the 20-day mid-winter window) was not related to local density of seed-producing trees across years ( $r^2 0.05$ , p = 0.53, n = 10) or to mid-winter *torpid time* in either year (low-food year:  $r^2 0.19$ , p = 0.47, n = 5; high-food year:  $r^2 0.31$ , p = 0.33, n = 5). Furthermore, burrow  $T_{soil}$  during the deepest and the longest torpor bout expressed in mid-winter was not a significant predictor of the depth and duration of those bouts in either the low-food (lowest  $T_{skin-min}$ :  $r^2$  0.23, p = 0.41; longest TBL:  $r^2$  0.19, p = 0.47, n =5) or the high-food year (lowest  $T_{skin-min}$ :  $r^2 0.09$ , p = 0.62; longest TBL:  $r^2 0.07$ , p = 0.67, n = 5; Fig. 4). Thus, although the depth and duration of individual torpor bouts tracked seasonal variation in  $T_{soil}$  (see preceding paragraph and Appendix B), at a given time point (e.g., mid-winter) or torpor state (e.g., deepest torpor bout of the hibernation season), among-individual variation in burrow  $T_{soil}$  did not account for significant amongindividual variation in torpor expression.

#### Discussion

Relating torpor expression of free-ranging eastern chipmunks to the local density of seedproducing trees and microclimatic conditions over two years of vastly different tree-seed production leads to the following four conclusions:

*There is substantial individual variation in metabolic traits expressed in nature*. All our study animals live within a 25 ha study site that consists of a relatively homogenous stand of mature beech-maple forest. Despite this, during the entire hibernation, time spent torpid by different adult individuals varied between 3% and 39% within a single winter, and between 3% and 87% across two winters. Based on metabolic measurements made by Wang and Hudson (1971) and calculations presented in the methods, the individual expressing the least torpor in the high-food year would have expended, over the course of a 200-day winter, more than three times as much energy as the individual expressing the most torpor in the low-food year (2,920 kJ vs. 9,620 kJ). This variation in the winter metabolism of individuals of the same species, living within the same 500 m<sup>2</sup> forest stand, exceeds the 2-fold variation in average chipmunk torpor patterns observed between two populations spaced more than 500 km (Munro et al. 2005) and approaches the 3- to 6-fold differences in average resting metabolic rates of extreme outliers in inter-specific mammal scaling relationships (e.g., Lovegrove 2000, 2003).

When resources are scarce and chipmunks express deep, prolonged torpor bouts, microclimate constrains maximum torpor expression. Prevailing  $T_a$  in the hibernaculum defines minimum torpor  $T_b$  of hibernators ( $T_b \ge T_a$  constraint) and low  $T_b$  decreases torpor metabolism and the frequency of costly arousals. Thus,  $T_a$  dictates the maximum energy savings offered by torpor.  $T_{soil}$  at 80 cm depth varied from a seasonal maximum of 7 to 9 °C in early November to a seasonal minimum of 2 to 3 °C in March or April, but the precise timing and value of these minima and maxima varied spatially across the study site and temporally between years. However, in a given year within a given time period (i.e. 20-day mid-winter window),  $T_{soil}$  varied among burrows by 1 to 4 °C and was

not a significant predictor of individual variability in torpor expression (Fig. 4). Yearly differences in  $T_{soil}$  did not explain yearly differences in torpor expression, as observed torpor bouts were longer and deeper in the year with warmer  $T_{soil}$ . Nevertheless, in the low-food year, when chipmunks expressed deep and prolonged torpor bouts,  $T_{soil}$  explained a majority of variation in  $T_{skin-min}$  and the average  $T_{skin-min} - T_{soil}$  differential was less than 2 °C. Thus,  $T_a$  constrained maximum torpor depth, as has been shown repeatedly in other hibernators (Geiser and Broome 1993, Buck and Barnes 2000, Ortmann and Heldmaier 2000, Humphries et al. 2002).

Spatial and annual differences in resource availability generate substantial variation in torpor expression. Torpor expression was reduced and more individually-variable in years of high tree-seed production than in years of low tree-seed production. Within years of high tree-seed production, individuals with burrows surrounded by fewer seed-producing trees were characterized by deeper and longer torpor bouts than individuals with burrows surrounded by more seed-producing trees (Fig. 4). The causal basis of these relationships is supported by previous experimental studies conducted on captive and free-ranging eastern chipmunks showing that torpor expression is drastically reduced in response to hoard supplementation (French 2000, Humphries et al. 2003a, Munro et al. 2005). Presumably, food is related to torpor expression in the absence of a strong effect of food on body mass and of body mass on torpor, because chipmunks store energy externally as food rather than internally as fat (Humphries et al. 2003b). Although chipmunks are known to travel more than 150 m to exploit localized food sources, individuals most intensively use a core area within 30 m of their burrow (Elliot 1978). Thus, although eastern chipmunks can and do exploit distant resources, their total hoard

accumulation is likely to be primarily dictated by food resources in close proximity to their burrow. The mobility of seed predators has the potential to homogenize the trophic consequences of spatial heterogeneity in seed fall (Curran and Leighton 2000, Ostfeld and Keesing 2000, Schnurr et al. 2002), but our results show that fine-scale spatial heterogeneity in resources can translate directly into fine-scale spatial heterogeneity in the metabolism of consumers. The cascading effects of local resources on hoard accumulation and torpor expression generate a remarkable degree of intra-specific metabolic diversity within a small forest stand.

The fundamental metabolic niche of hibernating chipmunks is imposed by microclimate, but their realized metabolic niche is determined primarily by local resources. Because cold  $T_a$  enables low metabolism in torpid animals and imposes high metabolism in euthermic animals, the fundamental metabolic niche breadth of hibernating animals is broadest in late winter when  $T_a$  is at its annual minimum (Fig. 2). The need for all hibernating endotherms to periodically arouse from torpor constrains the lower bound of the realizable metabolic niche above the lower bound of the predicted fundamental niche as defined by continuous minimum torpor metabolism. Nevertheless, under conditions of resource scarcity, individuals approach the lower bound of the fundamental metabolic niche by expressing deep and prolonged torpor bouts (Fig. 2). Access to abundant resources, resulting from a high local density of seed-producing trees in a year of high tree-seed production or from experimental food supplementation, leads to a drastic reduction in torpor expression and an upward shift in the realized metabolic niche, much closer to the upper bound of the fundamental metabolic niche (Fig. 2). Thus, the fundamental metabolic niche of hibernating chipmunks in cold environments is extremely

broad and defined primarily by climate, whereas the realized metabolic niche of chipmunks is highly variable among individuals and years and is determined primarily by resources. Chipmunks and other food-storing hibernators that exploit pulsed resources are likely to have particularly broad realized metabolic niches because they can rapidly accumulate very large energy reserves when resources are abundant and substantially reduce energy expenditure via torpor expression when resources are scarce. The relationship between hibernaculum temperatures and individual- or species-level variation in the torpor set-point temperature is likely to be another important determinant of the realized and fundamental metabolic niche of many hibernators (Lyman et al. 1982, Buck and Barnes 2000).

Additional laboratory and field studies are required to better understand the physiological basis and the selective advantages of highly plastic torpor expression in eastern chipmunks, including why chipmunks use available resources to reduce their use of torpor rather than maintaining deep torpor expression and conserving these resources for the following spring (Humphries et al. 2003b). Similar approaches need to be applied across larger spatial scales and more species to evaluate whether the climate and resource influences on the metabolic niche identified in this study also apply to broader spatial and taxonomic scales. Nevertheless, our study generates three conclusions of general relevance to the metabolic ecology of endotherms: there is extensive fine-scale, intraspecific variation in metabolic traits in nature, torpor greatly enhances the metabolic niche is shaped by both the abiotic and biotic environment.

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### Figure Legends

Fig. 1. Inter-annual variation between the low-food year (2005-2006; black lines and symbols) and the high-food year (2006-2007; grey lines and symbols) in soil temperature ( $T_{soil}$ , daily average from 32-33 soil probes), air temperature ( $T_{air}$ ; daily average measured at a weather station within 20 km of the study site) and snow depth (measured daily at the same weather station) during the hibernation period. Dashed lines indicate six-month temperature averages from November to April of each year. We evaluated the statistical significance of inter-annual variation in monthly  $T_{soil}$  by comparing the monthly averages (circles  $\pm$  SE) of 33 soil probes in the low-food year and 32 in the high-food year, which were distributed systematically across the study site; annual differences in  $T_{soil}$  were statistically significant in every month (in all cases, t > 3.0, df = 63, p < 0.002, which is less than the Bonferroni adjusted critical value of 0.008 for six comparisons). Monthly averages of  $T_{soil}$  and seasonal average of  $T_{air}$  were warmer and snow accumulation was less in the low-food year.

Fig. 2. The fundamental and realized metabolic niche of four hibernating eastern chipmunks, expressing the most and least torpor in the high-food and the low-food year. In the low-food and the high-food year respectively, we monitored the torpor expression of 8 and 25 chipmunks. Upper panels present observed skin temperature ( $T_{skin}$ ; black lines) and soil temperature ( $T_{soil}$ ; grey lines) at approximate burrow depth (80 cm below surface) over the hibernation season. Lower panels present predicted metabolic rate based on measurements by Wang and Hudson (1971). Dashed lines indicate the fundamental metabolic niche as defined by the effects of  $T_{soil}$  on minimum torpor metabolic rate (lower dashed line) and euthermic metabolic rate (upper dashed line). Solid lines

bounded by grey shading indicates the realized metabolic niche based on the metabolic consequences of observed  $T_{skin}$  at the prevailing  $T_{soil}$ , presented as a 14-day moving average to smooth spikes associated with periodic arousals. The extent of the grey shaded area reflects the range of predicted metabolism based on maximum and minimum values reported by Wang and Hudson (1971) and the black line indicates the mid-point of this range. Gaps in the time series of the individual expressing the least torpor in the low-food year reflect missing data resulting from weak transmitter signal reception by our automated telemetry system.

Fig. 3. Inter-annual comparisons (mean  $\pm$  SE), between the low-food and the high-food year, for a) the percent of time spent torpid (*torpid time*), b) the average torpor bout length (*TBL*), and c) the average torpor bout minimum skin temperature (*T<sub>skin-min</sub>*) during three 20-day windows (early, mid- and late winter) with all adult individuals monitored in each window. Significant differences between years, from Wilcoxon-Mann-Whitney tests, are indicated with single (0.001 < *p* < 0.05) and double (*p* ≤ 0.001) asterisks. The number of individuals monitored in each window in each year is given below the bar, with the number in parentheses indicating the number of individuals that expressed torpor.

Fig. 4. Resource and microclimate correlates of torpor variation among eastern chipmunks in mid-winter of the low-food and the high-food year. The resource measure is the average number of mature seed-producing trees (American beech, sugar maple, and red maple with DBH > 10 cm) per 100 m<sup>2</sup> in the local vicinity of an individual's burrow, whereas the microclimate measure is soil temperatures ( $T_{soil}$ ) at approximate burrow depth (80 cm) within 2 m of an individual's burrow chamber. In each year, during 20

days in mid-winter, we related the percent of time spent torpid (*torpid time*) to burrow  $T_{soil}$  (averaged over that same 20-day window) and the lowest minimum torpor skin temperature ( $T_{skin-min}$ ) and longest torpor bout length (TBL) to burrow  $T_{soil}$  (averaged over the duration of each torpor bout). Significant (p < 0.05) and marginally significant (0.05 ) linear relationships are indicated by solid and dashed lines respectively.







Fig. 2



Fig. 3



Fig. 4



# Appendices

Appendix A. Comparisons (mean  $\pm$  SE) among four age and sex classes (AF: adult female, AM: adult male, JF: juvenile female, and JM: juvenile male), in the percent of time spent torpid (*torpid time*), average torpor bout length (*TBL*), and the average torpor bout minimum skin temperature ( $T_{skin-min}$ ) in three 20-day windows (early, mid- and late winter) within the low-food year (2005-2006) and the high-food year (2006-2007). Note the only significant difference (bold italic; p < 0.05 Wilcoxon-Mann-Whitney tests) between age and sex classes in mid-winter of the high-food year, with juvenile males expressing less torpor than juvenile females and adults. Sample sizes for every age and sex classes in each window in each year are indicated in parentheses with the number of individuals that expressed torpor given after the colon.

	Year	Age & sex	Torpid time	TBL	T <sub>skin-min</sub>
Window		$(n_{\text{total}}:n_{\text{torpor}})$	(%)	(day)	(°C)
· · ·	Low-food	AF (3:3)	82.5 ± 2.1	$3.2 \pm 0.3$	$8.7 \pm 0.4$
Early winter		AM (5:5)	$80.7 \pm 4.4$	$5.8 \pm 1.8$	$13.9 \pm 5.8$
		AF (9:2)	6.3 ± 4.8	$0.9\pm0.2$	$16.6 \pm 2.5$
	High-food	AM (4:1)	$1.4 \pm 1.4$	$0.4 \pm n/a$	17.9 ± n/a
		JF (5:0)	$0.0 \pm 0.0$	n/a	n/a
		JM (7:0)	$0.0 \pm 0.0$	n/a	n/a
Mid-winter	Low-food	AF (2:2)	$90.2 \pm 0.5$	$4.9 \pm 1.0$	$5.9 \pm 0.1$
		AM (3:3)	90.7 ± 1.5	$6.1 \pm 0.8$	$6.0 \pm 0.3$
	High-food	AF (7:6)	33.4±13.2	$1.0 \pm 0.3$	15.6 ± 3.1
		AM (4:3)	$20.5 \pm 12.6$	$0.9 \pm 0.3$	$14.0 \pm 2.1$

		JF (5:4)	$15.2 \pm 6.7$	$0.7 \pm 0.2$	$17.5 \pm 1.4$
		JM (6:1)	0.2 ± 0.2	$0.2 \pm n/a$	$22.0 \pm n/a$
	Low-food	AF (1:1)	$82.9 \pm n/a$	$4.3 \pm n/a$	$8.6 \pm n/a$
		AM (2:2)	$88.2 \pm 0.7$	$4.0 \pm 0.8$	8.6 ± 1.7
Late winter		AF (7:0)	$0.0 \pm 0.0$	n/a	n/a
	High-food	JF (2:0)	$0.0 \pm 0.0$	n/a	n/a
		JM (2:0)	$0.0 \pm 0.0$	n/a	n/a

Appendix B. Mixed model repeated measures analysis of  $T_{skin-min}$  for all observed torpor bouts including a random effect of individual and a fixed effect of year interacting with burrow soil temperature ( $T_{soil}$ ; average during a given torpor bout). a) Fit statistics with individual variance parameters pooled for both years or separated by year. The model with two individual variance components (separated by year) had better fit statistics with lower Akaike's and Bayesian Information Criteria (AIC and BIC respectively) values than the model with one individual variance component (pooled for both years). b) Tests of fixed effect parameters (year,  $T_{soil}$ , and year by  $T_{soil}$  interaction) with individual variance separated by year. There was no significant effect of window and a significant interaction effect between year and  $T_{soil}$  on torpor bout  $T_{skin-min}$ .

a)	Fit statistics			
Variance parameters	AIC	BIC		Variance parameter estimates
1 variance (pooled for	355.3	357.0	Pooled years	6.56
both years)				

2 variances (separated by	345.4	347.1	Low-food year	0.0
year)				
			High-food year	22.89
	4			

b)				
Fixed effect	Numerator df	Demonimator df	F-statistics	p
parameters				
Year	1	5.84	0.34	
T <sub>soil</sub>	1	78.5	247.85	
Year* T <sub>soil</sub>	1	78.5	54.59	< 0.001

## **GENERAL CONCLUSIONS**

This thesis examined burrow site selection and investigated fine-scale relationships between burrow microhabitats and individual variation in behaviour, winter torpor expression and energetics in a free-ranging population of eastern chipmunks. Woody debris availability best explained patterns of burrow microhabitat use; better than did burrow microhabitat features too spatially and temporally variable (local food availability) or too spatially invariant (hibernacula microclimate). Chipmunks occupying burrows surrounded by more woody debris are in a more complex, less risky microhabitat, with more low risk travel routes, and good quality refuges and perch sites, and should thus have improved survival and fitness, through direct anti-predator benefits and indirect influences on time and energy allocation.

Even though woody debris availability was most important to burrow microhabitat selection, burrows were associated with higher local density of seedproducing beech trees. This indicates that burrow microhabitat features related to local food availability might contribute to patterns of burrow use by affecting individual success through fine-scale influences on food acquisition and energetics. During the active season of a high tree-seed production year, chipmunks extensively consumed and hoarded tree-seeds by foraging on red maple seeds in mid-summer and on beech and sugar maple seeds from late-summer to late-autumn. Accordingly, low tree-seed production was associated with increased energy conservation needs, resulting in more intense winter torpor expression and reduced winter energy consumption. In contrast, with high tree-seed production, the need for conserving energy was reduced and resulted

in a drastic decrease in torpor expression and a more than 3-fold increase in total winter energy consumption.

Tree-seed abundance was associated with increased variability in torpor expression and energetics among hibernating chipmunks. This fine spatial scale individual variation was explained by density of seed-producing trees around individuals' burrow. Individuals with burrows surrounded by more seed-producing trees expressed less torpor than individuals with burrows surrounded by fewer seed-producing trees. The causal basis of this relationship is supported by the drastic reduction in torpor expression associated with hoard supplementation (French 2000, Humphries et al. 2003, Munro et al. 2005). The cascading effects of local resources on hoard accumulation and torpor expression generated a remarkable degree of intra-specific metabolic variability within a small forest stand. This provides evidences that fine-scale spatial and temporal heterogeneity in resources can translate into fine-scale spatial and temporal heterogeneity in consumers' expression of a plastic metabolic trait.

There is extensive intra-specific variation in metabolic trait expression (e.g., McLean and Speakman 2000, Thomas et al. 2001a, Speakman et al. 2004), including torpor (e.g., Young 1990, Wilz and Heldmaier 2002), and a growing body of evidences suggesting that some inter- and intra-population variability is habitat-related (Thomas et al. 2001b, Speakman et al. 2003, Lehmer and Biggins 2005, Lehmer et al. 2006, Careau et al. 2007). However, spatial and temporal habitat-related variation in metabolic trait expression is most often concealed rather than accounted for. In order to resolve ecological drivers and roles of metabolic variation, causes and consequences of habitatrelated metabolic variation needs to be considered at different spatial and taxonomic scales, with more individual traits and a more rigorous spatial and temporal quantification of resource- and climate-related habitat components.

In the present study system, causal relationships between habitat and metabolic trait expression still need to be resolved. In order to achieve that, further investigation of underlying mechanisms directly or indirectly liking habitat, behaviour, physiology, and energetics are required. A more spatially-oriented approach, at a larger spatial scale with a fine-resolution assessment of resource- and climate-related habitat components, integrating more individual traits, would contribute to the understanding of the complex causal chain between habitat and metabolic variation in naturally heterogeneous landscapes. In this case, laboratory studies on food quality, physiology and energetics could help disentangling some of the factors involved in habitat-related metabolic variation observed in nature.

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# APPENDIX I: ANIMAL USE PROTOCOL