SWARMING BEHAVIOUR AND FALL ROOST-USE OF LITTLE BROWN (*Myotis lucifugus*), AND NORTHERN LONG-EARED BATS (*Myotis septentrionalis*) IN NOVA SCOTIA, CANADA.

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Swarming Behaviour and Fall Roost-use of Little Brown (*Myotis lucifugus*), and Northern Long-eared Bats (*M. septentrionalis*) in Nova Scotia, Canada

By Amanda Lowe, August 2012

ABSTRACT

Temperate bats exhibit a poorly understood behaviour during the fall known as swarming, which has both survival and reproductive consequences. The goal of this project was to characterize how variation in physical conditions influence the movement patterns and resources used during the swarming season of the little brown bat (*Myotis lucifugus*), and the northern long-eared bat (*M. septentrionalis*) in Nova Scotia, Canada. The objectives were to: 1) investigate if the swarming behaviour of male little brown bats is influenced by individual differences in body condition and reproductive status; and 2) characterize the roosts used by both species during the season. Swarming behaviour was not influenced by body condition and reproductive status alone, although the data indicate that males of a lower body conditions do return more often, and swarm for longer durations. Roosts used during the swarming season had a predominantly south-western orientation unlike summer roosts, but were most often found in mid-late decay stage trees of conifer-dominated forests.

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Chapter 1

An Introduction to the Swarming Behaviour of Little Brown and Northern Long-eared Bats

An introduction to the swarming behaviour of temperate bats

To characterize the resources required for the reproduction and survival of individual animals (i.e., resources that increase fitness), an understanding of the seasonal variation in resource-use is necessary (Harris et al. 1990; Knight and Gutzwiller 1995:14). As energy demands and resource availability changes, so must behaviours (Schooley 1994; Szaro et al. 1990). Base-line data that identify the seasonal changes of a species' behaviour and requirements for reproduction and survival can provide natural-resource managers with knowledge to make informed decisions on how a species might be impacted by disturbances (Westman 1985). However, if the daily behaviour of an animal remains unknown during any particular season, estimating or measuring the impact of a disturbance during that season for that species remains difficult, if at all possible.

Temperate-zone animals alter their behaviour from season to season to facilitate the acquisition of energy as the abundance of available food varies accordingly among seasons. Some animals, like squirrels, beavers, mice, and some birds (e.g., jays), will stock-pile food (Aleksiuk 1970; Smith and Reichman 1984; O'Connell 1989), and significantly reduce the size of their home range during the winter (Shradin and Pillay 2006). Others migrate long distances to regions where food is more abundant (e.g., caribou (*Rangifer tarandus*), Cichowski 1989; passerines, Schaub and Jenni 2000; and insects like the Monarch butterfly (*Danus plexippus*), Urquhart and Urquhart 1978). But other animals will choose to wait out the seasonal lack of food by lowering their

metabolisms and entering into prolonged periods of inactivity, known as 'hibernation' (Buck and Barnes 2000).

One group of mammals known for their use of hibernation, are the insectivorous bats that remain in the temperate-zone year-round (Order Chiroptera: Vespertilionidae; Twente et al. 1985). Hibernating bats remain in a dormant state of torpor (Willis 2006), with their body temperatures at, or below, ambient temperature for approximately 12 days at a time without arousal (Twente et al. 1985; Humphries et al. 2006). The greatest source of energy expense and activity in hibernation occurs during and following arousals (Thomas et al. 1990); bats will groom themselves, re-hydrate, expel built-up urine and metabolic wastes (Speakman and Racey 1989; Thomas and Cloutier 1992), and sometimes copulate before re-entering their inactive state (Thomas et al. 1979; Barclay and Thomas 1979).

In contrast to the less-active winter, males and females live busy lives during the summer. Females of many species form maternity colonies of up to 1000's of individuals in which to have their young (Davis and Hitchcock 1965; Fenton 1970), roosting sometimes exclusively in tree cavities (Broders and Forbes 2004), while other species use man-made structures, such as attics and bell towers (Griffin 1940; Davis and Hitchcock 1965). Males, on the other hand, roost solely or in small groups (≤ 5, Kalcounis and Hecker 1996; Broders and Forbes 2004), and as best we know, bear none of the young-rearing responsibilities. While nights are spent foraging on seasonally abundant insects (Henry et al. 2002; Murray and Kurta 2004; Lacki et al. 2007), days be spent in a shallower and shorter form of hibernation known as 'torpor', to conserve energy (Kurta and Kunz 1988; Hamilton and Barclay 1994; Dietz and Kalko 2006).

Although many summer and winter behaviours of temperate bats have been studied since the 1940's (the little brown bat in particular, Griffin 1940; Twente 1955; Davis and Hitchcock 1965), there remains an under-studied season (McCracken and Wilkinson 2000). Fall is an important time of year during which year-round temperate bats must put on sufficient fat stores to sustain a winter spent in hibernation (Kunz et al. 1998; Cryan and Veilleux 2007:153). Fat storage is facilitated by seasonal changes in roosting behaviour to select cooler roosts that favour torpor and energy conservation (Ingersoll 2010), and the reduction of energy expending behaviours during the fall (Speakman and Rowland 1999). However, not all behaviours exhibited by bats during the fall seem to conserve energy.

Beginning in early August, and lasting until hibernation in October, bats partake in a behaviour known as *swarming* (Davis and Hitchcock 1965; Fenton 1969). During these 6-8 weeks, male and females of several species fly in and around the entrances of hibernacula. At some sites, thousands of individuals can swarm in a single night (Schowalter et al. 1979; Parsons and Jones 2003; Rivers et al. 2006). The swarms are typically male-biased (Fenton 1969; Schowalter 1980), especially in the early and late stages of this period (Davis and Hitchcock 1965; Cope and Humphrey 1977). New individuals join the swarm throughout the night (Davis and Hitchcock 1965; Hall and Brenner 1986), but may only swarm for < 2 hours (Fenton 1969), spending the day away from the swarming site (Thomas et al. 1979). Furthermore, based on mark-recapture studies, it seems that few bats return to a single swarming site within the same season (Fenton 1969, Parsons et al. 2003; Rivers et al. 2006), and < 16 % of bats captured during swarming will return to hibernate at the same site (Twente 1955; Fenton 1969; Whitaker

and Rissler 1992; Furmankiewicz 2008). There are records of bats visiting a different swarming site in the same season (Davis and Hitchcock 1965; Hall and Brenner 1968; Fenton 1969; Rivers et al. 2006; Glover and Altringham 2008; Suba et al. 2008). Whether making trips between a swarming site and summering sites, or visiting multiple sites within a single season, it is probable that swarming behaviour expends additional energy.

There are multiple hypotheses to explain swarming including that it functions as a method of familiarizing newly volant juveniles with the location of hibernation sites (Fenton 1969; Cope and Humphrey 1977; Veith et al. 2004). Researchers also acknowledge swarming as an opportunity to assess the conditions of the hibernacula (Davis and Hitchcock 1965; Furmankiewicz and Gorniak 2002), and the beginning of a mating season (McCracken and Wilkinson 2000; Parsons et al. 2003; Kerth et al. 2003). The hypothesized relationship between swarming and mating is supported by a physiological peak in sperm production of males (Gustafson and Damassa 1985; Entwistle et al. 1998), and the observation of mating behaviours during swarming season (Davis and Hitchcock 1965; Fenton 1969; Thomas et al. 1979; Kerth et al. 2003). However, the entirety of the mating season may not be limited to the fall (Watt and Fenton 1995); female and male bats of several species can store sperm for up to 7-8 months following either copulation, or the cessation of spermatogenesis respectfully, (Gustafson 1979; Racey 1972; Racey et al. 1987; Wai-Ping and Fenton 1988; Entwistle et al. 1998; McCracken and Wilkinson 2000), and copulations have been observed during mid-winter arousals from hibernation (Thomas et al. 1979; Wai-Ping and Fenton 1988). As a result, it is unclear which copulations contribute to the majority of successful

fertilizations, (Burland et al. 2001; Rivers et al. 2005; Senior et al. 2005), and the importance of swarming behaviour in reproduction.

With a limited understanding of the movements of bats during the swarming season, and even less of what motivates individual differences in bat swarming behaviours, wildlife managers remain unable to make informed decisions on how to minimize the impact of human disturbances to temperate bats during every season. Two European-based studies (Parsons and Jones 2003; Furmankiewicz 2008) and 3 North American studies (Wethington et al. 1996; Neubaum et al. 2006; Ingersoll et al. 2010) have investigated where bats roost during the fall swarming period using radio transmitters and telemetry tracking, but most species remain to be studied.

As such, the goal of this project was to investigate the fall behaviours of two North American bat species that stay in the temperate zone year-round: the little brown bat (*Myotis lucifugus* LeConte 1831) and the northern long-eared bat (*M. septentrionalis* Trouessart 1897). Chapter 2 highlights the complexity of swarming behaviours among the adult, male *M. lucifugus* that visit a swarming site in Rawdon, Nova Scotia. I investigate if the swarming behaviours of males reflect a trade-off between two activities presumed to positively influence fitness (i.e., fat storage for survival and swarming for reproduction). I hypothesize that males of a higher body condition and reproductive status will remain at, and closer to, a swarming site more than males of a lower body condition and reproductive status. In Chapter 3, I document the resources used for roosting by both males and females of *M. lucifugus* and *M. septentrionalis* during the swarming season, in Nova Scotia, Canada. Each of the above mentioned chapters are

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written as standalone manuscripts prepared for publication. In Chapter 4, I summarize the major findings of both Chapter 2 and 3, and highlight aspects of fall swarming behaviour among the study species that require further study as a result of the current findings.

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Chapter 2

Body condition of adult male little brown bats (*Myotis lucifugus*) explain little of the inter-individual variation of swarming behaviour in Nova Scotia, Canada

Body condition of adult male little brown bats (*Myotis lucifugus*) explain little of the inter-individual variation of swarming behaviour in Nova Scotia, Canada

By Amanda Lowe, August 2012

ABSTRACT

Fall is a busy transition period for insectivorous bats that survive the temperate winter in hibernation. In addition to storing fat, these bats partake in a poorly understood behaviour known as *swarming*; both of which have direct and competing fitness consequences. Swarming occurs over 6-8 weeks prior to the onset of hibernation at hibernacula. One hypothesis to explain this behaviour is courtship and copulation. This study investigates if inter-individual differences in the amount of stored fat (i.e., body condition) impacts reproductive status and influences the swarming behaviour of adult male *Myotis lucifugus* in Nova Scotia, Canada. It was predicted that bats with a high body condition would be reproductive and would remain at, and closer to, a swarming site than males of a lower body condition and reproductive status as these individuals must focus on fat storage. Males in an advanced state of reproduction had a significantly greater body condition than non-reproductive males. However, contrary to the prediction, males with a high body condition entered the hibernaculum significantly less often and spent significantly less total time swarming than males with a low body condition . There was no difference between radio-tagged bats of a low and high body condition in the probability of their relocation. Of the individuals that were relocated, there was also no difference in the distance they roosted from the swarming site. Variation in behaviour among males of different body condition suggests that one or more other factors have a significant influence on inter-individual variation in swarming behaviours.

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Introduction

The investigation of individual-animal behaviours is important because it permits inference on the variation of survival and reproduction, and thus natural selection (Kingsolver et al. 2001; Davies et al. 2012). Because of inter-individual variation in behaviour, group level averages may mask important variation (Thomas and Taylor 1990; Schooley 1994; Hayes and Jenkins 1997). Variation in behaviours among individuals can explain alternative strategies which maximize fitness, can be associated with other phenotypic differences among individuals, whereas averaged behaviours may result in spurious inferences (Bolnick et al. 2012).

Bats that overwinter in temperate areas must gain at least 2.3 grams of body fat to sustain 7-9 months of hibernation (Kunz et al. 1998). However, during the fall when this fat storage is occurring, bats also partake in a poorly-understood behaviour known as swarming, which has been described as pattern-less and dynamic (Davis and Hitchcock 1965; Fenton 1969; Furmankiewicz 2008). Swarming takes place at the entrances of hibernacula (Fenton 1969; Davis and Hitchcock 1956) where large mixed-sex groups of multiple bat species will congregate for a 6-8 week period before hibernation in October (Navo et al. 2000; Furmankiewicz and Gorniak 2002; Parsons et al. 2003; Glover and Altringham 2008; Suba et al. 2008). Some explanations for these seasonal congregations include information-transfer between adults and young-of-the-year about the location of hibernacula (Fenton 1969), and it permits a seasonal assessment of hibernacula to ensure suitable over-wintering conditions (Davis and Hitchcock 1965). Further, it is recognized that swarming is an important time for mating (Thomas et al. 1979; Racey and Entwistle 2000; Kerth et al. 2003; Parsons et al. 2003; Veith et al. 2004; Nicola et al. 2005; Rivers

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et al. 2005, 2006; Glover 2006; Furmankiewicz and Altringham 2007; Furmankiewicz 2008). In late-August and early-September, the reproductive condition of males of several *Myotis* species peak (Gustafson 1979; Gustafson and Damassa 1985; Encarnacao et al. 2004b), and there have been many observed copulations during this time (Fenton 1969; Thomas et al. 1979; Schowalter 1980).

Swarming activities have been documented in several European (Furmankiewicz and Gorniak 2002; Parsons et al. 2003; Rivers et al. 2006; Glover and Altringham 2008; Suba et al. 2008) and North American species (Davis and Hitchcock 1965; Fenton 1969; Thomas et al. 1979; Schowalter 1980; Whitaker and Rissler 1992), but the inter-individual variation in behaviour during swarming is not understood. It has been documented that *Myotis lucifugus* remain at a swarming site for ≤ 2 hours (Thomas et al. 1979; Fenton 1969) and data suggest that most bats rarely re-visit a swarming site within one season (Fenton 1969; Parsons et al. 2002; Rivers et al. 2006). However, some individuals do return to the swarming site more than once (Fenton 1969; Parsons and Jones 2003; Rivers et al. 2006; Glover and Altringham 2008). This results in a high hourly turnover of individuals in the swarms (Hall and Brenner 1968). Often, ≤ 20 % of swarming bats are recovered hibernating at the same site in the winter following their initial capture (Twente 1955; Fenton 1969; Whitaker and Rissler 1992; Furmankiewicz 2008). In fact, bats tagged at swarming sites are more likely to be re-located hibernating at the site 2-3 years after the initial capture (Davis and Hitchcock 1965; Hall and Brenner 1968; Parsons et al. 2003; Suba et al. 2008). Additionally, there are records of same-season movements between swarming sites (Davis and Hitchcock 1965; Hall and Brenner 1968; Fenton 1969; Rivers et al. 2006; Glover and Altringham 2008; Suba et al. 2008),

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Interpretation of these movement patterns is difficult, since there is little consistency in the documented movements of swarming bats, and a poor understanding of what influences the behaviour of bats during the fall (Parsons and Jones 2003).

As such, the goal of this project was to characterize the movement patterns of individual bats during the swarming season and to investigate factors that may explain inter- individual variation. Both fat storing and mating activities occur during the fall (Fenton 1969; Ewing et al. 1970; Speakman and Racey 1986; Kunz et al. 1998; Speakman and Rowland 1999; Ingersoll et al. 2010), but the trade-off between these competing activities (i.e., fat storage promoting winter-survival and courtship and copulation promoting reproduction) has not been quantified (Ingersoll et al. 2010). Evolutionary theory predicts that animals will allocate energy in a way that maximizes fitness (Krebs and Davies 1993). In situations where the costs associated with reproduction are high enough to significantly decrease an individual's over-winter survival, a strategy that reduces investment in reproduction may be adopted (Skogland 1986; Clutton-Brock 1991; Kuerca 1991). As such, individuals must balance activities that promote fat storing and reproduction during the fall such that fitness is maximized (Speakman 1997).

I investigated if inter-individual variation in swarming behaviour of adult male little brown bats (*Myotis lucifugus;* 6-9g) can be explained by variation in body condition (BC; an indicator of body fat content) and reproductive status (RS). The little brown bat is a long-lived species (≤ 30 years, Keen and Hitchcock 1980), with a wide distribution encompassing most of North America (Fenton and Barclay 1980). Individuals of this species roost in trees, rocks, or buildings during the summer and hibernate in caves and

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abandoned mines for the winter (Fenton and Barclay 1980). Males and females are mostly segregated until they re-unite at swarms (Fenton and Barclay 1980), where they can be captured in large numbers (Davis and Hitchcock 1965; Schowalter 1980; Whitaker and Rissler 1992). The mating system of this species is thought to be promiscuous (Thomas et al. 1979; Wai-ping and Fenton 1988), although some have found skewed reproductive success towards certain males (Racey et al. 1987; Watt and Fenton 1995).

A direct positive relationship between male bats with a high BC and a high RS has been identified for 2 species (*Plecotus auritus*, Speakman and Racey 1986; Entwistle et al. 1998; *Myotis daubentonii*, Encarnacao et al. 2006a). The first objective of this study was to quantify the relationship between the BC and RS of adult male little brown bats captured during the swarming season. The second objective was to assess the hypothesis that the residency of adult male *M. lucifugus* at a swarming site will be a function of the individual's BC and RS so that males with a high BC and RS will invest more in reproduction than males with a lower BC and RS. This hypothesis assumes that there is an energetic or other cost associated with travelling among swarming sites, and that a primary reason to visit a swarming site is to mate (Fenton 1969; Thomas et al. 1979; Racey and Entwistle 2000; Kerth et al. 2003; Parsons et al. 2003; Veith et al. 2004; Nicola et al. 2005; Rivers et al. 2005, 2006; Glover 2006; Furmankiewicz and Altringham 2007; Furmankiewicz 2008). Thus, to test this hypothesis, I predicted that males with a high BC and RS will 1) re-visit the hibernaculum more 2) swarm for longer durations, 3) roost closer to the swarming site, and 4) be more likely to be re-located after release than males of a lower BC and RS. Among polygynous animals, a male's reproductive success is limited by his access to reproductive females (Clutton-Brock

1991), driving males to secure as many copulations as possible to maximize fitness (Krebs and Davies 1993). Among bats, a male-biased sex-ratio at swarming sites and a higher occurrence of male re-captures during swarming (Parsons et al. 2003; Rivers et al. 2006), support the contention that male bats visit swarming sites on multiple occasions seeking additional copulations (Thomas et al. 1979; Kunz et al. 1998; Parsons et al 2003; Glover and Altringham 2008; Furmankiewicz 2008; Ingersoll et al. 2010). One might expect that those males attempting to mate with as many females as possible during the swarming season might make frequent trips to a swarming site (Furmankiewicz 2008), remain for a long time, and roost in areas close to the swarming site to reduce the costs of commuting (Parsons and Jones 2003; Furmankiewicz 2008). However, some males may not be able to afford the energetic costs of finding multiple mates, and returning to a swarming site multiple times (Thomas et al. 1979; Wai-Ping and Fenton 1988; Senior et al. 2005). Such behaviours may decrease the amount of fat an individual is able to store (Speakman 1997; Henry et al. 2002; Speakman 2007). As a result, bats with little stored fat (or a low BC) may minimize energetically-demanding behaviours (e.g., swarming), trading reproductive behaviours for those that maintain fat stores above a critical level, and increasing an individual's ability to survive the winter (Speakman and Racey 1989). Instead, low BC males might exhibit less energetically-costly behaviours that promote fat storage (e.g., foraging and torpor), thus increasing their probability of survival and future reproduction (Brodie 1989; Speakman and Rowland 1999; Racey and Entwistle 2000; Henry et al. 2002; Dietz and Kalko 2007; Speakman 2007).

Material and Methods

General Methods

Bats were caught during swarming (August-October, 2009-2011) at an abandoned gold mine in Rawdon, Nova Scotia (45.055740°; -63.839840°, Figure 1) using a harp trap (Austbat Research Equipment, Lower Plenty, Victoria, Australia). Only adult male *M. lucifugus* were used for this study. Adults were identified by the degree of epiphyseal-diaphyseal joint fusion (Kunz and Anthony 1982), and held for at least an hour before processing to allow stomach contents to be purged. Data collected from processed bats included: species, sex, age, mass (using a digital scale to the nearest 0.01g), the average of 3 forearm measurements (using a digital calliper to the nearest 0.01 mm), as well as a visually assigned reproductive status (Table 1). Every bat captured before 5 September was PIT-tagged (EID-ID 100 implantable transponders, EIDAP Inc., Sherwood Park, Alberta, Canada; Gibbons and Andrews 2004).

All statistical analyses were done using Minitab (Minitab Inc., State College, Pennsylvania, USA), with $\alpha = 0.05$. For any two-sample comparisons, t-tests were used in the case of normal data (Anderson-Darling test, $p \leq 0.05$), and the Mann-Whitney Wilcoxon test (W) was used for non-normal data.
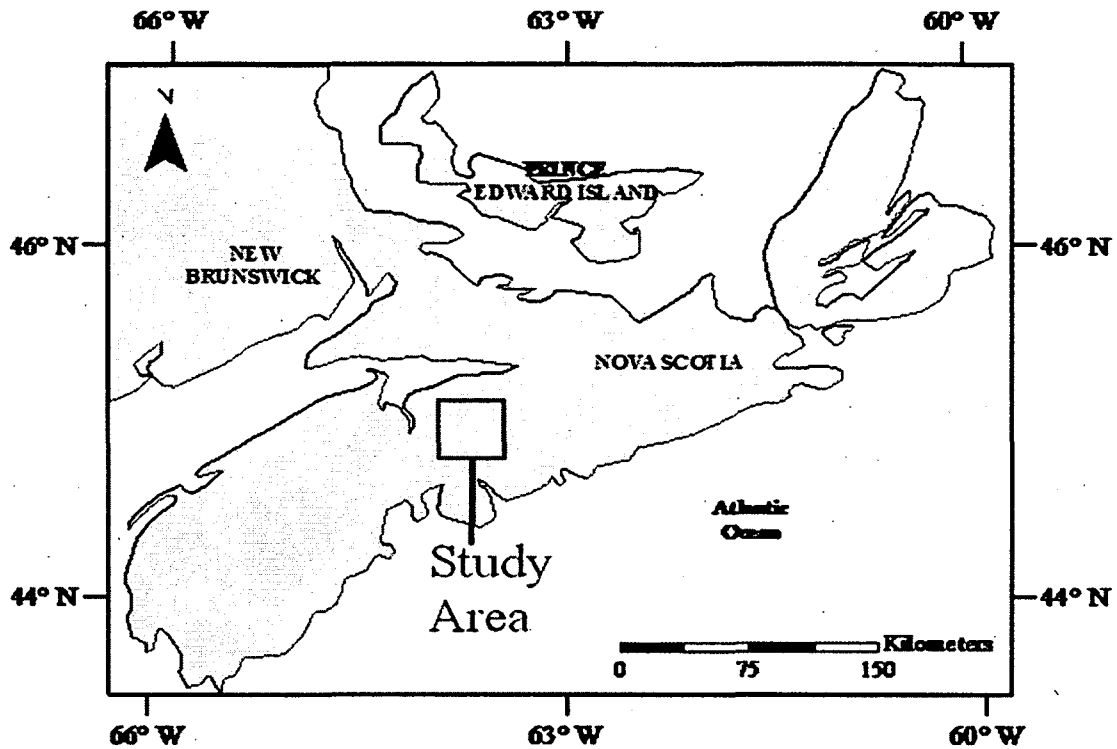
Figure 1. The approximate extent of the study are which was centered on a swarming site at an abandoned mine in Rawdon, Nova Scotia, 2009-2011.

Objective 1: the relationship between body condition and reproductive status

Body condition (BC) was used as an indicator of body fat (or potential energy, Kunz et al. 1998; Entwistle et al. 1998; Encarnacao et al. 2004a, 2006a; Senior et al. 2005; Jonasson and Willis 2011), and is measured as the ratio of body mass to forearm length (g/mm). Reproductive status (RS) was used as a metric for the stage of spermatogenesis and amount of sperm stored (Encarnacao et al. 2004b; Dietz and Kalko 2006). Reproductive status correlates positively with food intake (Damassa and Gustafson 1985), and has been found to vary between individuals depending on the quality of summer roost- and foraging-areas (Speakman and Racey 1986; Senior et al. 2005), or time spent in torpor (Kurta and Kunz 1988; Dietz and Kalko 2006). Adult *M.*

lucifugus begin spermatogenesis in the spring, and reach a peak (characterized by testes of maximum size) in late-summer (Gustafson 1979). Following this peak, matured spermatozoa pass from the testes into the epididymides for storage until copulation, resulting in the involution of the inactive testes, epididymal distension, and a displacement of pigmented granules in the tunica vaginalis (Racey 2009). For the current study, the reproductive status of adult *M. lucifugus* was visually gauged using physiological descriptions of each reproductive stage (Gustafson and Damassa 1985; Gustafson 1979) and an adapted version of the reproductive categories used by Speakman and Racey (1986; Table 1). Lowe A.J. was responsible for assessing RS for all bats. A one-way ANOVA, Tukey's post-hoc test, and a significance value of $\alpha \leq 0.05$ were used to determine if the BC of males vary among bats of different reproductive statuses.

Table 1. Description of the four categories of reproductive status visually assigned to adult male *M. lucifugus* caught during swarming at an abandoned gold mine in Rawdon, Nova Scotia (Aug-Sep 2011). *

Category:	Description
(1) Early reproduction	Testes: small to medium.
	Epididymides: 67-100% black, no sign of filling or distension.
(2) Partially reproductive	Testes: medium to large.
	Epididymides: 33-67% black, partially distended, less than 50% filled with sperm.
(3) Reproductive	Testes: large and swollen.
	Epididymides: 0-33% black, $\geq$ 50% distended, $\geq$ 50% filled, ballooning surface.
	Penis: may be swollen and purple.
(4) Post-reproductive	Testes: medium to small.
	Epididymides: 0-33% black, 100% distended, swollen or slightly deflated.
	Penis: swollen and purple.

* Not all criteria had to be met as described for a bat to be assigned the status, but testes and epididymides descriptors informed most classifications(adapted from Gustafson 1979, Speakman and Racey 1986, and Encarnacao et al. 2004b).

Objective 2: predicted behaviour of males with a high body condition

Standardizing body condition over time

An individual's BC is not static throughout the swarming season (Kunz et al. 1998), making analysis among individuals captured at different trapping events problematic. To account for this, the BC_0 of each male captured in 2011 was standardized to its predicted BC_s on 6 September, before comparing the behaviours of Objective 2.

The expected average BC of mid-swarming season ($\hat{BC}_{Sept\ 6}$) and population variability was estimated by modeling the change of BC over time from 211 adult *M. lucifugus* males captured at Rawdon during the 2009-2011 swarming seasons. Linear and polynomial functions were fitted to the data to determine which best explained the pattern

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of change in body condition over time for adult male *M. lucifugus,* for data from each of 2009-2011. If there was no significant inter-annual variation, the best-fit line using data (from all three years) was used to model the pattern of change in BC over the swarming season for adult males at Rawdon. Using this model, I predicted the standardized body condition of each bat. A residual for each male was then calculated by finding the difference between the observed BC of the male (***BC₀***) and the expected average BC for the date the bat was trapped ($\hat{BC}$ date; Equation 1 and 2). Following this, the residual value of each male was then used to return a standardized BC (***BC_s***) relative to the expected BC of mid-swarming ($\hat{BC}_{\text{Sept 6}}$; Equation 3).

Equation 1: $$\hat{BC}_{(date)} = \beta_0 + \beta_1(date) - \beta_2(date)^2$$

Equation 2: $$residual = BC_0 - (\hat{BC}_{date})$$

Equation 3: $$BC_s = residual + (\hat{BC}_{Sept6})$$

Assessing the extent of seasonal variation

To test for the possibility that individuals of different BC exhibit swarming behaviours only during a particular periods of the 6-8 week swarming season, I compared the BC_s of bats with re-located roosts, or who had re-visited the swarming site at least once, to those re-located or returning individuals prior to- and post- mid-swarming season (6 September), before combining the data for analysis. The total number of bats that returned to the swarming site, and the distances roosted from the swarming site prior to-

and post- 6 of September were also compared. The duration of swarming events were not tested due to an insufficient sample size.

Testing for the predicted behaviours of males with a high body condition

Adult *M. lucifugus* caught at the Rawdon swarming site were radio- and PIT-tagged to test predictions. All PIT-tagged adult males were used to test prediction 1. The number of re-visits made to the hibernaculum by these males were recorded via a PIT tag scanning antenna fixed at the entrance of the mine for 51 nights, from 31 July to 11 October, 2011. Not all bats that return to the swarming site were expected to enter the hibernaculum (Rivers et al. 2006). Thus the PIT-tag records are a conservative measure that reflects strictly those bats that enter the hibernaculum and not necessarily the number of bats that re-visit the swarming site. For each individual, any PIT tag records within the same night were counted as part of a single return to the hibernaculum. Quantitative comparisons were done by regressing BC against the proportion of nights that each bat entered the hibernaculum out of the total nights the bat carried a PIT tag. A proportion was used because some bats received a PIT tag later in the season than others. To further test if males of a high BC behave differently when at the swarming site, a two-tailed t-test was used to compare the BC of PIT-tagged males that entered the hibernaculum versus those that did not.

Males that had a high or low BC and RS, (relative to other males captured on the same night) were fitted with transmitters to track how long a bat would visit the swarming site, how far from the swarming site it would roost, and if it could be re-located within the search area the day following its initial capture and release. Transmitters that

were less than 5 % of the bats' body mass were glued to the mid-scapular region of males (Ag337 model; Lotek Wireless Inc, Newmarket, Ontario, Canada and LB-2N model; Holohil Systems limited, Carp, Ontario, Canada; ranging from 0.28-0.38 g). The duration that radio-tagged males spent swarming (i.e., prediction 2) was recorded with an automated radio receiver that was stationed at the swarming site. The receiver was fitted with 4 5-element yagi antennas (Lotek Wireless Inc., New Market, Ontario) fixed at 90 degree orientations in each of the cardinal directions from one another. Preliminary tests were conducted to verify that this setup was able to consistently detect transmitters ≤ 100 m from the presumed centre of the swarming site (the mine), in any direction. Any two records that were < 30 minutes apart were considered part of a single swarming event, and the time between the first record and the last was the duration of the swarming event. The total time that an individual spent at the site, as well as the average time of all swarming events per individual for the duration of the transmitter's battery life was plotted against BC_S using a linear regression.

Daily, ground-based searches over an area of approximately 314 km^2 centered on the swarming site were conducted for radio-tagged bats to locate day-roosts and calculate the distance each individual roosted from the swarming site, and if the bat remained within the search area the night following capture and release. Additionally, aerial searches were performed every 8-10 days over an approximate 707 km^2 search area, and any radio-tagged bats located from the air were verified from the ground. The location of all roosts were geo-referenced (eTrex Legend, Garmin International Inc., Olathe, Kansas, USA), and plotted using ArcMap 10 GIS software (Environmental Systems Research

Institute, Inc., Redlands, California). An ETGeo Wizard Point-distance tool (ET Spatial Techniques, Pretoria, South Africa) was used to calculate the distance of roosts from the swarming site, which was then plotted against BC_S for each individual using a linear regression. The average distance of roosts from the mine was used when plotting the distance of roosts from the swarming for male bats that had multiple roosts during the study. For males that were re-located at least once, the average standardized BC_S was compared to the BC_S of males that were never found during 2010 and 2011 using a two-tailed two-sample t-test.

Results

Objective 1: The relationship between body condition and reproductive status

In each year (2009-2011) the BC of adult males at the swarming site increased from an average of 0.19 in early August to an average of 0.26 in early September and then tapered off to approximately 0.23 in early October (Figure 2). Although the pattern of change in 2011 seems to be somewhat different, there were limited trapping nights in this year. Since there was little inter-annual variation, (Levene's test = 1.22, p = 0.224) the datasets of 2009 - 2011 were combined (n=211), and a second order polynomial was used to model the pattern of change in BC_0 throughout the swarming season: averageBC = - $0.00005(JD)^2$ + 0.00318(JD) + 0.18930 (R^2 = 0.26, df = 208, p ≤ 0.001; Figure 2d).
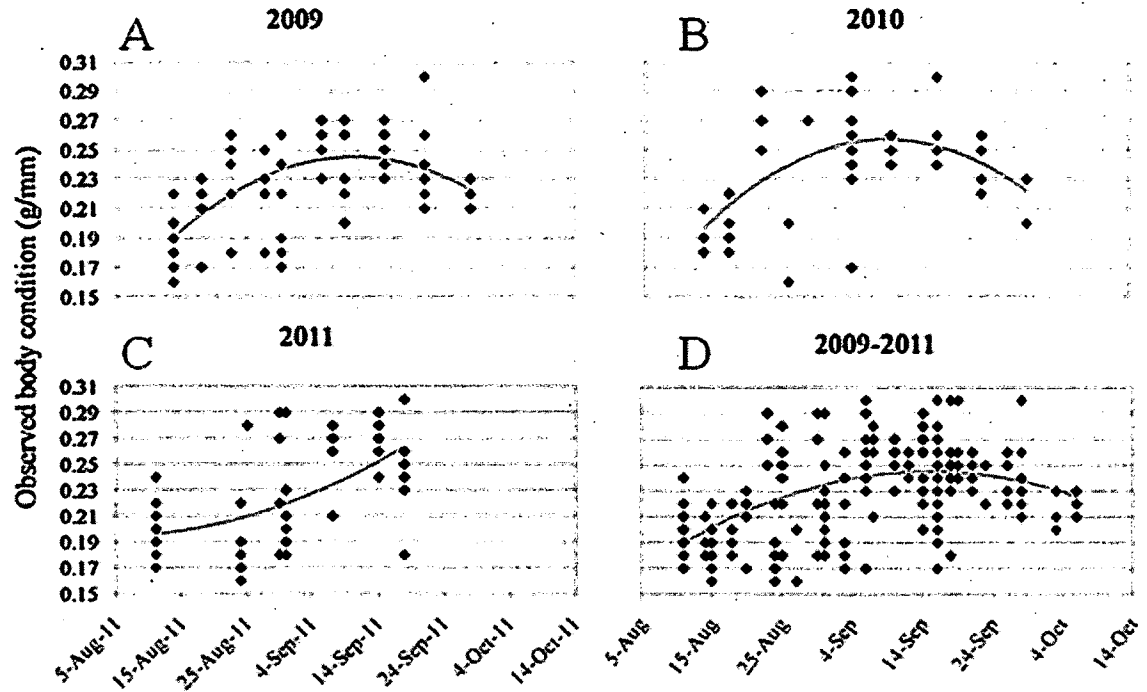
Figure 2 a-d. Body condition of individual adult male *M. lucifugus* caught during swarming at an abandoned gold mine in Rawdon, Nova Scotia, during 2009-2011 (n = 211), fitted with a second order polynomial best-fit-line.

The proportion of males in an advanced state of reproduction (i.e., category 4) that were caught increased as the swarming season progressed (y = 0.05JD - 1965; R^2 = 0.24, df = 60, p < 0.001). Because of a limited number of captures with RS categories 2 and 3, theses were combined for analysis. Males with a high RS (i.e., category 4) had significantly higher BC_0 values (average BC_0 = 0.28 ± 0.03SD), than males with a low RS (category 1 average BC_0 = 0.25 ± 0.03; ANOVA $F_{2,58}$ = 9.94, p < 0.001; Tukey HSD; Figure 3). Males in reproductive categories 2 and 3 did not have a significantly different BC_0 than males with either a high or low RS. BC_0 varied among RS categories as predicted, hence BC alone was used for all further analysis.
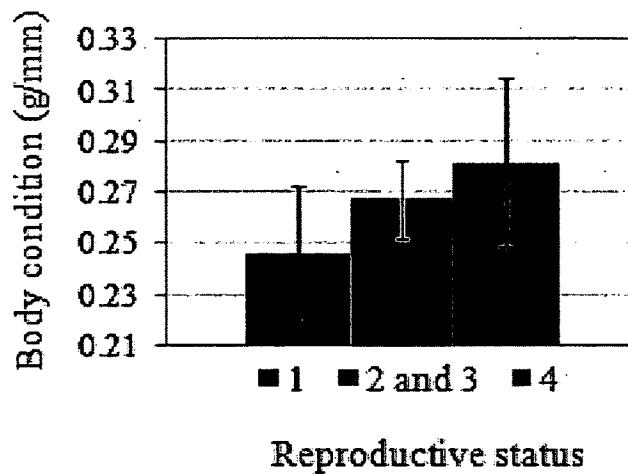
Figure 3.The average observed body condition of adult male *M. lucifugus* caught during swarming at an abandoned gold mine in Rawdon, Nova Scotia, during 2009-2011 (n = 61), assigned to each of the reproductive status categories.

Objective 2: Predicted behaviours of males with a high body condition

The BC_0 of all 2011 adult males ranged from 0.16-0.30 g/mm (mean ± SD: 0.22 ± 0.04) before standardization, to 0.20-0.34 g/mm (0.265 ± 0.033) after standardization. There was no evidence of seasonal variance in the swarming behaviours observed throughout the summer (all Ps > 0.05). Although the average BC of bats caught after the first week of September was less than prior, this was not significant (all Ps > 0.05). Further, the number of re-visits and the distance of roosts from the swarming site did not differ between early and late swarming season (all Ps > 0.05).

i) Number of re-visits to the hibernaculum

During 2011, 17 of 42 PIT-tagged bats (40.5 %) were recorded entering the hibernaculum between August and the end of September (2.30 ± 2.59 SD nights re-

visited/bat; range 0-16). Males carrying transmitters and PIT-tags returned to the

hibernaculum through the PIT tag antenna on only 65% of the nights re-visited (n = 8),

suggesting that not every bat that swarms will enter the hibernaculum. Of the bats that re-

visited the hibernaculum, BC_S did not explain the variation in number of revisits per

individual (R^2 = 0.04, df = 15, p = 0.461; Figure 4). However, the average BC_S (±SD) of

those bats that did re-visit the hibernaculum (0.24 ± 0.028; n = 17) were significantly less

than those that did not (0.26 ± 0.034; n = 25; two-tailed test; t = 2.39, df = 39, p = 0.022).
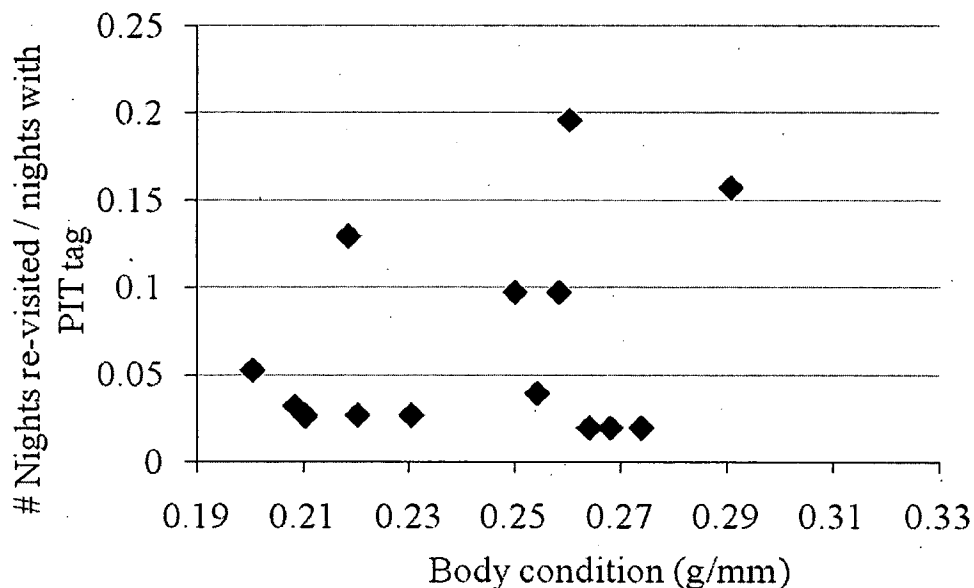
Figure 4. The proportion of nights a PIT tag carrying bat re-visited the swarming site and entered the hibernaculum (n =17/42) during 2011.

ii) Duration of swarming events

On average, an adult male remained at the swarming site for 24.6 minutes (± 43.8 SD, range 0.02-3.41 hrs). Of the 9 radio-tagged males that returned to swarm at least once (32 % of bats with transmitters, n = 35), 7 returned multiple times (range 2-12 re-visits). The duration of swarming events varied, even between visits made by the same individual. Contrary to the prediction, there is a negative relationship between body condition and the total time spent swarming (y= -60.2x + 18.2; R^2 = 0.53, df = 8, p = 0.016; Figure 5). The duration of each swarming event varied even among individuals, however the average duration spent swarming per individual was not explained by BC_s (y = -22.4x + 6.80; R^2 = 0.27, df =6, p = 0.133), despite there being a negative trend.
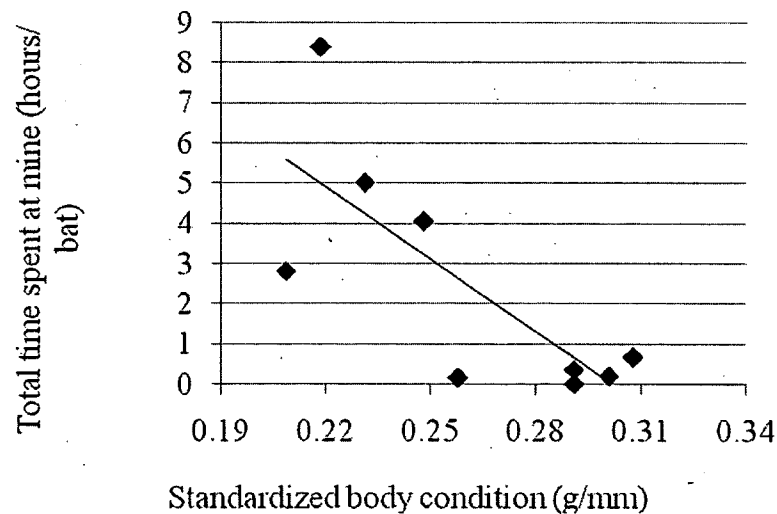
Figure 5. The total time an individual spent swarming in 2011 while carrying a functional transmitter (n = 9; R^2 = 0.53, df = 8, p = 0.016).

iii) Distance of roosts from the swarming site

Roosts were found up to 13.2 km from the swarming site (2.56 km ± 2.99 SD; Figure 6), but 75% of all re-located bats (n = 18) roosted within 2.5 km from the swarming site. The distance that a bat roosted from the swarming site decreased as BC_s increased, but the pattern was not significant (y = - 29.7x + 10.3; R^2 = 0.08, df =23, p = 0.09; Figure 7).
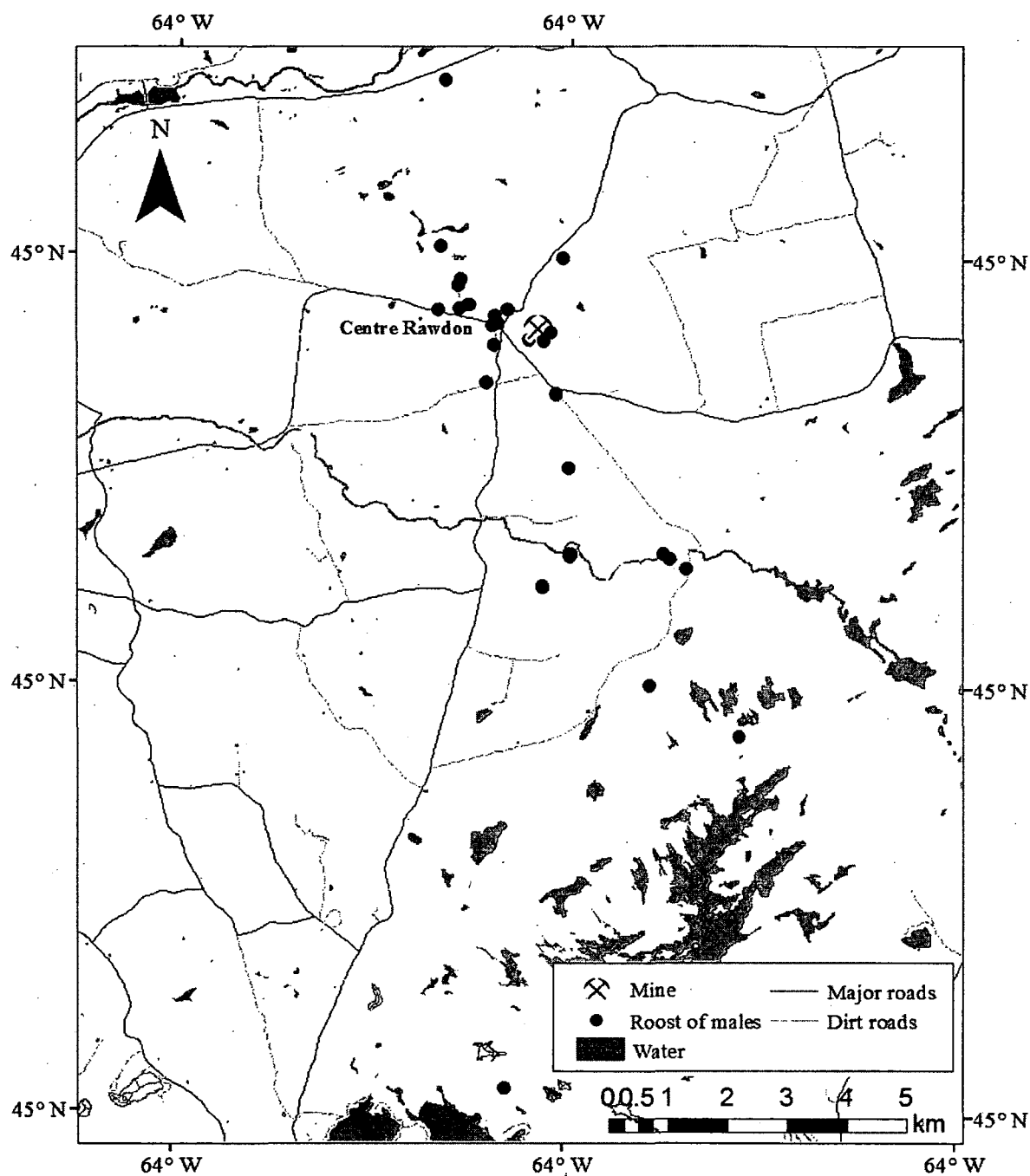
Figure 6. The locations of each roost in relation to the mine for the adult male *Myotis lucifugus* caught during the 2010-2011 swarming seasons in Rawdon, Nova Scotia.

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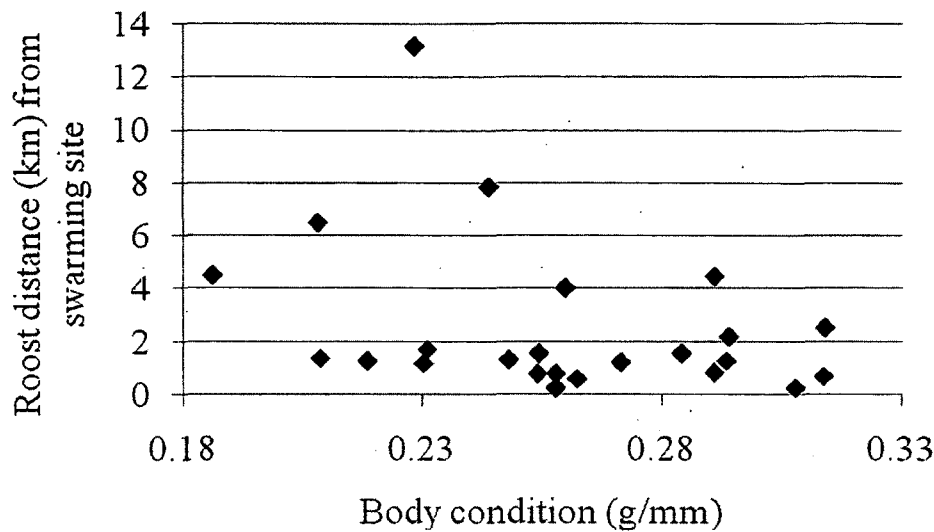
Figure 7. The distances of roosts of radio-tagged adult male *M. lucifugus* from the Rawdon swarming site in Nova Scotia, 2010-2011 (n = 24; R^2 = 0.08, df = 23, p = 0.09).

iv) Likelihood of relocation

The roosts of 24 radio-tagged bats (68.6 %) were re-located at least once during 2010 and 2011 (see Appendix 1). Re-located bats were tracked for 3.17 ± 3.97 (SD) days on average (range 0-13). Only 7 individuals were tracked for > 9 days. The average BC_S of bats with roosts that were re-located (0.26 ± 0.03 g/mm), was not significantly different than the BC_S of males that were not re-located (n = 11; 0.27 ± 0.04 g/mm; two-tailed, t = 0.69, df = 16, p = 0.503).

During the first two weeks of August, no bat was re-located within the search area for > 1 day, and only after 31 August was any bat found for ≥ 3 days. Males that had no record of returning to the swarming site (i.e., no automated receiver or PIT antenna data; n = 13), roosted in the search area for ≤ 3 days. Bats that were re-located in the search

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area for ≥ 3 days, returned in the evenings to swarm on 53 % of the days they were located (n = 6, via automated receiver; Appendix 1). In the 2011 season, I was not able to locate the roost of 4 of 11 males, but each of the 4 were later recorded at the swarming site via the automated receiver, or the PIT-recording antenna (recorded 11, 12, 17, and 34 nights post-release).

v) Re-captures

There were 4 PIT-tagged bats in this study that are at least 2 and 3 years old, according to their first capture record. Two of the re-captured bats (Bat 5059 and 5075) thought to be 3 years old, were also recorded entering the hibernaculum the most among surveyed bats in 2011 (Appendix 1). Both bats have at least 2 records of hibernation at the Rawdon gold mine, and 1 record of swarming in previous years. Bat 5075 used a group of roosts 4,445 m away from the swarming site for 13 consecutive days, during which it made 4 different visits to the swarming site.

Discussion

Body condition and reproductive status

In male *Myotis lucifugus,* body condition (BC) was positively related with reproductive status (RS), as was observed in two other species (Speakman and Racey 1986; Entwistle et al. 1998; Encarnacao et al. 2006a). Further, as the swarming season progressed the proportion of reproductive bats at the site increased (Gustafson 1979).

The increase in the average BC of males caught at the swarming site from the second week of August until the second week of September, suggests that this is the period of fat accumulation in Eastern Canada. The average increase in body mass of 2.3 g within one month for Rawdon bats is similar to the body mass changes observed in male *M. lucifugus* of New Mexico (Ewing et al. 1970), Vermont (Kunz et al. 1998), and Massachusetts (Townsend et al. 2008). A body mass increase to this extent would represent an increase in 25 % of a bat's entire body mass (for a bat with the average BC of 0.25, and a mass of 9.38 g in September), which is likely to contribute considerably to winter survival, as bats at latitudes similar to Quebec are thought to burn up to 29% of their entire body mass during 193 day hibernation (Thomas et al. 1990; Fenton 1970).

In north-temperate areas, several studies have found a decrease in the average body mass of bats at swarming sites after the second week of September, similar to the decreasing pattern observed among the Rawdon males (Schowalter 1980; Entwistle et al. 1998; Kunz et al. 1998; Townsend et al. 2007; Ingersoll 2010). There are at least two possible hypotheses to explain why the BC of males at swarming sites might decrease

during this time. First, it is possible that males with a high BC have already entered hibernation (Davis and Hitchcock 1965). As a result, less-fat individuals (Encarnacao et al. 2004b, 2006a) may dominate the captures during late September. Another is the potential inability to distinguish adults and juveniles (Davis and Hitchcock 1965; Thomas et al. 1979). For this reason, I emphasize that the model focuses on the average body condition of only those bats at the swarming site, not the average body condition of all local bats.

An alternative hypothesis would be that individuals experience a loss of body mass during the late swarming season. Schowalter (1980) recorded a decrease in the individual body masses of all 7 adult *M. lucifugus* re-captured between August and late September of the same swarming season. These males lost between 0.5-2.25 g of their body mass. An individual decrease in mass may be due to energy expenditure during swarming activities (Schowalter 1980), or due to the sub-optimal temperatures for torpor in hibernacula during early hibernation (Jonasson and Willis 2011).

Predicted behaviour of males with a high body condition

The hypothesis that the residency of an adult male *M. lucifugus* at a swarming site is a function of that individual's BC and RS was not supported. Body condition explained little of the variation in patterns of swarming among adult males. Since there is little understanding of how bats interact during swarming (Thomas et al. 1979), there are likely other factors influencing these patterns which were not accounted for in the current study; such as courtship or mating behaviours. This may explain why at least two of the predictions suggest that males with a low BC are present at swarming sites more often.

For instance, maybe males with a high BC and RS attract females sooner, and leave the swarming site right away for courtship and copulation. Additionally, male little brown bats with a high BC may have a competitive advantage over males with a low BC when attracting a mate (as in *Myotis daubentonii*, Senior et al. 2005). If so, less competitive bats (or males of a low BC) might have to spend more time at a swarming site to find receptive females, or potentially to find a torpid female located inside the mine (Thomas et al. 1979).

The documented variation among bats of a similar BC might support the idea that there are multiple strategies with which swarming bats seek mates. Having more fat stores, males of a high BC may be able to achieve reproductive success by choosing to either, 1) defer mating until hibernation, 2) swarm at multiple sites within the same season, or 3) stay and swarm at a single site. Kunz et al. (1998) speculated that male *M. lucifugus* with greater relative fat stores have a reproductive advantage over males with less stored fat, because they may be able to sustain mating during winter arousals (Thomas et al. 1979). Additionally, more fat stores may fuel visits to multiple swarming sites, without jeopardizing a bats' chances of winter survival. The small number of same-season movements recorded among swarming sites (Davis and Hitchcock 1956; Hall and Brenner 1968; Fenton 1969; Whitaker and Rissler 1992; Rivers et al. 2006; Glover and Altringham 2008; Suba et al. 2008) supports the idea that only some males choose to visit other swarming sites. If these three choices are available to males of a high BC (i.e., swarm less to facilitate winter-mating, leave and swarm elsewhere, or stay and swarm), the use of multiple strategies might explain why some Rawdon individuals spent < 1 hour swarming on average over 10 days, while others spent > 2 hours over a similar 10 day

period at the swarming site; or why some males with high BCs left the search area immediately (i.e., re-located ≤ 3 days), and others could be reliably re-located in a roosting area for at least 13 days.

Additionally, not all bats visiting a swarming site may be attempting to mate. Bats with less fat may have a reduced chance of survival in a hibernaculum with a variable temperature regime, because the amount of stored fat limits the amount of affordable arousals before starvation occurs (Humphries et al. 2006). Thus, investigating hibernacula conditions during swarming may be a priority for re-visiting males with a low BC. Furthermore, the cool temperatures of the hibernaculum might provide ideal conditions for torpor during the mid-late swarming season, which facilitates fat storage (Ewing et al. 1970; Humphries et al. 2006). It may be less of a necessity for males with a high BC to investigate the thermal conditions of a hibernaculum, because the greater amount of stored fat that they carry is sufficient to sustain winter hibernation, even in a hibernaculum with a variable temperature regime (Willis 2006).

Lastly, age may influence a bat's ability to store fat, and thus his swarming effort. If young bats have a limited amount of time or a reduced ability to store enough fat before winter (Davis and Hitchcock 1965), as well as a limited ability to reach sexual maturity during their first summer (Entwistle et al. 1998; Encarnacao et al. 2006b), they may be less likely to allocate energy toward fall swarming behaviours. Although I was unable to determine the exact age of re-captured bats relative to others swarming at the Rawdon hibernaculum, the current study had three re-captured bats whose date of original PIT-tagging makes them at least 3 years old. These 3 individuals had the highest number of re-visits to the mine during the 2011 swarming season (Appendix 3), but had

average BCs (i.e. between 0.25 and 0.29). Encarnacao et al. (2006b) found that age was positively correlated with BCs and RSs of male *M. daubentoni*, but the relationship between BC and age in *M. lucifugus* has not been characterized, and the number of re-captures in the current study was very small.

Although this study was limited to Rawdon, the patterns of behaviour observed here can be used to relate to other bat species worldwide. Swarming behaviours of Rawdon bats appear to be highly variable among individuals, but similar overall to some swarming patterns documented elsewhere. The percentage of re-located radio-tagged bats (i.e., 68.6 %) and bats that returned to the Rawdon swarming site at least once (40.5 %) were similar to the re-location success and banded bat re-capture numbers recorded in Europe and New England (61% re-location success, Parsons and Jones 2003; 42 % of fall banded-bats in hibernation, Davis and Hitchcock 1965). In addition, Rivers et al. (2006) also recorded bats entering the hibernaculum on < 65 % of re-visits made to swarming site. However, the average time spent at the swarming site in Rawdon was less than that estimated in Ontario (Fenton 1969), and some individuals swarmed for < 10 minutes, while others remained for > 3 hours. In addition, the duration of visits made by individuals to the swarming site was highly variable when comparing successive visits.

Speakman (1997) cautions that predicting the behaviours of small endothermic animals based on laboratory-determined physiological limits may result in predicted behaviours that are rarely exhibited in the field. He suggests that this is partly because animals operate at an optimal level of energy expenditure which is often well below their physiological limits, and that the optimal level varies with RS, and with season. The variation of swarming behaviours among the males of a high BC in the current study may

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support Speakman's (1997) suggestion that behaviours (such as swarming) are not performed at a level of maximum energy-expenditure, but within a large range of optimal swarming behaviours that vary individually, and from day-to-day. Furthermore, the ability of males with a high BC to copulate during hibernation (Barclay and Thomas 1979), and the longevity of bats (Keen and Hitchcock 1980) likely reduces the need of these animals to maximize their energy out-put during swarming, producing a wide range of swarming effort among bats of a similar BC.

To summarize, the movement patterns of bats during swarming do not appear to be influenced by BC and RS alone, but are likely a conglomeration of multiple strategies based partially on BC and RS and a balance between the costs and benefits of swarming and fat storing behaviours. It is likely that several different factors influence the individual variation in swarming behaviours and movements during the fall, some of which may include the use of a swarming site for purposes other than mating, whether or not competition among males exists (Senior et al. 2005), the location of additional swarming sites, the ability to reproduce in the winter, where the summer roosting area is located (Parsons and Jones 2003), the age of the bat (Encarnacao et al. 2006b), and what the bat did the night before in addition to BC and RS. To date, there is little literature on the energy demands experienced by bats during the swarming season, making the interpretation of movements at this time of year difficult. To further this understanding, it would be of interest to investigate the direct relationship between individual body mass loss and swarming activity. A larger sample size of re-captured bats within the same season would help clarify if an individual decrease in body mass during late-swarming, early-hibernation is common for *M. lucifugus*. Currently, passive monitoring techniques,

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(such as the PIT tag antenna used in this study), might provide the best method for gathering re-capture data on which bats will visit multiple swarming sites in a non-invasive way (Rigby et al. 2012). With such a broad spectrum of variation in swarming behaviours, further swarming studies at the individual-level will likely provide the pieces of information necessary for drawing the larger picture of temperate bat swarming patterns.

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Chapter 3

The fall roost-use of the Little Brown bat (*Myotis lucifugus*) and the Northern Long-eared bat (*M. septentrionalis*) during swarming in Nova Scotia, Canada

The fall roost-use of the Little Brown bat (*Myotis lucifugus*) and the Northern Long-eared bat (*M. septentrionalis*) during swarming in Nova Scotia, Canada

By Amanda Lowe, August 2012

ABSTRACT

Roosts are a vital resource for temperate bats (Order Chiroptera: Vespertilionidae) and despite the many studies characterizing the roost-use of bats, few have characterized roost-use during the fall swarming and migration period. This study characterizes the roost-use of the Little Brown bat (*Myotis lucifugus* LeConte 1831) and of the Northern Long-eared bat (*M. septentrionalis* Trouessart 1897) during this time, in Nova Scotia, Canada. All bats for this study were captured and released at a swarming site after being fitted with a radio-transmitter. Those that were re-located (31 of 43 bats) were within13 km of the capture site, and switched to roosts within 4 km of the tree used previously. Little Brown bats used several roost structures including trees, tree stumps, rocks and houses, but Northern Long-eared bats roosted only in trees or tree stumps. Although tree types used as roosts were highly variable (species, diameter at breast height, etc.), most roosts were on the south side of the tree. Despite the high variation in roost types used relative to expected based on summer roost selection, coniferous snags in mid- to late-decay stages (4-7) found in predominantly coniferous forests were also important roost-resources for these species during the fall. Preliminary results suggest that males and females of both species may not select roosts of similar characteristics, which may reflect the selection of micro-climates best suited to the energy demands associated with the behaviours typical of swarming season. This study provides a basis upon which future studies might be modeled to help determine how roost-resource use varies between the summer and the fall for temperate bat species, and whether resource-use differs between males and females.

Introduction

A major focus of conservation biology is management of human-induced degradation of the resources and conditions that determine the distribution and abundance of a species (i.e., habitat *sensu* Hall et al. 1997, Aubry et al. 2003). For forest-dwelling species, tree-harvesting and urbanization typically degrades a forest (Kohm and Franklin 1997) and may have dire consequences. For example, *Glaucomys sabrinus* (Shaw 1802; the Northern-flying squirrel) depends on the occurrence of deep cavities in standing snags for shelter during the winter (Bakker and Hastings 2002). However, where tree-harvesting is common, snag trees are removed because they are considered a safety hazard and provide little economic benefit (Weingand and Burditt 1992), reducing the roost-resources available for such cavity-dwelling species.

To limit disturbance, forest managers attempt to design and implement management plans that emulate a forest structure like that prior to disturbance (Gerson 1984; DeBell et al 1997; Guldin et al. 2007). However, the formation of effective management plans is dependent on a solid understanding of the resources and conditions that define the forest relevant to a species throughout a full annual cycle, during which required conditions may vary from one season to the next (Schooley 1994).

Other cavity dwelling-mammals that may be negatively impacted by cavity-roost disturbances include several species of temperate bat (Order Chiroptera; Safi and Kerth 2004; Boyles and Storm 2007). Sixteen out of 45 bat species found in North America rely on trees as roosts (Kunz and Lumsden 2003; Brigham 2007; Barclay and Kurta 2007). The maternity colonies in which the females of many species will rear their young are often located under loose bark, in hollow cavities, and in the cracking heart wood of

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standing dead trees, (i.e., snags), that provide shelter from the weather, protection from predators, and a microclimate that facilitates energy conservation (Brigham et al. 1997; Foster and Kurta 1999; Kerth et al. 2001; Kunz and Lumsden 2003). Solitary males will use shingling bark and splits in living trees and snags to find cool roosts that facilitate energy conservation via torpor (Vonhof and Barclay 1997; Ford et al. 2006). Because of the important role that trees play in the daily life of a bat, the loss of snags and other mature-forest structure may be responsible for the decline of several species (Altringham 1996; Neuweiler 2000; Evelyn et al. 2004). Knowing the roost-requirements of bats may allow forest managers to better predict how disturbances may impact populations (Gerson 1984; Fenton 1997; Miller et al. 2003).

Studies identifying roost-resources used by some bats during the summer (e.g., Humphrey 1975; Hamilton and Barclay 1994; Lewis 1995; Waldien and Hayes 2001; Kerth et al.2001; Henry et al. 2002; Owen et al. 2003; Dietz and Kalko 2006; Lausen and Barclay 2006; Broders et al. 2006; Garroway 2006; Willis and Brigham 2007), and winter (e.g., Pearson 1962; Fenton 1970; Whitaker and Rissler 1992; Veith et al. 2004; Furmankiewicz and Altringham 2007; Jonasson and Willis 2011), have greatly focused our understanding of temperate bat-ecology during these seasons. However, variation in roost-use according to seasonal changes in behaviour should also be accounted for if the goal is to develop effective forest management plans for wildlife (Wethington et al. 1996; Fenton 1997; Zimmerman and Glanz 2000; Broders and Forbes 2004; Cryan and Veilleux 2007).

For bats, there is a 6-8 week transition period between the summer and winter seasons when they participate in a behaviour called swarming (Fenton 1969). Both male

and female bats of several species congregate around the entrances of hibernacula for mating, from mid-August until the onset of hibernation in October (Thomas et al. 1979). Although swarming is a behaviour observed in several North American and European temperate-bat species (Davis and Hitchcock 1965; Hall and Brenner 1968; Schowalter 1980; Navo et al. 2002; Furmankiewicz and Gorniak 2002; Parsons and Jones 2003; Rivers et al. 2006), the primary function of this behaviour is not fully understood. Several hypotheses include the introduction of juveniles to suitable hibernacula (Fenton 1969; Humphrey and Cope 1976), and beginning of the mating season (Thomas et al. 1979; Veith et al. 2004; Furmankiewicz 2008). In addition, the roost-requirements of temperate bats during this period are also largely unknown (Cryan and Veilleux 2007, but see Neubaum et al. 2006; Ingersoll et al. 2010). Very few of the bats that swarm at a site will roost in the hibernacula during the day (Humphrey and Cope 1976), and even fewer will be re-captured at the swarming site within the same season (Hall and Brenner 1986; Rivers et al. 2006).

Cryan and Veilleux (2007) suggested that with the change of seasons and the weaning of young, the energy demands of females should be similar to those of males, resulting in similar roosting patterns. However, it is possible that males and females still experience different energy needs, resulting in the use of different roost-resources during the fall. Several authors have suggested that a male-biased sex ratio (Fenton 1969; Thomas et al. 1979), and a higher re-capture rate of males at swarming sites (Parsons et al. 2003), is due to males seeking multiple opportunities to mate with females (Cope and Humphrey 1977; Thomas et al. 1979; Kunz et al. 1998; Parsons et al 2003; Veith et al. 2004; Rivers et al. 2006; Furmankiewicz 2008; Glover and Altringham 2008; Ingersoll et

al. 2010). If male bats are swarming more than females, it is likely that males are spending less time foraging and storing fat, and thus experiencing different energy demands.

A small number of studies have documented the roost-resources used during the swarming season of two European species (Furmankiewicz 2008), and three North American species (Wethington et al. 1996; Neubaum et al. 2004; Ingersoll et al. 2010), but bat species common to eastern North America have yet to be studied. The objective of this study was to characterize some of the roost-resources of *Myotis lucifugus* LeConte 1831 (Little Brown bats; LBB) and *M. septentrionalis* Trouessart 1897 (Northern Long-eared bats; NLE) during the fall swarming period in Nova Scotia, Canada.

Methods

Field-site Description

The study area was centered on an abandoned gold mine that is used as a swarming site and hibernaculum in Rawdon, Nova Scotia, Canada (45°3'20.66" N; 63°50'23.42" W, see Figure 1), where bats were captured. The study region is characterized by rolling hills and ridge-lands of shale and slate, promoting shade-tolerant hardwoods when un-harvested (i.e., *Acer rubrum* and *Acer saccherum*, Red and Sugar Maples; *Betula alleghaniensis,* Yellow Birch; and *Fagus americana* American Beech). The Rawdon community was established in the late 1800's as its gold-mining population increased. Currently, lumber harvesting and farming are major industries in this region, resulting in a patchwork landscape of regenerating mixed-wood forests including *Picea arubens* (Red Spruce), *Tsuga canadensis* (Eastern Hemlock), *Pinus strobus* (White Pine), *Abies balsamea* (Balsam Fir), *A. rubrum* and *A. saccherum* (Red and Sugar Maples), *B. alleghaniensis* and *B. papyrifera* (White and Yellow Birch) (Davis and Browne 1997).
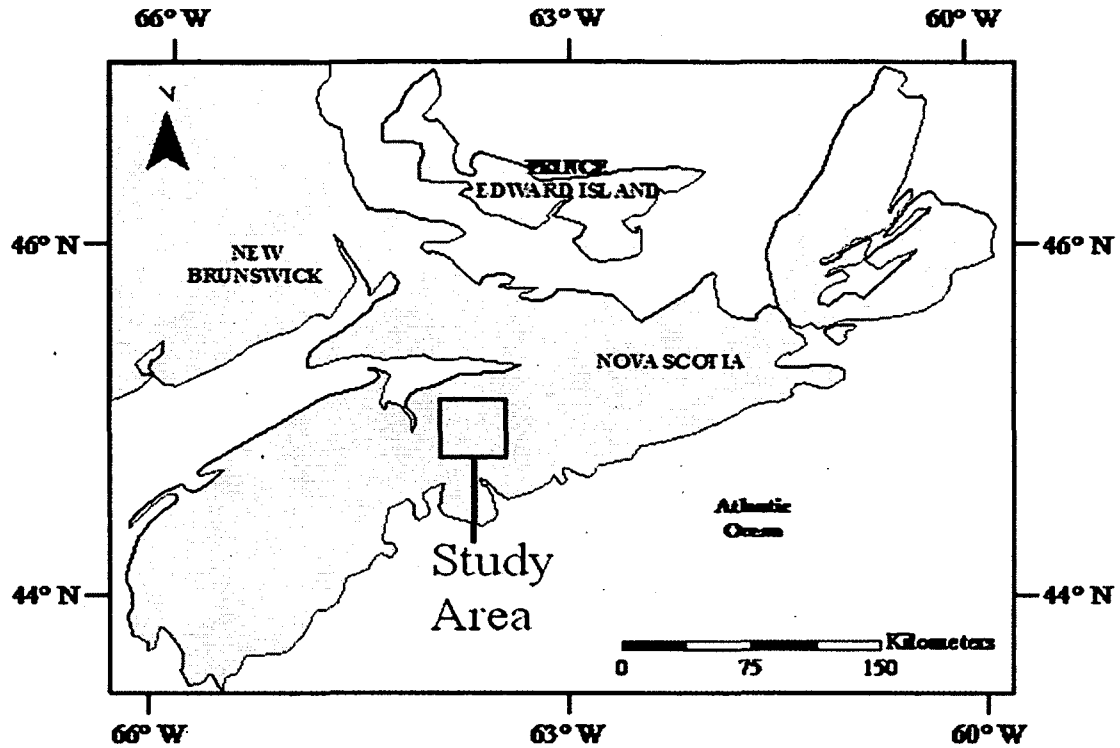
Figure 1.The location of the study area in Rawdon, Nova Scotia, Canada.

General capture and tracking methods

All bats were captured during swarming (i.e., early-August to late-September 2010-2011) using a harp trap (Austbat Research Equipment, Lower Plenty, Victoria, Australia) placed 2 m from the mine entrance. The sex and species of each bat was recorded, and the age of bats was estimated based on the degree of epiphyseal-joint fusion (Kunz and Anthony 1982). Male and female LBB (n=35 males, and n=1 female) and NLE (n=3 males, and n=4 females) were fitted with 0.28-0.42g radio-transmitters (model LB-2N; Holohil Systems limited, Carp, Ontario, Canada, and model Ag337; Lotek Wireless Inc, Newmarket, Ontario, Canada).

Roosts were searched for each day following release, until the transmitter battery had expired (approximately 8-12 days). Ground searches were conducted daily from a network of road-side telemetry stations (Appendix 1), within a 10 km radius from the swarming site. Aerial searches were performed every 8-10 days covering an approximated 700 km^2 area around the swarming site. A "homing-in" technique (Kenward 1987) was used to pin-point roosts with a radio-receiver (R2000 Scientific Receiver, Advances Telemetry Systems Inc., Isanti, Minnesota) and a three-element Yagi antenna (AF Antronics, Urbana, Illinois). The occupied roost tree was identified by triangulating the signal from at least three alternate directions to eliminate neighbouring possible trees.

Characterizing roost-use during swarming

For each re-located bat, we measured the characteristics of the roost and the surrounding forest within a 0.1 ha plot (17.8 m radius) in a way consistent with similar studies (e.g., Brigham et al. 1997; Broders and Forbes 2004; Jung et al. 2004). The roost characteristics measured included, roost-type (e.g., tree: bark, crevice; house: chimney, attic), tree species, the height of the roost, canopy and roost tree, and the diameter breast height (DBH), decay class, and percent canopy closure of all tree roosts. Percent canopy closure was also measured for rock roosts.

The height of roosts, roost trees, and average dominant canopy trees (calculated from five random trees of the upper canopy) were measured with a clinometer (to the nearest 0.5 m; model PM-5/1520; Suunto, Vantaa, Finland). Roost height relative to canopy height (Roost vs. Canopy) is the difference between the height of the dominant

canopy from the roost height (Menzel et al. 2002; Henderson and Broders 2008; Park and Broders 2012). Roost tree height relative to the canopy (Tree vs. Canopy) is calculated by taking the difference between the height of the canopy from the roost tree (Broders and Forbes 2004). The decay class (1-7) of tree roosts were assessed with criteria used by Park and Broders (2012), (adapted from Maser et al. 1979). The orientations of all roosts were determined using a compass. The average percent canopy closure from each of the cardinal directions at the base of the roost was taken by two field personnel independently using a spherical densitometer (Suunto).

To characterize roost plots, estimates of the number of deciduous and coniferous trees (any tree > 4 m tall) and the number of snags (decay class 2 and higher; Broders and Forbes 2004) were averaged between 2 independent counters. Counters recorded the number of coniferous and deciduous trees within the 0.1ha plot. Forest-type was determined by the percentage of trees within the 0.1 ha survey plot that were deciduous. Plots with ≤ 40% deciduous trees were considered "predominantly-coniferous" forest, while plots with ≥ 60% deciduous trees were considered "predominantly-deciduous" forests. Any plot with ≥40% but ≤60% deciduous trees was considered a "mixed-wood" forest. The number of snags over the total number of trees within 0.1 ha plot were used to determine the proportion of snags within the roost plot (Henderson and Broders 2008).

Roost locations were geo-referenced with a global positioning system (eTrex Legend, Garmin International Inc., Olathe, Kansas) and plotted with ArcMap GIS software (version 10.0, Environmental Systems Research Institute, Inc., Redlands, California). An ETGeo Wizard Point-distance tool (ET Spatial Techniques, Pretoria, South Africa) was used to calculate the distance of roosts from the swarming site. For

bats with multiple roosts, the average distance was used for analysis because most roosts were within a small (< 4 km) distance from previously used roosts.

Statistical methods

Any comparisons between roost characteristics were tested for normality (Anderson-Darling, $p \leq 0.05$), and compared using t-tests (when comparing two groups, and normal), and Mann-Whitney Wilcoxon (W, when either of the two groups were non-normally distributed). The Levene's test was used to compare the variance of measurements. Statistical tests and comparisons were conservatively used due to the small sample sizes of male and female Northern Long-eared bats. Oriana software (version 3.21, Kovach Computing Services, Anglesey, Wales) was used to perform circular stats when determining the prevalence of roost orientations (Glover and Altringham 2008), and the V test (a modified Rayleigh test for uniformity, Zar 1999: 626) was used to test if the orientations of the roosts were non-uniformly distributed around a mean direction (estimated from plotted data).

Results

Radio-transmitters were fitted to 35 male Little Brown bats (LBBs), 1 female LBB, 3 male Northern Long-eareds (NLE), and 4 female NLE. Of these, 10 male LBB and 1 female NLE were never re-located following release from the swarming site. Bats that were re-located were tracked for up to 13 days (4.38 ± 3.68 SD) until the 1st of October, during which 55 roosts were found (1 female and 42 male LBB roosts and 5 female and 7 male NLE roosts).

Male LBB were found roosting in 9 different tree species (Balsam Fir, Red Spruce, White Spruce (*Picea glauca*), White Pine, Eastern Hemlock, Yellow Birch, White Birch, Red Maple, Trembling Aspen (*Populus trembuloides*), and Large-toothed Aspen (*Populus grandidentata*)), but roosted in coniferous species most often (e.g., 41.6% of roosts were in Balsam Fir and Red Spruce, and 20.7% were in White Pine and Eastern Hemlock). The female LBB roosted in a White spruce snag. Male and female NLE roosted in both coniferous and deciduous trees, although 57% of roosts used by male NLE were in White Spruce snags and stumps.

All but one roost was re-located within 8 km of the swarming site (Figure 2), and bats that switched roosts (n=10) traveled ≤ 4 km (1.09 ± 1.21 SD) from any previous roost. Male LBB roosted anywhere from 225 - 13,154 m away from the swarming site, but were most often (79.2% of roosts) found within 2,500 m (Table 1). The roosts of NLE were evenly distributed over distances within 7,328 m from the swarming site (Levene's $p = 0.949$).
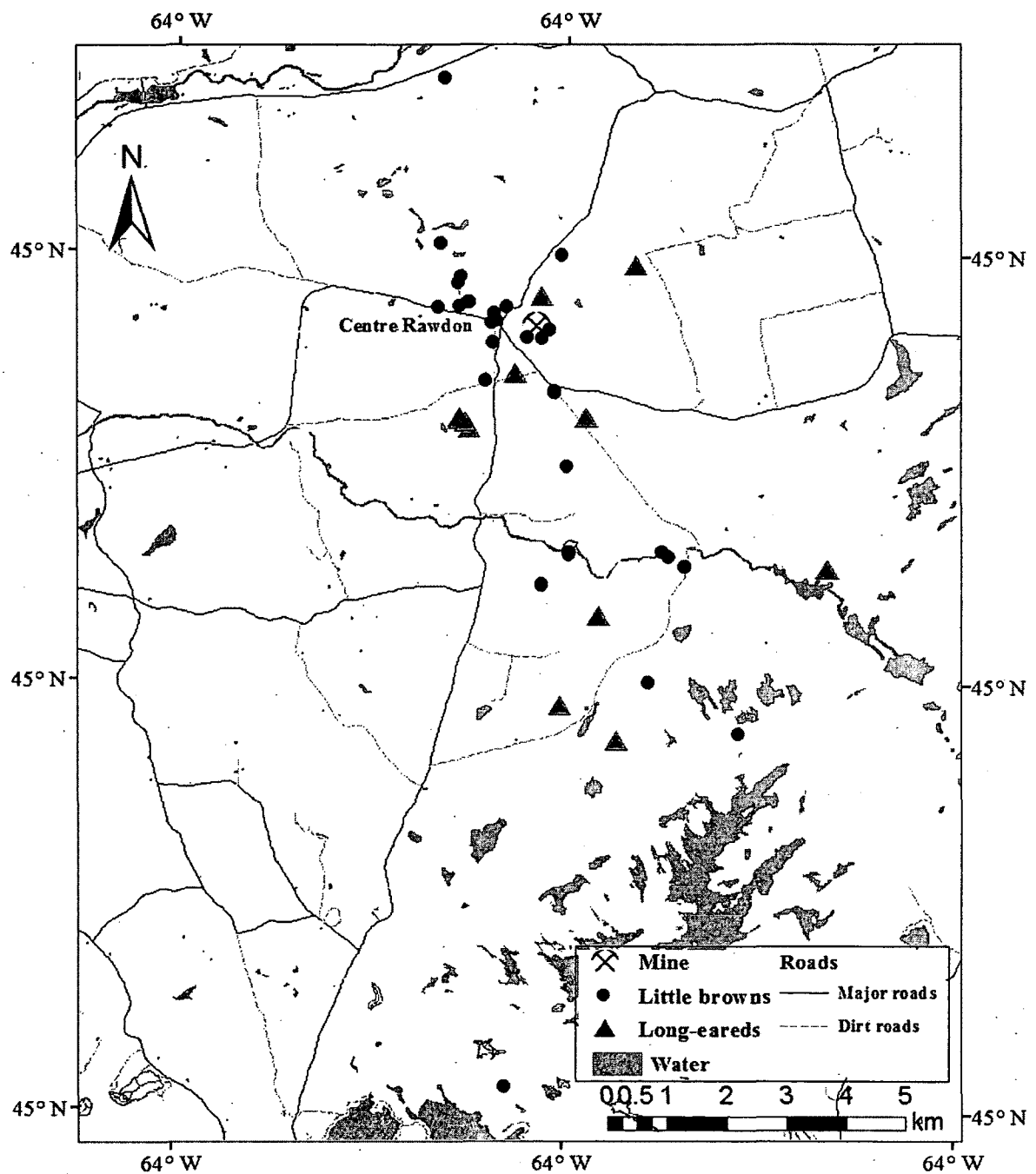
Figure 2. The roosts of all re-located bats found after release from the abandoned mine swarming site during the fall swarming seasons of 2010 and 2011 in Rawdon, Nova Scotia, Canada.

Roost-tree and roost-plot characteristics

Male LBB roosted in a variety of roosts including, trees (57 %), houses (26 %), rock crevices (9.5 %), and a stump (< 1 m above the ground, Table 1). House roosting bats were found in attics, chimneys, under tar-paper, and behind the shutters. Sixty-eight percent of tree-roosts used by male LBB (excluding stumps), were in trees as tall as, or taller than the surrounding canopy (range: 2 below - 10 m above the crown), while roosts were 2 m or more below the crown. The DBH of roost trees ranged from 13.97 - 64.77 cm, and were either found in trees that were dead or dying (i.e., decay class 6 or higher) or alive (i.e., decay class 1). Very few bats were found roosting in trees of mid-stages of decay (i.e., 2-5). Seventy-seven percent of males used a roost with canopy closure greater than 60 %. Roosts were regularly located in conifer-dominated or mixed-wood sites (ranging from 1 - 58.8 % deciduous) that had a small proportion of snag trees (i.e, $\leq$ 10 %). However, one male was found in a predominantly deciduous plot (93.5 %).

Table 1. The distance of roosts from the swarming site of roosts (m), the frequency of roost-types used (%), and the mean (standard deviation, SD) roost- and plot-characteristics for each bat group studied during the 2010-2011 fall swarming periods in Rawdon. "n" is the number of bats re-located, for which there may be multiple roosts. Roost characteristics are limited to tree roosts. Plot characteristic measurements include all tree, stump and rock roosts.

	Little Browns		Northern Long-eareds	
	Male (n = 24)	Female (n = 1)	Male (n = 3)	Female (n = 3)
Distance from swarming site (m)	2989 (2961)	283	3484 (2688)	4760.5 (3720)
Tree roosts	(n; %)	(n; %)	(n; %)	(n; %)
Bark	5; 11.9%	1	4; 57.1%	2; 40%
Crevice	4; 9.5%	-	-	2; 40%
Unknown	15; 35.7%	-	1	-
Rock roost	4; 9.5%	-	-	-
Stump roost	1	-	2; 28.6%	1
House roosts	11; 16.7%	-	-	-
Unknown roost structure	2; 4.7%	-	-	-
Roost-tree characteristics	(SD)		(SD)	(SD)
Roost height (m)	11.6 (6.3)	5.5	4.1 (4.0)	5.6 (2.1)
Canopy height (m)	15.1 (2.6)	14.4	8.9 (3.9)	10.9 (4.4)
Roost vs. Canopy (m)	-3.5 (5.7)	-8.9	-3.3 (3.8)	-5.3 (5.4)
Tree height (m)	16.5 (6.3)	6.3	8.8 (4.5)	12.1 (5.1)
Tree vs. Canopy (m)	0.4 (6.5)	-8.0	-0.1 (2.7)	1.2 (2.7)
DBH (cm)	30.5 (12.9)	16.1	16.4 (2.7)	25.8 (3.5)
Decay class	4.0 (2.5)	6.0	5.5 (1.0)	4.0 (2.5)
Plot characteristics (rock-roosts incl.)				
Canopy closure (mean %)	0.7 (0.2)	0.2	0.4 (0.2)	0.6 (0.1)
Forest type (% deciduous)	0.4 (0.2)	0.2	0.3 (0.2)	0.3 (0.3)
# Snag / 0.1 ha	10 (6)	21	25 (34)	13 (3)
# living trees / 0.1 ha	95 (59)	40	49 (42)	54 (24)
Total roosts characterized	42	1	7	5

There was a high degree of individual variability (see SD values, Table 1), as well as some inter- and intra-specific variability among the characteristics of roosts used by bats during swarming. NLE were never found roosting in man-made structures, or rocks (Table 1). Most males were found behind loose bark (57 %), while females were found in tree crevices and under loose bark. One NLE of each sex was also found roosting in a stump. Male and female NLE roosted in trees that were similar in height to the other trees within the plot (range: 2.5 below - 4 m above the canopy), and chose roosts 3 m or more below the crown of neighbouring trees. The average DBH of roost trees used by female NLE (ranging from 21.46 - 30.10 cm) were larger than the average DBH of trees roosted in by male NLE (ranging from 13.21 - 20.10 cm). There was a higher number of females found roosting in trees of an early decay stage than males (female range: 1-6; male range: 4-6). Male NLE used roosts with somewhat closed-canopies (ranging from 19-54 % closed). The roosts of female NLE had a higher canopy closure than those roosts used by males (41-65 % closed). Both male and female NLE roosted in conifer-dominated forests (ranging from 7- 42.9 % deciduous). There was only one bat (a female) that did not roost in a forest dominated by conifers. The proportion of snag trees within the plots of females were lower on average (ranging from 9- 42 %) than the proportion of snags in plots used by males (ranging from 8 - 68 %).

The orientations (mean $\pm$ 95% CI) of natural roosts (i.e., tree, rock and stump roosts) for both species and sexes were not randomly distributed, but rather had a strong south-west bias (V test expected mean = 225^{0}; V_{MYLU} male (mean) = 0.425, p = 0.004; V_{MYSE} male = 0.656, p = 0.01; V_{MYSE} female = 0.526, p = 0.049; Figure 3).
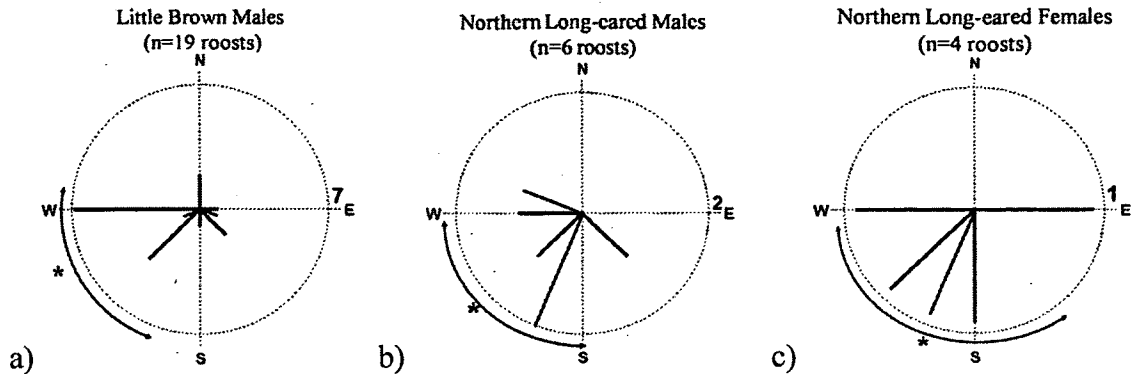
Figure 3. The mean (* ± 95% CI) orientation of all natural roosts (i.e., all roosts but houses) for a) Little Brown male (n = 19, mean = 235 ± 72.7°), b) Northern Long-eared male (n = 6, mean = 223 ± 52.5°), and c) Northern Long-eared female (n = 4, mean = 202 ± 60.8°) bats. Radius numbers on the right indicate the maximum number of bats with roosts in each direction, as represented by the lines.

Stumps used by the LBB male and the two NLE were each situated in areas that were clear-cut 4-5 years previous, and were ≤1.5 m (two were <30 cm above the ground). Stump roosts were free standing, with ample sun exposure and un-obstructed entrances. The entrances of rock crevices used by an adult and a juvenile male LBB were < 3 cm wide, and < 30 cm deep. The juvenile used a north-facing crevice 227 m upstream from the swarming site, in an area with very little sun-exposure, and large (≥ 20 m) mixed-wood trees (e.g., White Pine, Yellow Birch, Eastern Hemlock, White Ash). This roost was used for two successive days. The adult male however, was found using three different rock roosts along the steep banks (≥ -35 degrees) of a large river (≈ 7 m wide). One rock crevice in particular (the crevice with the most southern sun-exposure) was used on nine different occasions, but two Large-toothed Aspens were also used when not roosting in rocks.

Discussion

Many of the roost-resources used during the fall swarming season are similar to the resources used by Little Brown bats (LBBs) and Northern Long-eared bats (NLEs) during the summer, but there is a noted difference in the magnitude of distances traveled between the site of release and the roost, the orientation of roosts during the fall, the amount of variation in roost types. During the late summer and early fall bats store fat for winter (Kunz et al. 1998), complete spermatogenesis (Encarnacao et al. 2004, Dietz and Kalko 2006), and mate (Thomas et al. 1979). The intra-specific roost differences, and the variety of roost resources used during the fall may reflect the selection of roosts with specific micro-climates (Barclay and Kurta 2007), suited to the different energy demands associated with inter-individual variation in behaviour during this time.

Like the summer season, coniferous forests with trees in the mid- to late-decay stage (4-7) are important roost-resources during the fall (Broders and Forbes 2004, Menzel et al. 2002, Lacki et al. 2007). Bats switched between roosts within a small roosting area, similar to movements made between roosts during the summer, but traveled over larger distances between the site of release and the roosts used (Broders et al. 2006). Both species have been recorded travelling over 80 km when transitioning from summering areas to overwintering sites, and vice versa, during spring and winter (Griffin 1945, Davis and Hitchcock 1965). It is likely that the movements of swarming bats in Rawdon are representative of these seasonal flights from distant summering areas to the less numerous swarming sites, while summer movements between roosts and foraging

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areas are of a smaller magnitude, hence the large proportion (25%) of tagged bats that were never relocated.

The use of stumps and rocks by LBBs has been rarely documented, but it seems that these roosts are used in the fall just as they are in the summer (Fenton and Barclay 1980, Kalcounis and Hecker 1996, Park 2010). This study presents the first record of NLE bats using stumps. The suitability of stumps likely decreases with time as cleared-plots regenerate, and the stumps decay (Vonhof and Barclay 1997, Waldien 2000). Therefore, stump-use might be an opportunistic behaviour, used only during the fall as transient roosts, or as a result competition for roosts among a higher density of bats in areas surrounding the swarming site during this time of year. Little brown bats in this study have used rock-roosts located adjacent to rivers, similar to roosts used by Big Brown (*Eptesicus fuscus*) bats and NLEs during the summer (Jung et al. 2004, Lausen and Barclay 2003). The benefit of rock roosts adjacent to water may be the corridor that waterways provide for nightly commutes to foraging areas, or swarming sites. Lausen and Barclay (2002) found that crevices used by lactating Big Brown bats were 47 (± 4) cm deep, and had a stable temperature. However, the shallower rock-roosts used in the current study may have subjected bats to a more variable temperature regime (Chruszcz and Barclay 2002).

Intra-specific differences in roost-resources used during swarming

It has been reasoned that the differences in roost-use between males and females during the summer reflects the energy demands experienced by females when bearing young , that are not experienced by males (Foster and Kurta 1999, Cryan et al. 2001,

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Broders and Forbes 2004, Broders et al. 2006). Assuming the energy-demands associated with reproduction no longer limit the roost selection of females during fall, Cryan and Veilleux (2007) predicted that there would be little intra-specific difference in the roost-characteristics of bats during the swarming season. Alternatively, it may be reasonable to expect the fall roosts of males and females to be different because of different energy demands experienced by the sexes. Based on evolutionary theory (Krebs and Davies 1993), many authors have suggested that the male-biased sex-ratio at swarming sites (Cope and Humphrey 1977, Thomas et al. 1979), and the higher re-capture rate of males during swarming (Parsons et al. 2002) reflect the fact that males have more to gain from multiple copulations than females, and should thus swarm as much as possible (Kunz et al. 1998, Parsons and Jones 2003, Veith et al. 2004, Rivers et al. 2006, Furmankiewicz 2008, Glover and Altringham 2008, Ingersoll et al. 2010). Furthermore, males maintaining a high body temperature to complete spermatogenesis during the late-summer might also experience high energy demands (Entwistle et al. 1998). As such, swarming males or those completing spermatogenesis, likely use roosts of different micro-climates than those used by females during the swarming season.

Very few studies have characterized the summer roost-use of both female and male NLE. Comparable to summer studies on non-lactating bats (Garroway 2006), and separate male studies (Broders and Forbes 2004; Ford et al. 2006), the female NLEs tracked in Rawdon use larger roost trees (i.e., large DBH), with more clutter and less sun exposure (i.e., higher canopy closure) than males, and continue to travel longer distances than their male conspecifics (Broders et al. 2006); suggesting that the two sexes do not experience the same energy demands during swarming. However, as the sample sizes of

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Rawdon bats were small, further testing should be done to verify the noted findings. In Europe, male Brown Long-eared bats (*Plecotus auritus,* Furmankiewicz 2008), and Natterer's bats (*Myotis nattereri,* Parsons and Jones 2003) were also recorded roosting closer to the swarming site than their female conspecifics. The intra-specific difference in roost locations may be because females return to a familiar roosting- or foraging-area during the fall where search-effort is reduced (Hamilton and Barclay 1994, Parsons and Jones 2003, Furmankiewicz 2008), or because males reduce the costs of repeatedly commuting between roost and the swarming site by using near-by roosts (Furmankiewicz 2008). The use of coniferous trees and forests by females NLEs in Rawdon does not necessarily support the hypothesis proposed by Cryan and Veilleux (2007). Females predominantly use deciduous roosts during the summer (Lacki and Schwierjohann 2001; Broders and Forbes 2004, Foster and Kurta 1999, Menzel et al. 2002, Broders and Forbes 2004, Henderson and Broders 2008), but coniferous roosts and forests have been used by female NLEs during the summer (Sasse and Pekins 1996, Cryan et al. 2001, Lacki and Schwierjohann 2001, Garroway 2006, Park 2010). Without further study however, it will be difficult to determine if the use of coniferous roosts, or roosts within coniferous forests is a fall-behaviour, or if roosts in conifer-dominated forests is common during the summer in Rawdon.

Relationship between roost-characteristics and micro-climates

Variation in the roost characteristics and orientation of roosts used during swarming likely reflects the selection of roosts with different micro-climates suited to individual needs (Barclay and Kurta 2007). Larger roosts are thought to be better

insulated and more thermally stable, (Jung et al. 2004), while roosts with low canopy closure likely increases solar exposure and roost temperatures (Vonhof and Barclay 1996, Crampton and Barclay 1998, Garroway 2006). Males and females of both species used trees, rocks, and stump roosts with south-west facing exits, contrary to the south-east facing roosts used by these *Myotis* spp. in the summer (Jung et al. 2004). Roosts facing south-east in northern Ontario were thought to provide bats with heat from early morning sun-exposure, without getting too hot in the direct afternoon sun (Jung et al. 2004). North-west facing roosts received less direct solar exposure, and had considerably more stable temperatures than roosts in other orientations (Neubaum et al. 2006), while bats found in south-west facing roosts remained active throughout the day (Kalcounis and Hecker 1996), suggesting that roost temperatures were high and torpor was unfavourable. The south-western roosts used by both male *Myotis* spp. in Rawdon, (particularly those in stumps and small, highly exposed roost trees), may have had late-afternoon sun exposure and less stable temperature regimes (Vonhof and Barclay 1997), which subjected bats to temperature spikes late in the day (Kalcounis and Hecker 1996, Vonhof and Barclay 1997, Crampton and Barclay 1998). The late afternoon increase in the temperature of these roosts may have facilitated the passive-warming of torpid bats before engaging in swarming and foraging behaviours (Neubaum et al. 2006, Ingersoll et al. 2010), and facilitated the completion of spermatogenesis during the day (Kurta and Kunz 1988, Dietz and Kalko 2006). In contrast, roosts that received little solar exposure in rocks, or in larger trees with higher canopy closure (i.e., greater DBH and canopy closures) may have provided cooler, more stable micro-climates (Lausen and Barclay 2006, Menzel et al. 2002) for bats entering torpor to conserve energy, or store fat (Ingersoll et al. 2010).

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Inter-specific differences in roost-resources used during swarming

Little Brown bats still selected taller, larger trees characteristic of older forests as is documented during the summer (Owen et al. 2002, Broders and Forbes 2004), and unlike those used by NLEs. LBBs also roosted in man-made structures, while NLEs did not (Sasse and Pekins 1996, Foster and Kurta 1999). However, the amount of canopy closure of fall roosts was not as expected. It is thought that the NLE are often found in roosts of a higher canopy closure than that of LBB roosts during the summer (Broders and Forbes 2004, Foster and Kurta 1997), because the manoeuvrability of the former species allows it to exploit a dense and cluttered forest (Foster and Kurta 1999). But, simply because NLE bats can manoeuvre in an area with more clutter, does not imply that it is always beneficial to do so. The NLEs tracked during swarming in Rawdon used roosts in less cluttered, and more exposed forests than is typical of summer roosts (Sasse and Pekins 1996, Lacki and Schwierjohann 2001, Menzel et al. 2002, Owen et al. 2002, Jung et al. 2004, Broders and Forbes 2004). These smaller roosts with a higher solar exposure may have subjected bats to warmer temperatures, and a less stable micro-climate suitable for spermatogenesis (Kurta and Kunz 1988), or passive warming from torpor before engaging in nightly swarming behaviours.

Final conclusions

To date, studies investigating the roost-resources used by bats are predominantly conducted during the summer (Brigham 2007), but roost resources used during the highly active swarming season still require further investigation. The results of the current study suggest that there remain 4 distinct groups of bats (Little Brown male, Little Brown female, Northern Long-eared male, and Northern Long-eared female; Broders and Forbes 2004) that differ in their use of roost-resources during the fall. We also provide a basis upon which future studies might be modeled to further test the hypothesis of Cryan and Veilleux (2007), and help verify if the differences between summer and fall roost characteristics, orientations, and forest types documented in the current study are due to a seasonal or regional difference. Until such research is conducted, there remains an inability of conservation biologists and wildlife managers to understand and predict how *Myotis* spp. will respond to human-disturbance of the roost-resources used during each season of the year (Neubaum et al. 2006).

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Chapter 4

Swarming Behaviour and Fall Roost-Use:
Synthesis

The goal of this project was to investigate the fall behaviours of bats in Nova Scotia, eastern Canada during an under-studied time of the year; the fall swarming season. It is generally understood that a "swarming" bat is one who flies in front of a hibernaculum for only a short period of time (Davis and Hitchcock 1965; Fenton 1969), and may or may not enter the overwintering site (Rivers et al. 2006), partake in mating behaviour (Thomas et al. 1979), and potentially return on a different occasion (Hall and Brenner 1968; Parsons and Jones 2003; Glover and Altringham 2008). Other than this, our best understanding of the purpose of "swarming" is a collection of educated guesses, each of which need not be mutually exclusive. In addition to there being multiple hypotheses to explain these gatherings, there may also be multiple strategies with which a swarming individual can achieve any one of these purposes. As is, there remains a further need for studies investigating the activities of bats at, and outside of swarming areas, as this study has highlighted the complexity of behaviours exhibited by making the transition from active summer behaviours, to a less-active season of hibernation.

Swarming behaviour

Chapter 2 examined the variation in swarming behaviours of males. I showed that males with a high BC do not exhibit more swarming effort at a site than males of a low BC, but in fact enter the hibernaculum less, and spend less total time swarming than males of a low BC. However, there remains a large degree of variation in swarming behaviours, even among males of a similar BC suggesting that multiple factors in addition to the BC and RS may influence the behaviours of bats during the fall. As previously discussed, there may be multiple purposes to visiting a swarming site, resulting in some males visiting the entrance of a hibernaculum to re-evaluate the

conditions of the hibernacula (Fenton 1969), or to facilitate torpor and fat storage (Ingersoll et al. 2010), while other do not. Alternative factors influencing swarming patterns possibly include the competition for mates (Senior et al. 2005), and the use of different mating strategies which involve more time spent searching for an unoccupied female; perhaps even a torpid female inside the hibernaculum (Thomas et al. 1979; Barclay and Thomas 1979). Furthermore, the variation of swarming behaviours observed during the swarming season among males of a similar BC, (i.e., variation among the duration of time spent swarming, the distance roosted from the mine, and the re-location likelihood), alludes to the possibility that individuals may choose between multiple swarming strategies to secure a mate such as 1) investing the majority of a season swarming at a single site, 2) conservatively seeking mates while swarming during the fall and entering hibernation early to invest in winter-mating (Kunz et al. 1998), or 3) allocating as much fat as possible to fuel visits to multiple swarming sites within the same season.

Speakman (1997) demonstrates with several small mammal case-studies that there is an optimal range within which animals will exert energy; outside of which they will adapt their behaviours to favour energy conservation. He identifies the tendency of researchers to measure physiological capabilities that are extreme rather than optimal as a problem, biasing our ability to predict the behaviours of the study subjects outside of extreme conditions. For swarming bats, the optimal amount of energy output during swarming is likely a wide range of behaviour that changes throughout the season with BC change, and from day-to-day with weather, temperature, and food fluctuations, or simply with what the bat did the day before. Furthermore, due to the longevity of bats (Keen and

Hitchcock 1980) and the ability to copulate during hibernation (Gustafson 1979), maximizing the level of energy output during each swarming season may not be necessary, making the predictability of swarming behaviour difficult. Thus, it is important for future studies to consider the multitude of possible purposes of swarming, and the various strategies that individuals may use, even when swarming for the same purposes.

Fall roosting patterns

The amount of optimal-energy output is not necessarily similar for male and female bats during swarming. According to evolutionary theory, males have more to gain from multiple copulations than females, in terms of the number of resulting offspring that are possible (Krebs and Davies 1997). Male bats are notably more numerous in swarming captures (Furmankiewicz 2008), and also have a higher frequency of re-captures than females at swarming sites (Rivers et al. 2006; Furmankiewicz 2008), suggesting that their behaviour and associated energy demands are not the same as those experienced by the other sex, or by males during the summer. Furthermore, Dietz and Kalko (2007) documented a seasonal flip in the flight activity of male and female *M. daubentoni,* after females had weaned their young and males had begun the final stages of spermatogenesis, supporting the idea that the energy demands and behaviours of males and females need not be the same during the swarming season. Thus, as behaviour changes with seasons, determining the roost-resources used by males and females during the fall is necessary for managing forests in a way that is mindful of the resources used by bats throughout the year.

This initial characterization of roosts used by *Myotis lucifugus* and *M. septentrionalis* in Eastern Canada during the swarming season found that bats chose tall trees with large DBHs, and a mid-late decay stage in predominantly coniferous forests, as is observed during the summer (Kalcounis-Ruppell et al. 2005, Broders and Forbes 2004), with the exception of female *M. septentrionalis*. However, bats travelled larger distances, selected roosts with a south-westerly orientation during the fall, and intra-specific differences in the DBH and canopy closures of fall roosts were noted although the sample size was small.

Further studies investigating the fall roosts used by different temperate zone species, or *M. lucifugus* and *M. septentrionalis* of other geographic regions will help clarify if the selection of roosts with a south-westerly orientation is characteristic of fall roosting behaviour, and whether intra-specific differences in the use of roost resources also occur elsewhere in the temperate-zone, or among other temperate-species. Further studies on the roosting patterns of Rawdon bats during the summer would allow a clearer interpretation of the roost-resource use documented in this area during the fall. There exist few studies that investigate the use of natural roosts by male little browns during the summer (Kalcounis and Hecker 1996; Broders and Forbes 2004, Jung et al. 2004; Broders et al. 2006, Corning 2005; Park 2010), because the larger congregations of female little browns in buildings are often easier to locate and study (Kurta and Kunz 1988). Similarly, few summer studies of *M. lucifugus* roosting patterns have been conducted in Nova Scotia (Garroway 2006). Limited by the lack of studies conducted in Nova Scotia and the neighbouring Maritime provinces, it remains unclear how much of

the observed differences between summer and fall data are seasonally-influenced, and how much is simply due to a regional difference in roost-resource use.

Future work to be done

Swarming behaviours may be so individually-variable, that the generalized species- or population-level patterns may not be conceivable. If the number of bats caught at the Rawdon swarming site is equivalent to the capture success estimated in Europe (e.g. 10 %, Rivers et al. 2006), it is likely that a large portion of swarming bats were not caught, and further studies must be conducted to stitch together the larger picture of bat movements. Data that spans over multiple years, and that incorporates more re-capture data via PIT tag monitoring will likely help to achieve a good sample size, at which point behavioural patterns (if any exist) might be detectable. Other areas in need of study are the swarming behaviour of females, the energy demands experienced by bats during the fall, and the importance of swarming as a mating season. Advance in this understanding may equip researchers with the rationale needed to decipher the swarming behaviours of bats, including why some return to swarm at a single site multiple times, and why others leave immediately, or visits other swarming sites.

Finally, understanding the movements of bats during the fall transition period is an important step in understanding how White Nose syndrome might be spread (Foley et al. 2011). White nose syndrome is a disease that is transmitted from bat to bat during hibernation, killing over 1 million bats of several species since 2006 (Frick et al. 2010). Although symptoms of White nose syndrome subside from recovering bats during the summer season (Dobony et al. 2011), the visitation of bats to infected sites before leaving to visit another site during swarming (Davis and Hitchcock 1965; Hall and Brenner 1968;

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Fenton 1969; Rivers et al. 2006; Furmankiewicz 2008; Glover and Altringham 2008; Suba et al. 2008), has the potential to spread dormant spores from infected caves to other un-infected hibernacula. The extent and frequency of these movements have traditionally been unknown due to the difficulty of tracking bats over large distances and re-capturing transient bats at alternate sites, limiting our understanding of the spread of this traumatic disease. With the innovative implementation of the technologies mentioned above, future studies during this dynamic time of year may be able to detail more clearly how bats move during swarming, and provide an explanation for the dramatic spread of White nose syndrome.

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APPENDIX 1.

Re-visits to the Rawdon, Nova Scotia swarming site (# re-visits, via the PIT tag antenna and the automated receiver), and the number of days bats were known to be roosting within the search area (days located), for radio- and PIT-tagged adult male M. lucifugus in 2010 (n=7) and 2011 (n=28). The BC and RS were also recorded. The re-visits of males tracked in 2010 were not monitored, nor was RS data collected (?). A (?) also denotes individuals that were not re-located by ground or aerial search.

# re-visits (days located)	Date of transmitter	Record#	BC/RS	Distance of roost (m)
8 (13)	7-Sep-11	5075	0.29/ 4	4445.7
8 (10)	31-Aug-11	6791	0.22/ 1	1234.7
7 (10)	7-Sep-11	6796	0.23/ 4	1706.1
3 (9)	14-Sep-11	6799	0.26/ 1	762.5
3 (6)	18-Sep-11	6812	0.25/ 4	1294.4
1 (4)	31-Aug-11	6786	0.21/ 1	1363.9
0 (3)	24-Aug-11	6731	0.23/ 1	1174.1
0 (3)	14-Sep-11	6808	0.21/ 1	6465.1
1 (3)	7-Sep-11	6793	0.29/ 4	798.0
0 (2)	18-Sep-11	6813	0.26/ 4	227.8
0 (1)	11-Aug-11	6700	0.31/ 1	2495.8
0 (1)	11-Aug-11	6703	0.29/ 3	2162.2
0 (1)	11-Aug-11	6709	0.24/ 1	7824.4
0 (1)	11-Aug-11	6713	0.28/ 3	1526.5
0 (1)	11-Aug-11	6716	0.25/ 2	753.2
0 (1)	31-Aug-11	6790	0.23/ 1	13154.6
2 (1)	14-Sep-11	6809	0.31/ 3	256.0
2 (0)	7-Sep-11	6797	0.30/4	?
10 (0)	24-Aug-11	5059	0.26/3	?
1 (0)	24-Aug-11	6733	0.21/ 1	?
1 (0)	24-Aug-11	6745	0.20/ 1	?
0 (0)	25-Aug-11	6753	0.23/ 4	?
0 (0)	25-Aug-11	6754	0.32/ 4	?
0 (0)	18-Sep-11	6815	0.32/ 4	?
0 (0)	18-Sep-11	6818	0.27/ 4	?
0 (0)	18-Sep-11	6339	0.27/ 4	?
0 (0)	11-Aug-11	6714	0.26/ 1	?
0 (0)	31-Aug-11	6783	0.32/ 4	?
(3)	27-Aug-10	7639	0.19/?	4482.9

(9)	6-Sep-10	5663	0.25/?	1546.6
(10)	6-Sep-10	7854	0.26/?	3998.7
(1)	19-Sep-10	6250	0.26/?	595.0
(8)	19-Sep-10	7977	0.27/?	1200.8
(1)	30-Aug-10	6536	0.29/?	1270.3
(9)	6-Sep-10	4873	0.31/?	681.6

APPENDIX 2.
Telemetry stations about the swarming site used to daily search for bats.