FACTORS AFFECTING THE

DISTRIBUTION AND ROOST-SITE

SELECTION OF BATS ON THE ISLAND

OF NEWFOUNDLAND

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A Thesis Submitted to
Saint Mary's University, Halifax, Nova Scotia
in Partial Fulfillment of the Requirements for
the Degree of Master of Science in Applied Science

April, 2010, Halifax, Nova Scotia

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Date: April 23, 2010

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By Allysia C. Park

ABSTRACT

Ecological studies at the periphery of a species' distribution provide an opportunity to explore the limits of population viability under unique conditions. Research regarding specific factors that limit temperate bat distribution is lacking; therefore, the goal of this project was to characterize these factors for resident bats on the island of Newfoundland (NL) by species and sex (four bat groups in total). The first objective was to document the occurrence of little brown (*Myotis lucifugus*) and northern long-eared (*M. septentrionalis*) bats throughout NL, and relate their occurrence to stand and landscape factors. All bat groups were patchily distributed. *Myotis septentrionalis* were present in areas further east and north than previously documented but were not ubiquitous. Factors influencing distributional-limits were unique for each bat group, and included number of buildings and forest area in a landscape (for *M. septentrionalis* females and males, respectively); and number of snags and average tree diameter in a stand (for *M. lucifugus* females and males, respectively). The second objective was to compare female roost-site selection on NL to that of central areas in their North American distribution. Smaller and shorter softwood trees were common on NL, and frequently used as roosts. The final objective was to characterize roost-site selection of female *M. septentrionalis* at different reproductive stages (lactation and non-lactation). Sites used during the lactation period were within cavities of large diameter trees that maintained warm, stable microclimates.

Keywords: *Myotis lucifugus*, *M. septentrionalis*, Newfoundland, peripheral populations, roost-site selection, reproductive stage, AIC

April 23, 2010

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INTRODUCTION

Characterizing population dynamics in relation to resource availability and abiotic conditions permits inference regarding which factors are imperative to maintain viable populations (Holt and Keitt 2005, Bahn et al. 2006). Peripheral populations may contain unique, heritable traits that enable them to persist under conditions that individuals of conspecific populations might not be able to endure. Subsequently, if isolated, such selective pressures may lead to inter-population variation (e.g. morphologically, genetically, etc.) and, over time, speciation events (Lesica and Allendorf 1995). Therefore, peripheral populations promote evolutionary phenomenon and are important to consider when decisions are made for conservation and management purposes. Previous studies have focused on factors influencing species' limits (Kirkpatrick and Barton 1997, Case et al. 2005, Holt and Keitt 2005, Bahn et al. 2006); however, these studies are not common at northern extremes.

Though knowledge of roosting and foraging behaviours for temperate bats has increased significantly, little is known regarding specific resources and/or factors that limit species distribution (Parker et al. 1997, Lausen et al. 2008). Results of previous North American studies do however indicate that foraging and roosting conditions are the primary parameters that limit distribution (Humphrey 1975, Fenton 2003, Kunz and Lumsden 2003). Roosts themselves may be an essential resource that limits species distribution. Bats spend over half of their lifetime within roosts (Kunz and Fenton 2003), which provide protection from harsh weather conditions and predators (Fenton et al. 1994), and a location for thermoregulation, raising young (Hamilton and Barclay 1994, Crampton and Barclay 1998), and possibly socialization (Wilkinson 1992b, Jung et al. 2004). Forests provide roosts in

cavities, branches and foliage of trees (Kunz and Lumsden 2003). Selection of roosting areas by bats are thought to be determined by, among many other things, the presence of suitable foraging areas (Geggie and Fenton 1985, Crampton and Barclay 1998), which is based on specific foraging strategies of the bat species (Fenton and Bogdanowicz 2002). Forest type is thus an important factor to determine roost availability (Thomas 1988, Krusic et al. 1996, Crampton and Barclay 1998, Grindal and Brigham 1999, Kalcounis et al. 1999, Hutchinson and Lacki 2000, Patriquin and Barclay 2003, Broders and Forbes 2004, Ford et al. 2005, Loeb and O'Keefe 2006), and whether suitable foraging sites are present (Geggie and Fenton 1985, Furlonger et al. 1987) for forest-dependent bats.

The province of Newfoundland and Labrador, represents the Northeastern distributional limit of two species of North American bats: the northern long-eared bat (*Myotis septentrionalis*) and the little brown bat (*M. lucifugus*). Specifically, the island of Newfoundland (NL) contains biotic and abiotic attributes that are unique relative to other areas where these species have been studied previously. Thus, resource availability and the severity of abiotic factors on NL provide an excellent opportunity to examine peripheral populations of bats. Newfoundland and Labrador forests are softwood dominant and thirty-five percent of all trees in NL are small, shrub-like or bushy trees that do not exceed a height of eight meters (DNR 2008a). The province has a relatively low tree species diversity (20 species, versus 41 species found in adjacent Maritime Canada; Dept. of Natural Resources, DNR 2008a, b, respectively). This low diversity is likely due to the cool and moist climate, which slows nutrient cycling and soil drainage. The most dominant species, balsam fir (*Albies balsamea*; 49% of the total forest composition on NL; Singh 1977), thrives in wet

climates due to precipitation and fog (Campbell and Laroque 2007). The second most common species, black spruce (*Picea mariana*), constitutes approximately one third (34%) of the total forest composition (DNR 2008a). Abiotic conditions, such as low average summer inland temperatures of 13°C, proximity of the island to the foggiest waters in the world, and the high wind, make NL unique. The only previous study of bat biology in NL, recorded a low number of bats, and these bats were foraging in lower than typical temperatures (<10°C), in comparison to studies conducted in central areas of their range (Grindal 1999).

The distribution, life history and social structures of bats on the island of Newfoundland are unknown. Three species have been recorded, but one (the hoary bat, *Lasiurus cinereus*) is believed to be an extralimital record (Maunder 1988). *Myotis lucifugus* are known to exist across NL (van Zyll de Jong 1985), while the documented distribution of *M. septentrionalis* is restricted to the southwest portion (Caceres and Barclay 2000); however, systematic research has not been conducted outside of this area.

Myotis septentrionalis and *M. lucifugus* are sympatric throughout much of their distribution within North America, ranging from as far south as Wyoming to as far north as the Yukon (Fenton and Barclay 1980, Caceres and Barclay 2000). Both species differ in their foraging and roosting behaviours. *Myotis lucifugus* forage in a wide range of site types (LaVal et al. 1977), while *M. septentrionalis* appear to be forest specialists (Broders et al. 2003, Henderson and Broders 2008). Although both species forage in forested areas, only *M. septentrionalis* are obligate forest roosters (Caceres and Barclay 2000, Broders and Forbes 2004, Jung et al. 2004). However, there are rare instances where maternity colonies of *M. septentrionalis* have been found in human-made structures such as barns (Sasse and Perkins

1996, Foster and Kurta 1999, Henderson and Broders 2008). *Myotis lucifugus* typically form maternity colonies in buildings (Fenton and Barclay 1980, Anthony et al. 1981, Burnett and August 1981, Kalcounis and Hecker 1996, Riskin and Pybus 1998, Zimmerman and Glanz 2000, Broders and Forbes 2004), though they occasionally roost in natural structures as well (Fenton and Barclay 1980, Barclay and Cash 1985, Kalcounis and Hecker 1996). Both species display a sexual segregation during the summer such that males and non-reproductive females rarely roost with the maternity colony and remain solitary (Thomas 1988, Kunz and Lumsden 2003, Broders and Forbes 2004, Jung et al. 2004). For the purposes of this study, I therefore assumed that four distinct groups of bats exist in NL: male and female *M. septentrionalis*, and male and female *M. lucifugus*.

For the forest-dependent *M. septentrionalis*, certain characteristics of forest landscapes, stands and roost trees are essential for survival, especially for reproductive females, which have the greatest energy demands (Racey and Entwistle 2003); however, few studies characterize roosting patterns relative to reproductive stage. Females of most temperate bat species form maternity colonies that range from a few individuals to groups greater than 100 (Lewis 1993, Britzke et al. 2003, Garroway and Broders 2008). The presence and increasing size of colonies in cavity roosts, has been shown to positively influence roost temperature (Lewis 1993, Willis and Brigham 2007). Stable, warm microclimates within roosts promote normothermic (normal) body temperatures (Foster and Kurta 1999), offspring development during gestation, and milk production during lactation (Hamilton and Barclay 1994, Wilde et al. 1999, Kerth et al. 2001b, Jung et al. 2004). During gestation, selecting warm roosts reduces the amount of energy required to sustain normothermic body temperature, which

increases the amount of energy allocated towards rapid development of the fetus (Wilkinson 1992a, McLean and Speakman 1999, Kerth et al. 2001a, Kunz and Lumsden 2003). During lactation, the most energy intense period for both the mother and her offspring (Racey and Swift 1981, Kurta et al. 1989), females allocate the majority of energy reserves not spent on foraging towards milk production (Wilde et al. 1999).

The warmest roosts tend to be located in the tallest and largest diameter trees that are close to the canopy (Crampton and Barclay 1998, Kunz and Lumsden 2003). These attributes lead to warm, stable microclimates because roosts receive more solar radiation, house more individuals, and have greater isolative properties (Foster and Kurta 1999, Garroway and Broders 2008). Selecting warm roosts in regions of high latitudes seems important to ensure the rapid development of young, especially considering the shorter growing season at these latitudes (Racey 1988, Lewis 1993, Vonhof 1996, Cryan et al. 2000, Kerth et al. 2001b). Lacking the added stress of reproduction, males and non-reproductive females roost alone in cooler areas, and are able to enter torpor throughout the day to conserve energy (Barclay 1991, Hamilton and Barclay 1994, Lacki and Schwierjohann 2001, Jung et al. 2004, Carter and Feldhamer 2005, Ford et al. 2006). Because of variation in energy requirements during different reproductive stages, one can hypothesize that roost-site characteristics selected by females also vary to maximize energy efficiency and increase fitness. Since the most energy demanding period of reproduction occurs during lactation, I can predict that the most discrepant characteristics in roost-site selection arise when contrasting roosts used by lactating *M. septentrionalis* to those of non-lactating females (Garroway and Broders 2008).

The goal of this study was to characterize distribution-limiting factors of Newfoundland bats by species and sex (four bat groups in total), and relate these to areas where these species have been previously studied. Specifically, I hypothesized that because roosting and foraging requirements of each bat group varies, landscape- and stand-level factors that limit the distribution of each bat group on the island of Newfoundland would also vary. I also hypothesized that roost-site selection for females is a result of an interaction between reproductive condition, weather conditions and roost-site availability. I predicted that characteristics of roost-sites on the island of Newfoundland would differ from site characteristics used in the interior of their North American distribution. I also predicted that the characteristics of roost-sites associated with lactating *M. septentrionalis* would be distinguishable from those that were non-lactating, such that lactating females roost in sites with characteristics associated with warmer, more stable microclimates.

METHODOLOGY

Distribution of bat groups on the island of Newfoundland

This study occurred during the summers of 2008 and 2009. From June 02 to August 13, 2008, bats were sampled at fourteen forested areas across the island of Newfoundland (Figure 1). Each area contained at least one trail and one river. Trails were assumed to be a critical landscape feature for this study because they provide a linear element for commuting bats (Verboom and Huitema 1997, Law and Chidel 2002, Baxter et al. 2006, Downs and Racey 2006), and an ideal site for trapping bats using harp traps (Henderson et al. 2008).

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Research on Price Edward Island (P.E.I.), Canada, found rivers to be a key predictor of *M. septentrionalis* presence (Henderson et al. 2008), and they are also used as commuting corridors that provide drinking water and high prey concentrations (Racey and Swift 1985, Grindal et al. 1999, Downs and Racey 2006). These fourteen areas were pre-selected with no *a priori* knowledge of the presence of bats.
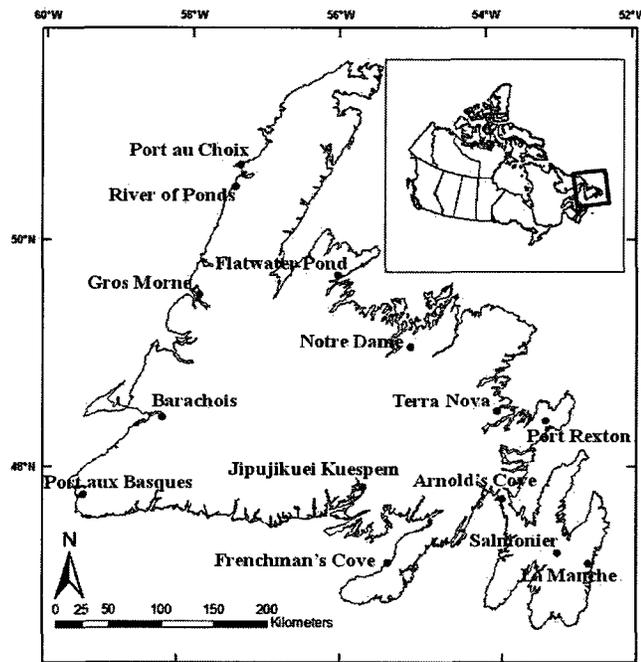
Figure 1: Fourteen areas across the island of Newfoundland sampled for the presence of forest-dwelling bats during the summer of 2008.

One to five forested trail locations were sampled within each area, for a total of 35 sampled locations. These 'locations' were the sampling units. To ensure that individual sampled locations were independent from each other and represented an independent statistical datum, all locations were at least 1000 m from one another. It was assumed that

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the resources available between sample locations separated by this distance were independent. To decrease the possibility of recording false absences, each sample location had two capture sites that were between 100 and 200 m apart, and each capture site was sampled on two nights. Therefore, four trap nights of sampling was conducted for each sampling unit (each of two capture sites were sampled for two nights for each location). Harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) were deployed at least a half hour before sunset and checked every half hour for three hours (Anthony et al. 1981, Barclay 1982, Hayes 1997, Wickramasinghe et al. 2004).

All bats captured were identified to species, weighed (with a pesola spring scale to the nearest 0.05 g), aged, sexed and noted for reproductive condition. The age of bats was determined by presence of cartilage in the metacarpal-phalangeal joint of the forth digit in their wing (Buchler 1980). Bats were identified as pregnant by carefully palpating the abdomen and as lactating via exposed skin around the nipple and/or presence of milk (Racey 1988). All bats were released at the site of capture after processing. On several occasions, only bat feces were found in the trap, which could not lead to a positive species or sex identification, therefore only bats processed by hand were considered for analysis. Bats are known to be less active when weather conditions are wet and cold, particularly reproductive females who have less tolerance for rainfall (Thomas 1988, Mills et al. 1996). Therefore there was no sampling on nights with heavy rain. The Saint Mary's Animal Care Committee, Parks Canada, and the Department of Environment and Conservation, NL approved methods of capturing and handling bats and/or provided permits to do so.

Following a thorough review of the literature, a series of three landscape- and two

stand- level metrics were selected to characterize the resources and conditions important to

M. septentrionalis and *M. lucifugus* biology for this study (Table 1). Each of these metrics was

quantified by analyzing Newfoundland Forest Inventory data (Department of Natural

Resources [DNR], 1999) and CanVec data (Centre for Topographic Information, NRCan,

ESS, 2007) using a Geographic Information System (GIS; version 9.1, ESRI, California,

USA) or by forest measurements taken in the field. For landscape level attributes, a two-

kilometer radius buffer was created (12.6 km^2) centered on the midpoint between both

capture sites of each sample location to ensure forest composition varied between sampling

locations (Henderson et al. 2008). This size buffer was chosen as this was found to be the

approximate flying distance of female northern long-eared and little brown bats (Broders et

al. 2006). In the two-kilometer radius buffer, total forest area was calculated by summing the

area (km^2) of polygons that were forest dominant. Proximity of the nearest river to the

capture site (in km) was calculated using the measure tool, and number of buildings was

determined by counting the identified points.

To characterize stand conditions, a 0.1 hectare (17.8 m) radius plot (Broders and

Forbes 2004) was used at both capture sites within a sampling location and averaged to

represent the entire sample unit. Originating at each capture site, a plot was centered at a

distance and direction determined from a list of random numbers. All plots were contained

within a distance of 100 m from the capture site to the forest interior. Tree diameter was

calculated by averaging the diameter at breast height (dbh; in cm) of five random, live trees.

Number of snags was determined by counting trees between decay classes four and seven (Table 2).

Weather was also expected to be an important abiotic variable that could significantly influence bat distribution for peripheral populations in NL; however, it was difficult to create a research design that would account for variability in temperature, precipitation and fog. Thus, historical data (temperature, number of days with rain or fog, etc.) were compiled from Environment Canada records for the 2008 period during hours sampled for bat group presence. This data were used in a descriptive manner to explore the potential impacts of weather on bat group presence in the vicinity where bats were captured. Weather data were not available for Jipujikuei Kuespem (47°53′N, 55°16′W), Lockston Path (48°22′N, 53°20′W), and Frenchman's Cove (47°13′N, 55°24′W; the southern-most area sampled).

Table 1: Landscape and forest level metrics measured at each trail location.

Variables
1. Average tree diameter in the 0.1 ha plot
2. Number of snags per 0.1 ha (Decay class of at least 3; Table 2)
3. Total forest area within a 2 km buffer
4. Proximity to the nearest river (km) in a 2 km buffer
5. Number of buildings within a 2 km buffer

Table 2: Decay class identification of trees adapted from Daniels et al. (1997).

Decay Class	Description
1	Live, healthy, no obvious defects
2	Declining live trees, browning needles
3	Recently dead, branches and twigs still present, little decay
4	Dead, no needles and only primary branches present, bark sloughing and detached
5	Dead, most branches and bark lost, top broken
6	Dead, no branches or bark remain, broken boles (height ± 10 m), boles hollow or crescent-shaped
7	Dead, stubs >3m height, heartwood soft, internal decay, outer shell may be hard

Analyses were performed on four bat groups; male and female *M. septentrionalis*, and male and female *M. lucifugus*. Logistic regression (Hosmer and Lemeshow 2000) was used to predict which forest parameters within both levels (landscape and stand) were related to the probability of presence of each bat group at a sample location. Bat groups present at a location were coded as 1, while those not present were coded as 0. Based on the variables measured and a review of the relevant literature of roosting and foraging behaviours, a set of nine *a priori* candidate models was created for all bat groups (Table 3). One area with two sampling locations (Frenchman's Cove) was not included in the analyses because data to record landscape variables were not available. Because only 33 forest plots were analyzed, all models were restricted to univariate or bivariate models to control for spurious effects and maintain parsimony (Hosmer and Lemeshow 2000, Burnham and Anderson 2002). Since logistic regression analysis are particularly sensitive to multicollinearity within models (Hosmer and Lemeshow 2000), a correlation matrix was constructed to ensure that no pair of the five independent variables contained within the model set were significantly correlated ($r \geq 0.7$; Perry and Thill 2007). To be conservative, any pair of variables with a correlation coefficient between or equal to 0.5 and 0.7 was not included within the same model.

Table 3: *A priori* candidate logistic regression models for predicting presence of four bat groups within forested trails of Newfoundland.

Model	Description
1	Tree diameter
2	Tree diameter, Number of snags
3	Number of snags
4	Proximity to river
5	Number of buildings
6	Total forest area
7	Total forest area, Proximity to river
8	Proximity to river, Number of snags
9	Proximity to river, Number of buildings

The candidate models were ranked by second order Akaike's Information Criterion (AIC_C) using SYSTAT 12 (SYSTAT software, Inc. 2001) to determine the most parsimonious model. AIC_C differences (Δ_i) were calculated for all models in the set to determine the amount of support in comparison to the best model. Akaike weight (w_i) was then calculated to determine the importance of each model, and its probability of being the best in the candidate set to fit the data. Models were ranked according to importance weights, and the top three that differentiated locations where each bat group was present were used for multimodel inference.

To identify which parameters in the top three models best differentiated locations selected by bat groups, and the direction of its effect, a model-averaging technique was used to give the parameter estimates (β_i) and unconditional standard errors (S.E.). Only parameters with estimates that were not overlapped by their respective standard errors were considered for making inferences. Model averaging reduces bias for obtaining parameter estimates when no one model in the candidate set clearly distinguishes itself as the best

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(Burnham and Anderson 2002). To determine magnitude of effect at the biological level, odds ratios (with 95% confidence intervals) were calculated as a measure of association for the likelihood that each parameter influenced presence of bat groups in a particular location (Hosmer and Lemeshow 2000). I predicted that proximity of the nearest river to capture site would be positively related to presence for all bat groups and therefore included it in more models than any other parameter (four out of nine).

Roost selection by female, forest-dependent Myotis septentrionalis

Year 2 (June 09 to August 11, 2009) field activities were conducted at a northerly area of NL (River of Ponds: 50°32′N, 57°24′W) where female *M. septentrionalis* were known to occur. Forested trails were sampled in an area managed for logging (approximately 30 km from the community of River of Ponds where females were caught in 2008), but trapping success was low. After ten unsuccessful trapping nights, sampling efforts were relocated to forested trails directly in the community. Sampling area relocation coincided with a shift in the reproductive season; therefore, only non-lactating females (four) were captured in the first sampling area. Adult, female *M. septentrionalis* were identified by reproductive condition and fitted with a radio-transmitter (0.42 g, model LB-2N Holohil Systems Ltd., Carp, Ont., Canada), to track them to roost sites. Females were assigned as lactating or non-lactating based on an assessment of reproductive status and not from the timing of the lactation period (the last day in which a pregnant bat was caught until the first day a juvenile was caught). Transmitters were placed dorsally between the shoulder blades, using surgical

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cement (Osto-Bond, Montreal Ostomy, Montreal, Quebec, Canada). Bats were retained for ten minutes to let the adhesive set, and then released at the capture site.

All bats were located on each subsequent day until the transmitter fell off or failed, using telemetry receivers (HR 2000 Osprey VHF Receiver, H.A.B.I.T. Research Limited, Victoria, British Columbia, Canada and R-1000; Communications Specialists Inc., Orange, California and R2000, Advanced Telemetry Systems Inc., Minnesota, USA) and 3-element yagi antennas (AF Antronics, Urbana, Illinois). Roost sites were georeferenced with a global positioning system (GPSMAP 76CSx, Garmin Ltd., Hampshire, UK). The average distance that individuals were tracked from their original capture site was calculated using ArcView GIS (version 9.3). Emergence counts were conducted at roost trees at dusk to estimate colony size (Broders and Forbes 2004). To determine if the number of roost-mates varied with reproductive condition, a two-sample Kruskal-Wallis test was performed on the non-normally distributed data. Ambient temperature (T_A) was measured every hour (for 18 days) using iButton® (±1 C. Dallas Semiconductor Corp., Dallas, Texas) data loggers located centrally within the study areas. Several data loggers were also placed in different roosts (range 6 t0 18 days) to measure and make an inference about variables affecting roost temperature (T_R) for bats in different stages of reproduction (i.e. lactating versus non-lactating).

To characterize differences in roost selection of female *M. septentrionalis* in NL to conspecific populations elsewhere in North America, a literature review was performed using the subject of roosts used by *M. septentrionalis*. Forest variables for each study, such as roost tree height and diameter, and the number of roost tree species, were summarized and

contrasted to results found for the River of Ponds study area. A series of two stand-, and

two local- level metrics were also selected from the review to characterize the resources and

conditions important to *M. septentrionalis* biology (Table 4). For the characterization of stand

conditions a 0.1 hectare (17.8 m) radius plot was sampled (Broders and Forbes 2004). Stand

plots were centered on roost-sites, and both live trees and snags were counted within them.

Local level attributes of roost trees were measured when no bats were known to be roosting

in the tree. Roost tree dbh was recorded in cm, and canopy height relative to roost height

was determined, using a clinometer (model PM-5/1520, Suunto, Finland), by subtracting the

height of the canopy (calculated from the average height of five random trees (in m)), from

the height of the roost. Since two areas were sampled for female northern long-eared bat

presence, variables measured at each scale had to be tested (using a 2-sample t-test for

normally distributed data), to ensure there were no significant differences, and that data from

both areas could be lumped.

Table 4: Stand- and local- level metrics measured at each roost location to differentiate roosts used
by lactating and non-lactating *M. septentrionalis* presence in River of Ponds, NL.

Variables
1. Number of live trees per 0.1 ha
2. Number of snags per 0.1 ha (Decay class ≥ 2; Table 2)
3. Roost tree diameter
4. Canopy height relative to roost height

Logistic regression (Hosmer and Lemeshow 2000) was used to predict which forest

parameters within both levels (local and stand) differentiated roost-sites used by lactating and

non-lactating females, as well as parameters that may be restricting the distribution of female

M. septentrionalis on Newfoundland. Roost trees used by lactating females were coded as 1,

while those used by non-lactating females were coded as 0. Based on the variables measured

and a review of the relevant literature of roosting behaviours for female *M. septentrionalis*, a set

of nine *a priori* candidate models were created (Table 5). Because only 36 roosts and their

respective stand plots were analyzed, all models were restricted to univariate or bivariate

models (Hosmer and Lemeshow 2000), with the exception of one model containing three

parameters. The candidate models and respective parameters were then analyzed in the same

fashion as in 2008 to reveal the best one(s) suited to differentiate lactating *M. septentrionalis*

presence from non-lactating females within an area or roost.

Table 5: *A priori* candidate logistic regression models for predicting the probability of presence of

female, lactating *Myotis septentrionalis* within River of Ponds, NL.

Model
1. Roost tree diameter, Canopy relative to roost
2. Roost tree diameter, Canopy relative to roost, Total number of live trees
3. Canopy relative to roost, Total number of live trees
4. Canopy relative to roost
5. Roost tree diameter
6. Roost tree diameter, Total number of snags
7. Total number of live trees
8. Total number of live trees, Total number of snags
9. Total number of snags

RESULTS

Distribution of bats on the island of Newfoundland

Fifty-one bats were captured at ten of the fourteen areas sampled to characterize the distribution of bats in 2008. Of these, 43.1% and 56.9% were *M. lucifugus*, and *M. septentrionalis*, respectively. For both species, females were captured more frequently than males (16 of the 22 *M. lucifugus* and 19 of the 29 *M. septentrionalis*). The only records for pregnant bats occurred on June 22 and July 04, 2008 for *M. septentrionalis*. The first occurrence of a lactating female was on July 07 (*M. septentrionalis*) at Terra Nova National Park (48°36´N, 53°58´W), and all other females of this species caught for the remainder of the field season continued showing signs of lactation. No juvenile *M. septentrionalis* were caught. The first occurrence of a lactating *M. lucifugus* was on July 18, followed by the first record of a juvenile bat on July 28. No other *M. lucifugus* were caught during the lactation period. Prior studies have controlled the sampling effort, by not trapping in conditions that are unfavourable for bat capture (i.e. heavy rain, strong winds or low temperatures (<10°C); Thomas 1988, Mills et al. 1996); however, in this study the average minimum temperature for a night when bats were caught was 9.9°C, and the minimum temperature was 4.6°C.

Both species appeared to be patchily distributed on NL. *Myotis septentrionalis* was found further east and north than previously documented (Figure 2). The most northerly area where both males and females were present occurred in River of Ponds (50°32´N, 57°24´W). There were no bats captured in the only area that was further north than River of Ponds (Port au Choix; 50°42´N, 57°22´W). *Myotis septentrionalis* was documented in three of the six southern-most areas sampled (two areas contained only males, while the third had

only females). Lockston Path was the eastern-most location where both sexes of *M. septentrionalis* were captured. *Myotis lucifugus* were trapped in only five of the fourteen areas but as a species were, like *M. septentrionalis*, also caught as far north as River of Ponds, however they were present further east than *M. septentrionalis* (Figure 2). Both sexes were trapped in Salmonier Nature Park (47°43′N, 53°47′W); however, they were not seen at the furthest eastern location, La Manche (47°10′N, 52°53′W).
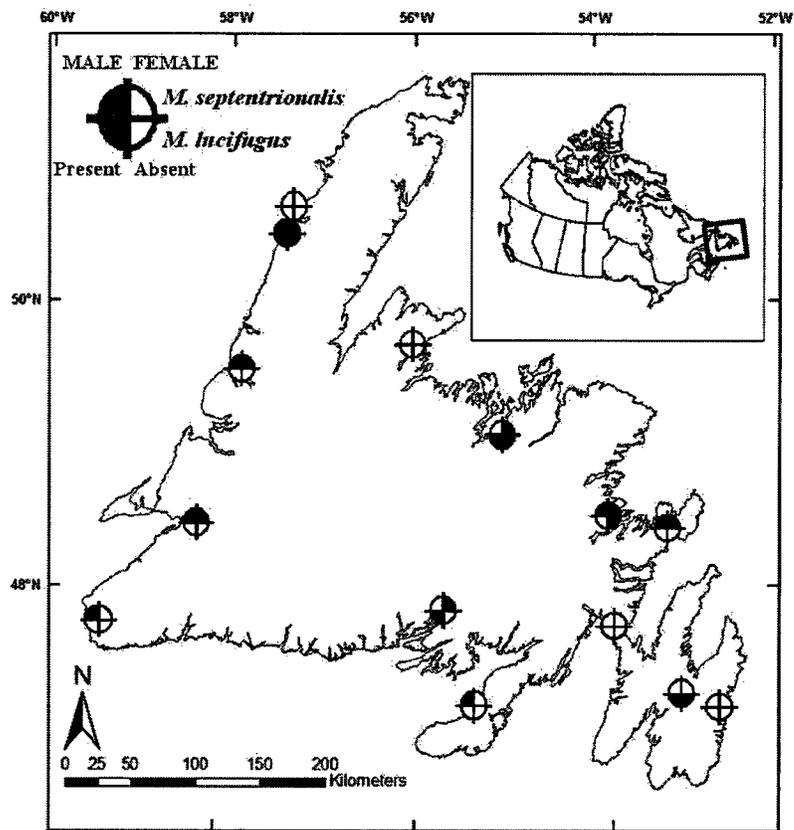
Figure 2: Distribution of male and female *Myotis septentrionalis* and *M. lucifugus* on the island of Newfoundland during the summer of 2008.

The three best models for differentiating locations where each bat group were and were not captured, were ranked along with their respective importance weights (Table 6). Because there was high model uncertainty, and importance weights were low, I focused on the parameters within the three best models to make inference. The best parameters to differentiate sampling locations were ranked according to their statistical effect size (parameter estimates (β_i), and standards errors (S.E.); Table 7). For each bat group, there was at least one parameter for which $\beta_i \pm$ S.E. did not overlap zero, and these have the most support. For female *M. septentrionalis*, the combined weight of importance for the top three models was 55%. In a 2-km radius landscape plot, for every decrease of ten buildings, the odds that this group would be present at a sample location increased by 1.22 times (95% CI: 0.91 to 1.64; Figure 3). For male *M. septentrionalis*, the combined weight of importance for the top three models was 76%. In a 2-km radius landscape, for every 2.0 km^2 increase of available forest, the odds that this group was present at a sample location increased by 2.58 times (95% CI: 0.93 to 7.15; Figure 3); and for every 0.5 km increase in distance from the nearest river, presence was 57% less likely to occur (95% CI: 0.09 to 2.11).

For female *M. lucifugus*, the combined weight of importance for the top three models was 78%. In a 0.1-ha stand, for every increase of five snags, the chances that a female *M. lucifugus* would be present at a sample location increased by 1.42 times (95% CI: 0.95 to 2.12; Figure 3). For male *M. lucifugus*, the combined weight of importance for the top three models was 52%. In a 0.1-ha stand, for every 2.0 cm decrease in average tree diameter, the odds that male *M. lucifugus* were present in a sample location increased by 1.55 times (95% CI: 0.68 to 3.56; Figure 3).

Proximity to nearest river from the capture site was prominently included in the model set, and was identified as an important parameter to determine bat presence in all groups except male *M. lucifugus*. In close examination, the statistical effect size across all models in each candidate set was stable (i.e. β_i was similar) for both groups of *M. septentrionalis*; however, biological significance was mostly weak because standard errors were large and overlapped parameter estimates (Table 7).

Table 6: Ranking of Akaike's Information Criterion (AIC$_C$) between the *i*th and the top ranked model (Δi) and Akaike weights (w_i) for all a priori models of each bat group, differentiating the characteristics of sites where bats were and were not captured.

Models	*Myotis septentrionalis* Female Rank	w_i	Male Rank	w_i	*Myotis lucifugus* Female Rank	w_i	Male Rank	w_i
Number of buildings	1	0.275	5	0.054	7	0.044	4	0.137
Distance to nearest river, Number of buildings	2	0.149	7	0.034	9	0.017	9	0.041
Distance to nearest river	3	0.123	3	0.098	4	0.055	5	0.131
Forest area	4	0.104	1	0.428	6	0.046	3	0.144
Number of snags	5	0.097	6	0.045	1	0.464	2	0.151
Tree diameter	6	0.095	4	0.057	5	0.047	1	0.229
Distance to nearest river, Number of snags	7	0.061	8	0.030	2	0.163	7	0.046
Forest area, Distance to nearest river	8	0.054	2	0.237	8	0.017	8	0.043
Tree diameter, Number of snags	9	0.043	9	0.017	3	0.148	6	0.078

Table 7: Model averaged parameter estimates (β_i) and unconditional standard errors (S.E.) for the parameters in the top three models of each bat group, to determine probability of presence of each bat group within forested trails of Newfoundland. Note: only those variables whose $\beta_i \pm$ S.E. did not overlap zero were used for inference.

Parameters	*Myotis septentrionalis*		*Myotis lucifugus*	
	Female	Male	Female	Male
	β_i (SE)	β_i (SE)	β_i (SE)	β_i (SE)
Number of buildings	-0.020 (0.015)	-	-	-
Distance to nearest river	-1.474 (1.522)	-1.688 (1.624)	-0.860 (1.569)	-
Forest area	-	0.474 (0.260)	-	0.101 (0.240)
Tree diameter	-	-	0.059 (0.182)	-0.220 (0.212)
Number of snags	-	-	0.070 (0.041)	-0.026 (0.056)

Female   Male

M. septentrionalis

Probability — Number of buildings

Probability — Forest area (km^2)

M. lucifugus

Probability — Number of snags

Probability — Live tree diameter (cm)
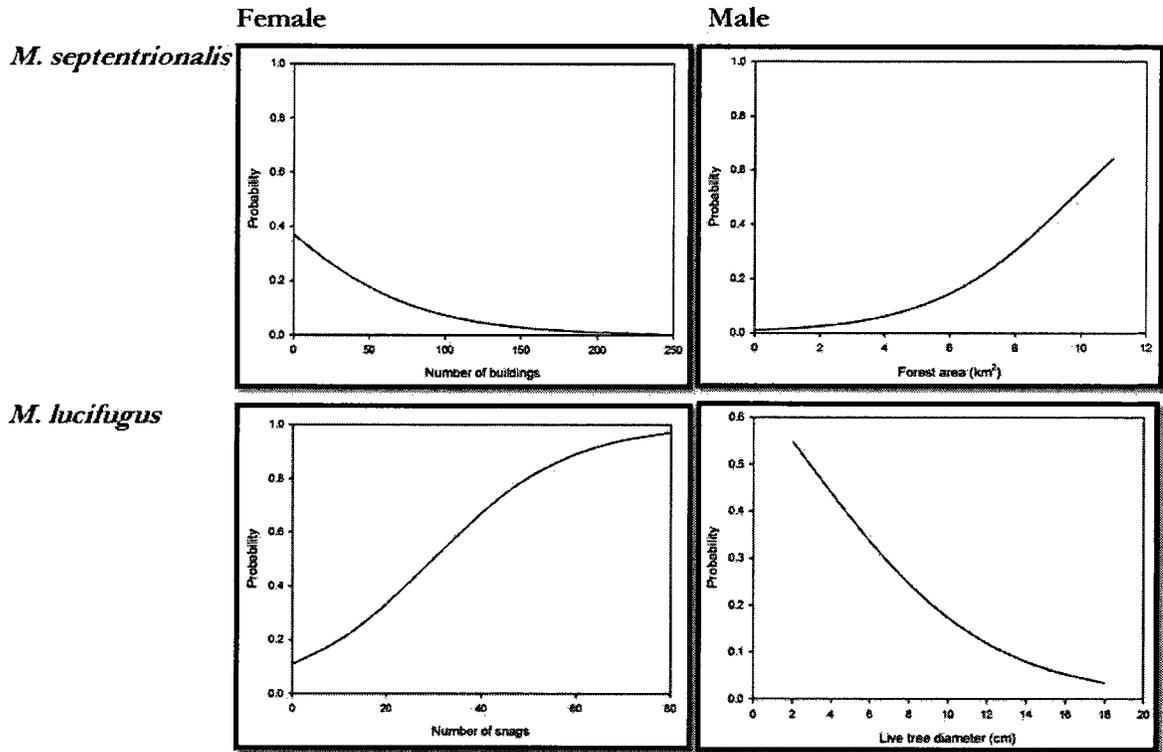
Figure 3: Probability curves for parameters that best differentiated locations where each bat group were present to where they were not present on the island of Newfoundland.

Roost selection by female, forest-dependent Myotis septentrionalis

From June to August 2009, 18 female *M. septentrionalis* (eight lactating, and ten non-lactating) were caught and tracked around the community of River of Ponds, NL using radio telemetry. The lactation period occurred from July 10 to August 02, during which, two non-lactating females were caught and tagged. The transmitters remained adhered to the bats for an average of 3.3 days (range 0 - 11 days). Of those, we did not record any data from four because of the inability to locate the bat, or the transmitter falling off the individual during

the first night of activation. A bat day was defined as one radio-tracked bat roosting in one tree for a single day.

In total, 18 *M. septentrionalis* were tracked to 35 roost trees, nine of which were used on more than one occasion (with 11 bat days being the greatest frequency of occurrence for any roost tree). On average, bats roosted 1,136 m from the capture site (range 71 – 2,375 m). At least three species of trees were used as roosts, two softwood (*Abies balsamea*, balsam fir (n = 13); *Picea mariana*, black spruce (n = 1)), and one hardwood species (*Betula papyrifera*, white birch (n = 10)). The remaining 12 trees were not identified due to their advanced class of decay. Three roost trees were used by more than one tracked bat either on the same or separate days. Of these roost trees, two contained both non-lactating and lactating bats either on separate occasions, or on the same day (a white birch snag and balsam fir snag, respectively). Roosts used by both non-lactating and lactating bats were predominately found in snags (87% and 92%, respectively; Table 8). Exit counts were estimated for 39 of the 60 total bat days. The mean colony size for roost trees that were occupied by non-lactating bats was 7.6 (range 1 to 28; n = 27), and for lactating was 9.0 (range 1 to 19; n = 12). The maximum roost group size was 28 individuals in a roost tree used by a tagged non-lactating bat. There was no evidence that colony size differed between lactating and non-lactating bats (U = 147, df = 1, p = 0.64).

Table 8: Number of snags and live trees of three species used for roosting by lactating and non-lactating *Myotis septentrionalis* in River of Ponds, NL, 2009.

Tree species	Non-Lactating		Lactating	
	Decay class 4-7	Decay class 1-3	Decay class 4-7	Decay class 1-3
Abies balsamea	7	1	5	0
Picea mariana	0	1	0	0
Betula papyrifera	3	1	5	1
Unknown	10	-	2	-

Forest Characterization

Studies used to review characteristics of roost-sites occupied by female *M. septentrionalis* were arranged geographically from areas towards the central portion of the North American distribution extending to the periphery (Table 9). Two of the eight studies found roosts of similar size (roost tree height of 8.7 m [±0.6] in Arkansas, *Perry and Thill*, *2007*; roost tree diameter of 21.3 cm in Kentucky, *Lacki and Schwierjohann, 2001*), to those characterized on the island of Newfoundland. The general trend, however, shows that compared to River of Ponds, NL, female *M. septentrionalis* in more interior regions of their distribution use roosts in trees that on average, are taller (16.5 versus 11.3 m in River of Ponds), larger (37.3 versus 25.8 cm dbh), and in areas that offer greater tree species diversity.

The *a priori* models selected to differentiate roosts used by *M. septentrionalis* during lactation and non-lactating in River of Ponds, NL were ranked with their respective importance weights (Table 10). The best parameters contained in the top three models were ranked according to their parameter estimates (β_i), and standards errors (S.E.; Table 11). The combined weight of importance for the top three models was 89%. At the local level, for

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every 2.0 cm increase in roost tree dbh, the odds that a lactating *M. septentrionalis* roosted in that tree increased by 1.23 (95% CI: 1.01 to 1.51). At the stand level, for every increase of five trees within a 0.1-ha plot, the odds of lactating *M. septentrionalis* presence increase by only 1.05 times (95% CI: 0.97 to 1.14). Concerning statistical effect size and magnitude, roost tree diameter appeared to have the strongest biological inferential power (Figure 4).

Table 9: Roosting ecology review for female *Myotis septentrionalis* across North America with a comparison to that of a periphery population in Newfoundland, Canada.

Reference	Province/ State	Roost tree height (m) [S.E.]	Roost tree dbh (cm) [S.E.]	Number of roost tree species (available)	n
Perry and Thill (2007)	Arkansas	8.7 [0.6]	18.7 [1.0]	5 (9)	49
Carter and Feldhamer (2005)	Illinois	15.8 [2.0]	37.3 [4.7]	5 (23)	19
Lacki and Schwierjohann (2001)	Kentucky	n/a	21.3	12 (13)	57
Foster and Kurta (1999)	Michigan	23.3 [0.2]	65.0 [1.0]	3 (14)	32
Menzel et al. (2002)	West Virginia	18.7 [1.5]	29.2 [1.6]	9 (14)	12
Owen et al. (2002)	West Virginia	17.8 [0.7]	27.2 [1.0]	11 (16)	43
Sasse and Perkins (1996)	New Hampshire	14.8 [1.0]	40.9 [2.8]	9 (13)	47
Broders and Forbes (2004)	New Brunswick	n/a	43.8 [1.8]	9 (11)	55
Garroway and Broders (2008)	Nova Scotia	17.8	42.0	6	44
Park (2010) M.Sc. thesis	**Newfoundland**	**11.3 [1.0]**	**25.8 [1.7]**	**3 (n/a)**	**36**

Table 10: Difference in Akaike's Information Criterion (AIC$_C$) between the ith and the top ranked model (Δ_i), Akaike weights (w_i), and sum of Akaike weights (Σw_i) for all a priori models, differentiating characteristics of sites and roosts used by lactating and non-lactating *Myotis septentrionalis*.

Model	Δ_i	w_i	Σw_i
Roost tree diameter, Canopy relative to roost	0.00	0.534	0.534
Roost tree diameter, Canopy relative to roost, Total number of live trees	1.54	0.247	0.781
Canopy relative to roost, Total number of live trees	3.22	0.107	0.888
Canopy relative to roost	4.03	0.071	0.959
Roost tree diameter	6.34	0.022	0.981
Roost tree diameter, Total number of snags	7.48	0.013	0.994
Total number of live trees	9.49	0.005	0.998
Total number of live trees, Total number of snags	11.81	0.001	1.000
Total number of snags	15.38	0.000	1.000

Table 11: Model averaged parameter estimates (β_i) and unconditional standard errors (S.E.) for the three top parameters to differentiate roost-sites used by lactating and non-lactating *Myotis septentrionalis* within roost trees of Newfoundland. Note: only those variables whose $\beta_i \pm$ S.E. did not overlap zero are used for inference.

Parameters	β_i (S.E.)
Roost tree diameter	0.105 (0.051)
Total number of live trees	0.010 (0.008)
Canopy relative to roost	0.051 (0.079)
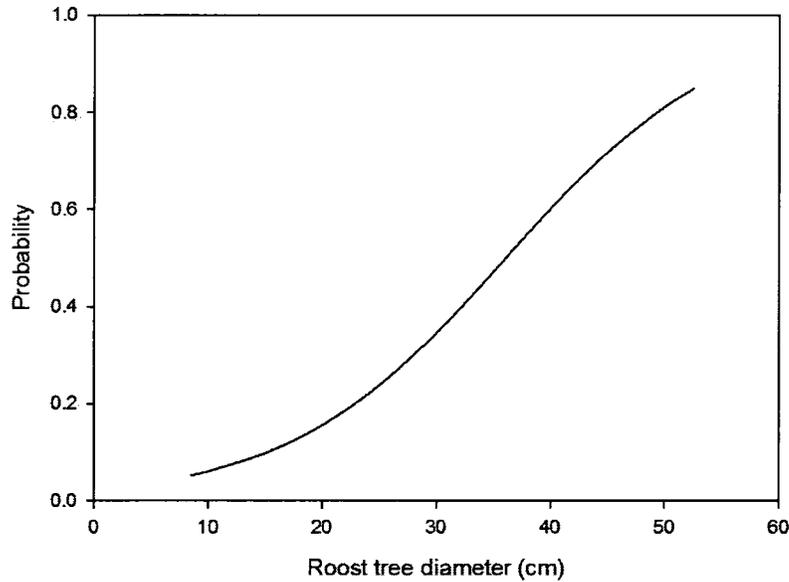
Figure 4: Probability curve for the parameter (roost tree diameter) that best differentiated roost-sites used by lactating to those used by non-lactating *M. septentrionalis* in Newfoundland.

Roost microclimate

A clear distinction between regressions of roost microclimate used by lactating and non-lactating bats was seen (Figure 5). The average slope of trend lines of ambient and roost temperatures were 0.60 for roosts used by lactating bats (n = 2; r^2 = 0.68 and 0.88). A slope less than one indicated that temperature was more stable and did not fluctuate as much inside the roost cavity compared to ambient conditions (range of 11.2 to 23.0°C, and 8.6 to 26.6°C, respectively). Slope was two times greater for roosts used by non-lactating bats (1.35; n = 4; range of r^2 = 0.62 to 0.86). A slope greater than one indicated that temperature fluctuated more inside the roost cavity than ambient (1.6 to 36.6°C and 4.9 to 27.2°C, respectively). The prediction that lactating bats roosted in trees with a small range in temperature fluctuation appeared to be true, however not all roosts within large diameter

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trees maintained these stable microclimates. This was the case for two roosts found in trees with a dbh of 23.7 and 34.5 cm that were used by non-lactating bats. The large variation in temperature of one roost was most likely attributed to the fact that the roost was not an internal cavity, but under a sheet of exfoliating bark; the other roost was composed of a cavity that opened from the top of the tree and had a split on one side. Both roosts were therefore more exposed to ambient conditions, and fluctuated accordingly. On average however, roosts in trees occupied by lactating bats were greater in dbh than roosts in trees of non-lactating bats (31.7 cm and 22.7 cm, respectively).
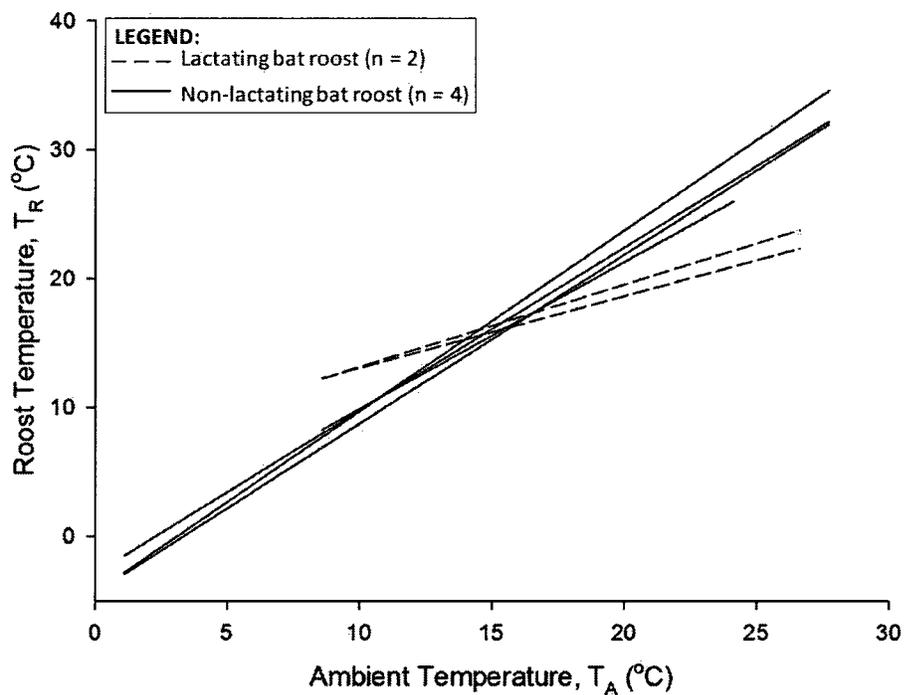

Figure 5: Microclimate of roosts occupied by lactating and non-lactating *Myotis septentrionalis* in River of Ponds, NL.

DISCUSSION

Prior studies have recognized that the distribution of temperate bats can be patchy (Dobbs 1983, Amelon and Burhas 2006, Henderson et al. 2008, Lausen 2009). My findings were consistent in that *Myotis lucifugus* was not ubiquitous and not present in the western-most areas sampled; *M. septentrionalis* appeared more restricted, and was absent from the southeastern-most areas. There were certain limitations with this study however, in that the lack of bat group presence in each sample location may not have been a result of their absence, but rather that trapping did not occur often enough, or on the right trails, etc. This study provided insight into the factors that account for the distributional pattern of bat groups on NL, and how these factors ultimately limit the distribution of bat populations. These data show that, as predicted, four bat groups were distinct from each other in terms of their roosting and foraging site-selection. The best forest parameters to differentiate locations where each bat group was present occurred at both the stand (0.1 hectare) and landscape (2.0 kilometer) levels and included the number of snags and tree diameter within a stand, and distance to nearest river, number of buildings, and amount of forest in a landscape.

Both sexes of *M. lucifugus* exhibited relationships with stand-level factors. Maternity colonies of *M. lucifugus* are frequently found in human-made structures throughout their range (Fenton and Barclay 1980, Anthony et al. 1981, Burnett and August 1981, Kalcounis and Hecker 1996, Riskin and Pybus 1998, Zimmerman and Glanz 2000, Broders and Forbes 2004). Although I did not track individuals to roosts, I did expect that maternity colonies primarily used human-made structures as roosts. Despite sampling locations being close to,

or containing buildings within the landscape (average = 34 buildings; range 0 – 102), this parameter was not identified as important differentiate presence and absence of female *M. lucifugus*. Instead, the most important parameter was the number of available snags in a stand. Although this result was not predicted to be important for this particular bat group, it may have been a function of the available forest area in the landscape. Maternity colonies of *M. lucifugus* have been documented in natural structures in previous studies (Fenton and Barclay 1980, Barclay and Cash 1985, Kalcounis and Hecker 1996), which may be indicative of their roosting preference before fabricated structures became available. Therefore, in isolated areas such as those on NL, where the percentage of forest area is high and the human population is sparse, *M. lucifugus* females may prefer to roost within forests. This does not support the results of the Alaskan study by Parker and others (1997), who suggested that maternity colonies of *M. lucifugus* were more likely to be in human-made structure despite a low human population. Certain limitations were apparent in the present study with respect to sample size, as female *M. lucifugus* were only captured in seven of the 33 sampled locations. Also, the majority of the forest inventory data used to characterize landscape variables were taken from data characterized in 1999. Therefore should any land cover changes have occurred since this time, they were not incorporated into this analysis as no updates have been made to the data set. Further research could therefore evaluate the roost-site selection of *M. lucifugus* maternity colonies in NL in relation to updated landscape, stand, and local variables. An increasing number of snags within a stand as an important factor to predict presence, support studies on other bat species or groups, which suggest that bats might have an affinity to a particular roosting area (Kalcounis and Hecker 1996, O'Donnell

and Sedgeley 1999, Broders 2003, Carter and Feldhamer 2005). A roosting area allows for a network of available trees to be used as roosts (Broders and Forbes 2004).

Broders and Forbes (2004) determined that in New Brunswick, an increasing number of available snags was most important to differentiate roost-site selection of male *M. lucifugus*. In this study, number of snags was initially identified as an important parameter for male *M. lucifugus* presence; however, the relationship carried weak biological significance and was not in the predicted direction, as odds of their presence was less likely with an increase in snag density. Decreasing average tree diameter in a stand was the most important parameter to distinguish locations where males were present, but again was not in the direction predicted. Prior studies have determined that males are more plastic in roost-site selection (Thomas 1988, Barclay 1991, Mills et al. 1996, Broders and Forbes 2004, Perry and Thill 2007) and will roost in trees that are smaller in diameter than females, which could explain why the odds of finding male *M. lucifugus* in these stand types increased.

Myotis septentrionalis have an even greater affinity towards forests as they are dependent on them for both roosting and foraging (Caceres and Barclay 2000, Lacki and Schwierjohann 2001, Broders et al. 2003, Carter and Feldhamer 2005). Parameters identified as important to distinguish locations where this species was found on NL were at the landscape level. Locations where male *M. septentrionalis* were captured were closer, on average, to rivers than locations where they were not captured. This supports results of prior studies and the prediction that rivers are essential areas to obtain drinking water, exploit foraging opportunities, and for commuting through landscapes (Racey and Swift 1985, Grindal et al. 1999, Downs and Racey 2006, Henderson et al. 2008). Most importantly,

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males were found in landscapes that were more forest-dominant than where they were not found. A similar relationship was observed in P.E.I. in that forest area was an important parameter in landscape buffers to differentiate areas where both male and female *M. septentrionalis* were captured (Henderson et al. 2008). In this study, the probability of female *M. septentrionalis* presence was highest within landscapes that contained fewer buildings. These findings reinforce the importance of forests to promote survival and fitness for both groups of the forest-dependent bat species. Additionally, these results suggest that *M. septentrionalis* has reached their northeastern distributional-limit on the island of Newfoundland because of the landscape structure, or more specifically, the lack of available forest in areas on the island of Newfoundland where *M. septentrionalis* was not found to be present.

Weather may also be a factor that has influenced the peripheral population of *M. septentrionalis* distribution on NL. For areas separated by the presence of both *M. septentrionalis* groups, the average temperatures were lower where neither group was captured (12.1°C compared to 13.0°C), and the number of fog days were greater (30 compared to 17 days). Low temperatures increase the amount of energy required to maintain normothermic body temperatures; while fog contains moisture that can accumulate on the fur of bats reducing its isolative power, and creates "clutter" in the air that has a negative effect on echolocation (Grindal et al. 1992, Burles et al. 2009). Since Newfoundland provides a unique view of temperate bat ecology, it is important to compare and contrast this perspective to that of the central North American distribution, where most studies occur. Forest-dependent, female *M. septentrionalis* were present in central areas sampled of NL and absent in the more

northern, eastern and southern portions. Males however, showed greater flexibility and were present in more of the southern areas, which is a common trend seen in other studies (Thomas 1988, Barclay 1991, Mills et al. 1996, Broders and Forbes 2004, Perry and Thill 2007). It is expected that, since males contribute little energy to reproductive costs, they be less constrained in site selection than females (Thomas 1988, Barclay 1991, Mills et al. 1996). Therefore, focusing on specific factors regarding roost-site selection of females may provide greater insight as to which factors are essential for survival and dictate distributional limits.

Throughout the interior of their range, female *M. septentrionalis* roost in a wide variety of tree species that are, on average, tall and large in diameter. In the majority of areas previously studied, hardwoods have been an important site for roosting (Sasse and Perkins 1996, Foster and Kurta 1999, Menzel et al. 2002, Owen et al. 2002, Broders and Forbes 2004, Carter and Feldhamer 2005, Ford et al. 2006, Garroway and Broders 2008). As studies progress to southern areas of the described distribution in North America, softwoods are also becoming a more common roosting substrate (Lacki and Schwierjohann 2001, Perry and Thill 2007). Interestingly, studies that identified softwoods as common roost-sites for female *M. septentrionalis*, also described average roost tree height and diameter to be on par with, or less than these in this study. Furthermore, on the island of Newfoundland softwood species (particularly balsam fir; *Abies balsamea*) were the most common roost tree species (58.3% of known roost tree species used, 38.9% of total roost trees). Though factors influencing selection of softwoods as roost-sites are unclear, in Newfoundland the reason could simply be due to their greater availability. On the west coast and northern peninsula of the island, where the study site was based in 2009, balsam fir is the dominant

tree species, with black spruce (*Picea mariana*) present in low-lying bogs and wet-site forests (Setterington et al. 2000, Thompson et al. 2003). Both softwood species comprise over 75% of the total forest composition on the island (DNR 2008a), which limits the selection of any other species of tree (including hardwoods) to be used as roost-sites. Balsam fir is known to be a short-lived species, such that "old growth" that has reached canopy height will typically only last 20-30 years (Thompson et al. 2003), which lessens the opportunity to grow to a large size. The amount of old growth forests has further been reduced in the western region of the island since the 1940s because of logging, and infestations of both hemlock looper (*Lambdina fiscellaria*) and spruce budworm (*Choristoneura fumiferana*) (Thompson et al. 2003). Smaller and shorter roost trees, compared to those available in central areas of female *M. septentrionalis* distribution in North America, are widely available in Newfoundland, and are chosen as suitable roost sites that meet the expensive costs of reproduction.

Energetic requirements of bats are not only differentiated by sex, but also by reproductive status. Non-reproductive females, like males, lack the energetic stress of producing offspring and can therefore be more flexible in selection of roosting sites (Thomas 1988, Barclay 1991, Mills et al. 1996). In this study, roost-tree and -site characteristics selected for by lactating *M. septentrionalis* appeared to coincide with energetic demands, relative to those that were non-lactating. Lactating bats selected roost sites with specific attributes at the local and stand levels, which included roost tree diameter, canopy height relative to the height of the roost in a tree, and the total number of live trees within a stand, all of which exhibited a positive relationship with lactating bat presence.

Both canopy height relative to roost height and number of trees in a stand did not exhibit the relationship predicted, and lacked a strong biological association in differentiating lactating northern long-eared presence from non-lactating. Only one other study has been performed on roost-site selection of *M. septentrionalis* in comparison to reproductive status. Garroway and Broders (2008) concluded that a shift in resource selection occurred based on an inference that, relative to non-lactating females, lactating bats preferred roosts exposed to increased solar radiation, and reduced clutter (i.e. roosts were situated high in tall trees that were surrounded by a relatively open canopy and a low number of trees in the stand). It would be expected that maternity colonies roost high in trees (i.e. close to the canopy) that are relatively void of clutter to gain warmth from exposure to sunlight (Vonhof and Barclay 1996, Betts 1998, Ormsbee and McComb 1998, Veilleux et al. 2009). Roosts that are higher in temperature boost development of young during parturition (Racey and Swift 1981, Vonhof 1996, Kerth et al. 2001b), which is especially important when the growing season is short compared to that at the interior of the species' distribution (Lewis 1993, Kerth et al. 2001b). Avoiding any conditions that would result in energetically costly roosting conditions is important to enhance fitness for both females and their offspring, notably at the northern extremes of their distributions (Lacki et al. 2009). In this study however, roosts of lactating females were located in cluttered stands.

On the island of Newfoundland, lactating *M. septentrionalis* most importantly, roosted in trees that were larger in diameter, relative to non-lactating females. This is further supported by trends seen in prior studies that have compared characteristics of roost trees used by female *M. septentrionalis* to that of random trees (Sasse and Perkins 1996), of trees

used by males (Perry and Thill 2007), and trees used by colonies to those by solitary females (Lacki and Schwierjohann 2001). Insulation and temperature of roost cavities is also largely dictated by the size of the tree in which it is located. Large diameter trees provide more insulation and are less affected by ambient conditions, enabling them to maintain more stable microclimates than trees with smaller diameters (Nicolai 1986, Vonhof and Barclay 1997). Maternity colonies required to maintain and conserve energy could therefore select particular roosts based on roost temperatures (Broders and Forbes 2004). Since a significant difference between colony sizes of lactating bats in comparison to non-lactating bats did not occur, this study does not support the trend that lactating females will select large diameter trees in order to form colonies of a greater size to socially thermoregulate. This study may have been constricted however, in that the sample size was not large enough to detect this trend.

Roost microclimate has not been widely studied in the past due to difficulty of access to cavities. For studies that have been successful, reproductive bats seem to select roosts with more stable microclimates, relative to roosts used by non-reproductive females (Burnett and August 1981, Kalcounis and Hecker 1996, Sedgeley 2001). This study also supported the prediction that the more energy-demanding lactating period resulted in females selecting roosts in trees that maintained stable microclimates, relative to the microclimate of roosts used by non-lactating *M. septentrionalis*. However, not all large diameter trees produced stable temperature ranges as predicted; in two instances where this occurred, non-lactating females were found roosting in large-diameter trees with unstable temperatures. The two roosts were under exfoliated bark and in a split in the top of a tree. A cavity within the trunk of a

tree that has a solid enclosure and small entrance, protects the roost from extreme ambient fluctuations and prevents temperatures from getting too cold, as well as too warm (Kalcounis and Hecker 1996, Sedgeley 2001). If the roost temperature becomes too cold, reproductive females run the risk of entering torpor, or expending a lot of energy to maintain normothermic conditions, which lowers the survival and growth rate of their offspring (Racey and Swift 1981, Thomas 1988, Barclay 1991, Mills et al. 1996). Additionally, if roost temperatures are too warm, it will exceed the thermoneutral zone for the particular species (Kalcounis and Hecker 1996). It is therefore necessary to consider that, along with tree diameter, roost type selected by females is also dependent on reproductive condition.

CONCLUSION

This study refined the range of *M. septentrionalis* on the island of Newfoundland and revealed factors that influence roost and foraging site selection for peripheral populations of temperate bat species. Analyses in this study identified multiple predictors for both species that occurred at the stand- (for *M. lucifugus*) and landscape- level (for *M. septentrionalis*). These predictors are therefore believed to influence the distributional pattern of resident bats on NL. Location preference was further differentiated by sex of both species. This implies that adequate roosting and foraging sites occur in diverse areas for all four groups of temperate bats.

For the more forest-dependent and energy restricted female *M. septentrionalis*, roost-site selection at the periphery of their range was found to differ from that at the interior of

their North American distribution. However, even at the Northeastern extreme, which contains forest features that are less likely to be chosen by *M. septentrionalis* females at the interior of their distribution, the overall trend of roost-site selection is similar. When differentiated by reproductive condition, females that were lactating and undergoing conditions that required significant energy resources, selected roost cavities that were enclosed in large diameter trees and had warmer, more stable microclimates, than those that were non-lactating. This suggests that reproductive females are more sensitive to distribution-limiting factors within peripheral populations of temperate bats. In future research, it would be beneficial to continue the examination of roost microclimate differences between lactating and non-lactating females to support my results, and to evaluate the relationship between temperature and metabolic rate of *M. septentrionalis*. Investigating torpor use by females, and relating it to roost microclimate would also evaluate the benefits or costs associated with utilizing torpor during different stages of reproduction. This would permit a stronger inference regarding the benefits of roost microclimate for reducing energy costs of reproductive females.

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APPENDIX A: LOCATION, FOREST MEASURES AND PRESENCE DATA OF SAMPLED LOCATIONS ON THE ISLAND OF NEWFOUNDLAND IN 2008

Location, forest measures, and presence (1) or absence (0) data for four bat groups, for each of the 33 sampled locations on the island of Newfoundland in 2008. UTM zone = zone of coordinates in NAD83 format, UTM E = easting coordinates in NAD83 format, UTM N = northing coordinates in NAD83 format, dbh = average live tree diameter at breast height (cm) in a stand plot, Snags = average number of snags in a stand plot, Forest area = total area of forest-dominated polygons (km²) in a landscape plot, D to river = distance to nearest river (km) in a landscape plot, # buildings = total number of buildings in a landscape plot, F *M.sept.* = presence of female *M. septentrionalis* in a sampled location, M *M.sept.* = presence of male *M. septentrionalis*, F *M.luci.* = presence of female *M. lucifugus*, M *M.luci.* = presence of male *M. lucifugus*. Note: UTM coordinates, forest measures of stand plots and presence data were averaged for both capture sites of a sampled location.

Location	UTM Zone	UTM E	UTM N	dbh (cm)	Snags	Forest area (km²)	D to river (km)	# buildings	F M.sept.	M M.sept.	F M.luci.	M M.luci.
Arnold's Cove 1	22	275833	5294380	11.4	22	1.02	0.16	81	0	0	0	0
Arnold's Cove 2	22	279224	5293785	12.1	0	4.16	0.29	3	0	0	0	0
Barachois 1	21	406972	5380373	9.7	10	3.92	0.39	0	1	0	0	0
Barachois 2	21	401205	5369576	9.0	0	9.23	1.04	1	0	0	0	0
Barachois 3	21	399204	5368029	9.7	0	8.01	0.65	0	0	0	0	0
Barachois 4	21	406989	5370581	10.6	14	8.05	0.04	2	1	1	0	0
Flatwater Pond 1	21	570270	5511679	12.4	0	4.97	0.04	132	0	0	0	0
Gros Morne 1	21	439816	5490806	8.1	15	10.33	0.02	0	0	0	0	0
Gros	21	435569	5487214	14.9	0	4.27	0.71	237	0	0	0	0

Location											
Gros Morne 2	21	432726	5497269	14.3	7	6.62	0.32	6	0	0	0	0
Gros Morne 3	21	431012	5498532	6.8	0	2.65	0.26	5	1	0	0	0
Gros Morne 4	21	446683	5475006	15.1	4	8.58	0.38	0	1	1	0	0
Gros Morne 5	21	596789	5304090	13.8	3	8.16	0.02	7	0	0	1	0
Jupujikuei Kuespem 1	21	599741	5306527	8.4	0	8.49	0.03	0	1	0	0	1
Jupujikuei Kuespem 2	21	605629	5308627	11.7	6	5.51	0.40	1	0	0	0	0
Jupujikuei Kuespem 3	22	356285	5225647	15.0	1	7.93	0.16	8	0	0	0	0
La Manche 1	22	357653	5224932	13.2	2	7.93	0.59	8	0	0	0	0
La Manche 2	22	324955	5367628	16.5	8	8.57	0.26	2	1	1	1	0
Lockston Path 1	22	325764	5366185	14.3	1	8.85	0.11	4	0	1	1	0
Lockston Path 2	21	332980	5294191	8.7	20	6.75	0.81	58	0	1	0	0
Port aux Basques 1	21	335240	5300567	12.9	13	4.09	0.28	55	0	0	0	0
Port aux Basques 2												

River of Ponds 1	21	473233	5596805	17.1	31	5.27
River of Ponds 2	21	473160	5598142	10.5	5	5.16
Salmonier 1	22	332604	5245845	12.8	21	5.18
Salmonier 2	22	327907	5238256	12.2	72	5.03
Salmonier 3	22	327277	5236885	11.5	26	5.13
Terra Nova 1	22	282198	5392250	12.2	0	8.89
Terra Nova 2	22	280801	5388563	15.6	16	8.97
Terra Nova 3	22	280181	5380283	14.0	1	6.88
Terra Nova 4	22	n/a	n/a	16.2	6	5.38
Terra Nova 5	22	280903	5377076	13.9	0	5.21
Notre Dame	21	567100	5403201	13.0	0	8.26
Port au Choix	21	476793	5617187	13.3	9	0.63

0.38	92	0	0	0	0
0.04	97	1	1	1	1
0.46	7	0	0	1	1
0.29	102	0	0	1	0
0.29	27	0	0	1	0
0.73	65	0	0	0	0
0.03	0	1	1	1	0
0.02	40	0	0	0	0
0.33	3	0	0	0	0
0.14	1	0	0	0	0
0.94	0	1	0	1	1
1.82	39	0	0	0	0

APPENDIX B: LOCATION, FOREST MEASURES AND PRESENCE DATA OF ROOST TREES USED BY LACTATING FEMALES ON THE ISLAND OF NEWFOUNDLAND IN 2009

Location, forest measures and presence of lactating (1) or non-lactating (0) female *M. septentrionalis* data for each of the 35 roosts sampled in River of Ponds, NL, in 2009. ID = identified roost tree, Long. = longitude in decimal degrees in WGS1984 format, Lat. = latitude in decimal degrees in WGS1984 format, Lact. = presence of lactating *M. septentrionalis*, Roost dbh = diameter at breast height (cm) of roost trees, Can. rel. roost = canopy height relative to roost height (m), Snags = number of snags in a stand plot, Live trees = number of live trees in a stand plot.

ID	Long.	Lat.	Lact.	Roost dbh (cm)	Can. rel. roost (m)	Snags	Live trees
R01T0715N09	-57.332	50.391	0	52.5	13.6	0	163
R02T0716N09	-57.332	50.398	0	23.7	11.8	20	48
R03T0717N09	-57.330	50.402	0	11.0	12.2	11	80
R04T0718N09	-57.331	50.403	0	16.5	14.9	18	143
R05T0719N09	-57.328	50.400	0	21.1	8.6	27	80
R06T0720N09	-57.337	50.404	0	8.5	14.6	18	118
R07T0721N09	-57.330	50.403	0	17.0	6.0	21	166
R08T0725N09	-57.326	50.399	0	31.5	8.7	7	22
R09ER0826N09	-57.328	50.399	0	24.4	4.4	15	108
R10H0328N09	-57.325	50.400	0	19.2	9.6	26	75
R12RoP1B13L09	-57.318	50.403	1	31.7	22.0	7	46
R13RoP1B14L09	-57.360	50.543	1	43.0	17.0	9	241
R14RoPER1315L09	-57.360	50.544	0	14.2	17.4	9	187
R15RoPER1316L09	-57.355	50.546	1	40.5	7.3	10	139
R16RoP1B16L09	-57.363	50.551	1	23.0	n/a	19	178
R17RoPER1316L09	-57.369	50.546	0	19.0	n/a	20	51
R18RoP1B17L09	-57.340	50.548	0	27.0	15.5	9	143
R18RoP1B17L09	-57.356	50.546	1	27.0	15.5	9	143
R19RoP1B18L09	-57.372	50.547	1	21.2	7.7	17	53
R20RoPER1318L09	-57.342	50.547	0	17.8	n/a	13	76
R21RoPER1319L09	-57.348	50.546	0	28.5	0.6	4	151
R22RoP2A23L09	-57.366	50.550	1	41.5	9.9	8	110
R23RoP2A23L09	-57.383	50.537	1	n/a	n/a	23	174
R24RoP2A24L09	-57.369	50.548	1	34.5	11.2	9	39
R25RoP2A25L09	-57.382	50.538	1	32.2	-0.1	17	169
R26RoP2A26L09	-57.376	50.544	1	27.5	14.3	12	123
R27R2628L09	-57.375	50.544	0	15.7	n/a	22	57
R28R2629L09	-57.375	50.544	0	24.0	n/a	15	119
R29RoP1B01A09	-57.383	50.538	1	35.0	16.8	25	236
R30RoP1B01A09	-57.383	50.538	1	22.7	18.8	19	230
R31RoP1C05A09	-57.373	50.513	0	34.5	19.1	13	44

R32RoP1C05A09	-57.373	50.513	0	25.6	n/a	7	58
R33RoP1C07A09	-57.368	50.518	0	15.7	12.0	13	74
R34RoP1C08A09	-57.372	50.515	0	14.5	n/a	13	82
R35RoP1C09A09	-57.372	50.515	0	37.5	n/a	14	71
R36RoP1C10A09	-57.372	50.515	0	22.4	n/a	14	100