

HABITAT USE WITHIN AND AMONG ROOSTS OF CHIMNEY
SWIFTS (*Chaetura pelagica*)

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Abstract

Habitat use within and among roosts of chimney swifts (*Chaetura pelagica*)

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Chimney swifts are listed as Threatened nationally and in many provinces within Canada due to rapid population declines. I examined large-scale spatial variation in the maximum size of chimney swift roosts at the northern edge of their range to identify where larger roosts occur. I used multi-sourced data collected across Ontario and Quebec between 1998 and 2013. I found that larger roosts were found at more northerly latitudes, and that very large roosts (>1000 birds) only occurred north of 45°. I also investigated fine-scale patterns of chimney swift positioning inside one of the largest roosts in Ontario. Using digitally recorded images, I calculated the angular position of swifts inside the roost relative to ambient and roost temperature. I found that swifts showed a strong preference for clinging to the south facing wall and clustered more when ambient air temperature was warmer. Thus, huddling in swifts provides additional or alternate benefits, other than serving purely to reduce costs of thermoregulation at low ambient temperatures. This research contributes to the understanding of chimney swift roosting ecology and identifies large roosting sites that should be retained for conservation.

Keywords: anthropogenic habitat, aerial insectivore, cavity roosting, chimney swift, *Chaetura pelagica*, communal roosting, conservation, group size, habitat use, huddling, social thermoregulation, species-at-risk

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CHAPTER 1:

General Introduction

Most wildlife ecological research focuses on areas of natural habitat and the relationships and dynamics within those areas. Scant attention has been paid to wildlife that has adopted anthropogenically-provided surrogate habitats; however, it is precisely this group of species that most directly comes into contact with many forms of human settlement and industry. Traditionally, conservation efforts have focused on protecting undisturbed habitat, and little conservation value has been placed on anthropogenic habitat (McIntyre & Hobbs 1999; Miller & Hobbs 2002). While there is no doubt that human modification of the landscape has a negative effect on many species and protection of natural areas is an important part of biodiversity conservation (Margules & Pressey 2000), some species that rely on human-altered habitat may face negative consequences if this habitat type is ignored altogether (Davison & Fitzpatrick 2010). Thus, to conserve biodiversity in all its forms, effective ecosystem management plans should follow an integrated approach that incorporates multiple land uses and varied ownerships (Knight 1999; Miller & Hobbs 2002; Marzluff & Ewing 2008).

The identification of habitat necessary to support and maintain healthy wildlife populations is required for effective conservation strategies. Identifying and protecting the habitat of species that use human-made habitat presents unique challenges, as the needs of both humans and wildlife must be considered. In species that predominantly use human-made structures (e.g., chimneys, barns, bridges), for which a return to their natural/historical habitat is not an immediately feasible option, how do we determine what structures to protect and over what time frame? In such cases, human safety and

maintenance costs are legitimate concerns as human-made structures have finite lifespans and face eventual deterioration. Recently, a policy amendment to Canada's Species at Risk Act (SARA) posits that anthropogenic structures can be identified as critical habitat if these structures are deemed necessary for the survival or recovery of a listed species (Government of Canada 2016). However, this anthropogenic habitat should only serve as an interim measure, with a return to natural habitat as the ultimate goal in recovery and management plans (Government of Canada 2016). Knowledge of how a species uses this anthropogenic habitat over multiple spatial and temporal scales is needed to contribute to the designation of critical habitat, which is especially important and urgent for synanthropic species in strong population decline.

A model synanthropic species

Aerially-foraging insectivorous birds of North America are experiencing widespread population declines (Nebel et al. 2010). Among this group, the chimney swift (*Chaetura pelagica*; hereafter, swift) has faced the most dramatic declines of the guild as shown by a 95% reduction in the Canadian population over the past 40 years (COSEWIC 2007). Consequently, swifts have been listed as Threatened both nationally and in many provinces. At the time of listing, the estimated breeding population of swifts in Canada was 12,000. (COSEWIC, 2007). A guild-wide trend in the decline of aerial insectivores suggests changes in food resources may be the common factor limiting these species and contributing to declines (Nocera et al. 2012). While few historical data on insect populations exist, a study of a historical deposit of swift guano provided evidence that the decline in swift populations may be linked to a shift in the type of insects consumed over

a 48-year period (Nocera et al. 2012).

Swifts are currently very closely associated with urban and suburban areas and rely almost exclusively on masonry chimneys for both breeding and roosting habitat (Steeves et al. 2014). Historically, the natural habitat of swifts was old hollow trees, but swifts quickly adopted man-made structures as North America was industrialized and virgin forest became rare (Graves 2004). In fact, the first record of swifts using human-made habitat in North America came as early as 1664 (Graves 2004), and today, reports of swifts using natural habitat are extremely rare due in part to the past destruction of large diameter trees by extensive and intensive logging practices (Zanchetta et al. 2014). However, declines in swift populations may now be affected by loss of their surrogate anthropogenic habitat (COSEWIC, 2007); a decreasing number of chimneys are available to swifts as the modernization of heating systems means fewer masonry chimneys are being constructed. Additionally, existing masonry chimneys are being capped or lined as safety precautions, which renders them unavailable to swifts. The primary recent conservation action for swifts has been the provision of supplementary habitat in the form of wooden towers for swifts to nest in (Kyle & Kyle 2005; Steeves et al. 2014). Despite being used by swifts in the southern United States, these structures have yet to attract a successful breeding pair in Canada (Finity & Nocera 2012; Nocera, pers. comm.), and in Ontario it may be because the availability of suitable nesting sites is not *yet* limiting swift populations (Fitzgerald et al. 2014).

While swifts roost communally, they do not breed communally. Generally only one pair of swifts occupies a nesting chimney, inside which they build a cup-shaped nest that is glued to the wall with sticky saliva (Fischer 1958). On average, swifts lay 4 or 5

eggs, and incubation and feeding are shared by both parents (Fischer 1958).

Occasionally, 1 or 2 helpers may join a breeding pair and share incubating and feeding duties (Dexter 1952). Eggs hatch after approximately 19 days and the young may take their first flight 28-30 days after hatching (Fischer 1958). Parents no longer feed the young after they leave the chimney, and once all the young have fledged, family groups may leave the nest chimney to join communal roosts. Swifts are monogamous and exhibit strong nest site fidelity from year to year (Dexter 1969). In comparison, chimneys used for communal roosting may contain hundreds or thousands of swifts when they gather during spring and autumn migration (Steeves et al. 2014). Roost chimneys are also used throughout the nesting season by non-breeding swifts (Dexter 1969).

While recent studies have focused on habitat use at or around nesting sites (e.g., Finity & Nocera 2012; Wheeler 2013), few studies have examined the availability or use of roosting sites. Roosting chimneys are often much larger masonry chimneys associated with schools, churches, and industrial buildings (Steeves et al. 2014). Such large masonry chimneys have not been commonly built since 1960, and many existing roost chimneys are nearing the end of their lifespan and/or are in need of repair, modification, or destruction (COSEWIC 2007). Therefore, the availability of suitable roosting structures may be a factor limiting swift populations, or is likely to be a factor in the future. For example, out of 98 roost sites that have been identified in Quebec since 1998, only 38 (39%) were still available to swifts as of 2010 (Rioux et al. 2010). To inform management decisions about the preservation of existing habitat or the possible provision of new habitat, it is necessary to first understand how swifts use and select preferred roost sites.

Communal Roosting

Communal roosting is common in several species of birds (Eiserer 1984; Beauchamp 1999), bats (Lewis 1995), and primates (Anderson 1998). Although the evolutionary origin of communal roosting is debated, the benefits of roosting as a group must outweigh the costs of roosting alone for those species that do it. Increased foraging efficiency through information exchange (Ward & Zahavi 1973; Caccamise & Morrison 1986; Bijleveld et al. 2010), decreased predation risk (Weatherhead 1983), and a decrease in the cost of thermoregulation (DuPlessis & Williams 1994; DuPlessis et al. 1994) are the primary, not mutually-exclusive, hypotheses for the formation of communal roosts.

The information centre hypothesis proposes that communal roosts are used to communicate knowledge about good foraging areas (Ward & Zahavi 1973); successful foragers provide information about good foraging areas to less successful foragers at the roost. In turn, successful foragers may receive alternate or additional benefits from communal roosting that make it advantageous to travel back to the roost each night (Richner & Heeb 1995; Bijleveld et al. 2010). One benefit is that communal roosts may provide increased predator protection; the presence of several individuals, both at the roost site and at foraging areas, increases predator detection and reduces one's chances of being predated through the dilution effect (Weatherhead 1983; Elgar 1989; Finkbeiner et al. 2012). Additionally, the location and physical characteristics of the roost site may also provide protection from predators (Townsend et al. 2009; Lambertucci & Ruggiero 2013). Finally, there is evidence to suggest that a reduction in the costs of thermoregulation is an important factor driving the occurrence of communal roosts (DuPlessis et al. 1994;

DuPlessis & Williams 1994; McKechnie & Lovegrove 2001; Hatchwell et al. 2009; Chappell et al. 2016). Roosting with others can reduce the energetic demands associated with thermoregulation in several ways. Groups of roosting birds can raise the local ambient air temperature, thereby decreasing the gradient between body temperature and ambient air temperature resulting in less heat lost to the environment (Walsberg 1990; Hayes et al. 1992; Willis & Brigham 2007; Paquet et al. 2016). By huddling close together, birds can reduce their surface area to volume ratio and further decrease heat loss (Vickery & Millar 1984; Canals et al. 1989; Hayes et al. 1992; Boix-Hinzen & Lovegrove 1998; Gilbert et al. 2010; Burns et al. 2013). Some communally roosting birds may further increase energetic benefits by roosting in cavities or other habitat that provides a favourable microclimate and additional protection from wind and rain (Buttemer 1985; Walsberg 1996; Cooper 1999; Sedgeley 2001; Douglas et al. 2017). Moreover, an individual's position within a roost may determine the degree of anti-predator and energy saving benefits received (Weatherhead 1983; McGowan et al. 2005). For example, an individual occupying a more central position within the roost would be less susceptible to predation and incur greater thermal benefits than an individual at the periphery.

As an obligate communally roosting species, swifts presumably receive some energetic and/or fitness benefits from communal roosting; however, little is known about swift behaviour inside the roost. A better understanding of why swifts use roosts can help to determine important habitat for conservation and contribute to designing effective supplementary habitat.

OBJECTIVES

In this study, I examined patterns in how swifts use roosting habitat on both large and small spatial scales. First, I investigated maximum roost size in relation to geographical position and human population density at the northern edge of the swift's range with the objective of identifying sites that support large numbers of swifts (Chapter 2). Next, I explored the positioning of swifts inside one of the largest single roost structures in Canada to determine if roosts are important for facilitating thermoregulatory behaviour (Chapter 3). The results of these two objectives will refine and improve the effectiveness of recovery and management plans for swifts. While little is known about how swifts select and use habitat in general, there has been some recent research on nesting and foraging habitat use (Finity & Nocera 2012; Wheeler 2013; Fitzgerald et al. 2014), but research on roost use is lacking. Because roosting sites may contain large numbers of birds (100s – 1000s) the removal of one of these sites may have severe adverse effects to the population as a whole. The results of this study will allow us to identify areas that are a high priority for conservation, as well as provide information useful for the design and placement of supplementary habitat. By understanding how and why swifts use roosts, it may be possible to construct artificial roost structures that are successfully used as habitat by swifts to supplement areas of low roost availability.

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CHAPTER 2:

Spatial patterns in roost size of chimney swifts at their northern range edge

ABSTRACT

Within the guild of aerial insectivores, the chimney swift (*Chaetura pelagica*) has experienced the steepest population declines in recent decades (COSEWIC 2007). Among other factors, reduced availability of suitable roosting and nesting habitat (primarily masonry chimneys) may be contributing to population declines of chimney swifts. However, this remains conjectural because swift roosting ecology is poorly understood despite the close association between chimney swifts and urban areas. We sought to determine whether patterns existed in how chimney swifts use roosts at a large landscape scale, and hypothesized that larger roost sites may occur in areas where there is less available habitat. Using human population density as a proxy for roost site availability, we tested the prediction that roost size would be larger in areas of low human population density. To do this, we analyzed roost count data collected across Ontario and Quebec between 1998 and 2013 in relation to latitude and human population density. We found that roost size increased with latitude (negative binomial regression; $z = 6.49$, $p < 0.001$, $n = 209$), but was not related to human population density, which does not support our hypothesis that larger roosts occur in areas with less available habitat. We also found that very large roosts (>1000 birds) only occurred at latitudes north of 45 degrees. Due to the large number of swifts these roosts support, the protection of these sites is important for swift conservation.

INTRODUCTION

Communal roosting, the gathering of mostly unrelated conspecifics for periods of rest, is common among several species of birds (Eiserer 1984; Beauchamp 1999). Communal roosting provides potential benefits to individuals through increased foraging efficiency (Ward & Zahavi 1973; Caccamise & Morrison 1986; Marzluff et al. 1996; Wright et al. 2003), increased predator protection (Weatherhead 1983; Elgar 1989; Townsend et al. 2009; Lambertucci & Ruggiero 2013), and reduced thermoregulation costs (Walsberg 1990; DuPlessis & Williams 1994; DuPlessis et al. 1994; Chappell et al. 2016). Communal roosting can also incur costs including increases in resource competition, conspicuousness to predators, and ectoparasite and disease transfer (Brown & Brown 1986; Davis & Brown 1999). Thus, the fitness benefits received from roosting communally are linked to the number of individuals occupying a roost (i.e., group size), and the cost-benefit trade-off suggests an optimal group size should exist (Beauchamp & Fernández-Juricic 2005). However, group size in birds is often highly variable, both within and among species, ranging from a few to thousands of individuals (Brown et al. 1990). Although the associated costs and benefits of varying group sizes are well studied (Brown & Brown 1986; Elgar 1989; Avilés & Tufiño 1998), it remains unclear why there is so much variation in group size (Brown et al. 1990; Beauchamp & Fernández-Juricic 2005; Brown et al. 2013).

Identifying large-scale geographic patterns in group size distributions may be useful in understanding why group size is so variable. Most studies of geographic variation in avian group size have been limited to breeding colonies (Laidre et al. 2008; Jovani et al. 2012; Brown et al. 2013) and few studies have considered variation in group

size at communal roosts (Chapman et al. 1989; Lambertucci 2013). It is important to distinguish between these two types of social groups, as the evolutionary consequences of breeding colonially may differ from those of roosting communally (Barta & Giraldeau 2001; Laughlin et al. 2014). Communally roosting birds may have access to several roost sites and can choose freely among these sites each night, whereas colonially breeding birds must return to the same site each day to care for nestlings. Determining geographical patterns in roost size may provide insight into the evolution of communal roosting, but is also particularly important to identify sites for conservation (i.e., habitat that supports a large number of individuals), especially for species undergoing population declines.

The chimney swift (*Chaetura pelagica*; hereafter, swift), is a communally roosting bird experiencing one of the steepest population declines of all North American birds, leading to a federal listing of Threatened in Canada (COSEWIC 2007). The swift is also provincially listed as Threatened in Ontario (ESA 2017) and Manitoba (Endangered Species and Ecosystems Act 2017), and Endangered in Nova Scotia (Nova Scotia Endangered Species Act 2017). Although a change in insect abundance has been shown to be a likely factor contributing to their decline (Nocera et al. 2012), swifts also face the added pressure of habitat loss (COSEWIC 2007). Historically, hollow trees in old-growth forests supplied natural nesting and roosting habitat, but swifts responded to the industrialization of North America by adopting anthropogenic structures, primarily masonry chimneys, for both roosting and nesting sites (Graves 2004). However, technical advances (e.g., gas or electric heating systems) in exhaust/ventilation have increasingly rendered chimneys unnecessary, or they are being capped or lined with metal, rendering

them unusable to the birds. Recent evidence suggests that the availability of suitable nesting sites is not yet limiting swift populations (Fitzgerald et al. 2014), however chimneys used for roosting are often much larger than chimneys used for breeding and are thus rarer across the landscape. Roosting chimneys are most often found on churches, schools, or industrial buildings and may be used by hundreds to thousands of birds during migration (Steeves et al. 2014). Large roosting chimneys are not as numerous as smaller nesting chimneys, and both types of chimneys are decreasing in number (COSEWIC 2007; Rioux et al. 2010). It follows that although swift populations are not seemingly limited by chimneys for breeding (Fitzgerald et al. 2014), they may instead be limited by chimneys for roosting, a hypothesis that has not been explicitly tested. Little is known about why swifts select preferred roost sites and how they use these roosts (Steeves et al. 2014). A better understanding of the roosting ecology of swifts will yield valuable conservation information and allow for informed management decisions about the preservation of existing habitat or provision of new habitat.

We used monitoring data from multiple sources to examine large-scale geographic patterns in the size of swift roosts at the northern edge of the species' breeding range in Ontario and Quebec, Canada. We hypothesized that roost size would be larger in areas where suitable roosting structures were less available, as swifts would be forced to congregate at fewer sites. Using human population density as a proxy for roost chimney availability (since swifts rely almost exclusively on anthropogenic structures), we predicted that roost size would be larger in areas with low human population densities and thus fewer larger chimneys. Similarly, since human population density generally

decreases with latitude (e.g., Balanovsky et al. 2011), we predicted roost size in our study area would increase with latitude.

METHODS

a) *Chimney swift monitoring data sets*

We used data from the citizen-science programs Ontario Swift Watch and the Quebec Chimney Swift Monitoring Program to identify locations (latitude and longitude) of swift roosts and the maximum number of swifts observed per roost (hereafter, roost size). Data were collected largely by community volunteers between 2009 and 2013 in Ontario and between 1998 and 2013 in Quebec. Volunteers used standardized survey methods (Bird Studies Canada 2009; Rioux et al. 2010) to record the number of swifts using each chimney. Gaps in volunteer-collected data were filled with data collected by Bird Studies Canada (Ontario) and the Canadian Wildlife Service (Quebec). Chimney observations began approximately 30 minutes prior to sunset and continued until 15 minutes after the last swift entered the chimney or it was too dark to visually detect swifts (approximately 30 minutes after sunset). Observers reported the total number of swifts using the chimney by counting the total number of swifts seen entering the chimney and subtracting the number of swifts seen exiting the chimney. Surveys were conducted once per week in Ontario and twice per week in Quebec, beginning approximately on 15 May and continuing for the duration of their occupancy, usually until early September (varies with location). Observations were not made during heavy rain due to the potential influence of rain on the behaviour of roosting swifts, as swifts have been observed entering the roost earlier than expected to seek shelter from heavy rain (Zammuto & Franks 1981).

Chimneys included in this study were identified by trained volunteers, Bird Studies Canada staff (Ontario), and Canadian Wildlife Service staff (Quebec). In Quebec, systematic searches of urban areas were conducted to identify chimneys occupied by swifts. The probability of locating roost chimneys was increased by concentrating searches in older neighbourhoods likely to contain masonry chimneys (see Rioux et al. 2010 for description of Quebec Swift Monitoring Program). In Ontario, chimneys were identified using an adaptive searching method that focused on areas known to have had or likely to contain chimneys used by swifts (large urban areas), complete inventories of open chimneys (small communities), or through casual observations of open chimneys (Fitzgerald et al. 2014). Swift presence or absence was then confirmed using the monitoring protocol described above.

We collected supplemental data for two recently identified roost sites located in Renfrew County, Ontario, in 2012 and 2013. We monitored these sites every 7 days, using the standardized survey protocol beginning on 15 May in 2012 and 1 May in 2013. We continued surveys until swifts departed for autumn migration and were no longer using the roosts (approximately 31 August). Due to the large number of swifts using these roosts (>1000 birds, at times), we confirmed the ground counts using a digital video recorder (Panasonic Lumix DMC-G2K, lens: H-FS 100-300) to video-record the swifts entering the roost and then counting the swifts using slow motion playback (VLC media player v.2.0.6).

Human population densities for municipal regions that contained roost sites were obtained from the 2011 federal census data on the Statistics Canada website (Statistics Canada 2011).

b) Statistical analyses

We quantitatively differentiated roost sites from nesting sites by excluding chimneys with maximum counts of ≤ 8 swifts. We chose a threshold of 8 swifts because groups of related individuals (i.e., family groups) of swifts can include the breeding pair, an average of four offspring, and occasionally 1-2 helpers at the nest (Dexter 1952; Fischer 1958).

Maximum roost size, the largest recorded count at each roost site in all years of observation, was used in all further statistical analyses.

Roost count data were overdispersed compared to a standard Poisson distribution (Overdispersion test (Cameron & Trivedi 1990): $z = 3.47$, $p < 0.001$). To address this issue, we used a negative binomial regression to examine the effect of latitude, longitude, human population density, month, and year on swift roost size. The negative binomial model includes an extra dispersion parameter that measures the extra variability, which allows more flexibility in modeling overdispersed data compared to Poisson models (Lawless 1987; Gardner et al. 1995; Hilbe 2014). Both latitude and human population density were included in the model as they were only weakly correlated (Pearson correlation coefficient = -0.3). Month was included as a categorical factor (levels: May, June, July, August, September) because the number of swifts occupying roosts throughout the breeding season varies with spring migration, nesting, post-nesting, and autumn migration (Steeves et al. 2014). Year was included as a fixed factor because swift populations have experienced declines over the period of time data were collected from. Upon inspection of scatterplots of each response variable plotted against maximum roost size, we also included squared latitude as a response variable due to a possible quadratic relationship.

Working from a global model (all variables listed in Table 2.1), we used a stepwise backward elimination approach to remove variables that were statistically insignificant ($\alpha > 0.05$), starting with the least significant, and had the poorest relative parameter estimates. We assessed overall fit of the model using half-normal plots and residual plots. All statistical analyses were conducted with the program R, version 3.0.1 (R Core Team 2013) and the MASS package for negative binomial regression (Venables & Ripley 2002). The ggmap package was used for mapping (Kahle & Wickham 2013).

RESULTS

We identified 209 roost sites across Ontario (92) and Quebec (117) between the years 1998 and 2014 (Figure 2.1). Roost size varied substantially, ranging from 9 to 2489 swifts with a median roost size of 48 swifts. Median roost size in Ontario was 41 swifts (range: 9 – 2489) and median roost size in Quebec was 60 swifts (range: 9 – 1610). We identified 6 very large roosts that had a maximum size of ≥ 1000 swifts. The largest roost was in Rolphton, ON, with a maximum count of 2489 swifts. The other large roosts were in Sault Ste. Marie, ON (2302 swifts), Mont-Laurier, QC (1610 swifts), Pembroke, ON (1358 swifts), Saint-Georges, QC (1311 swifts), and North Bay, ON (1000 swifts).

The best-fit model describing chimney swift roost size retained the variables of latitude, longitude, and month (Table 2.2). Variables related to squared latitude, human population density and year were not retained.

Roost size was most strongly associated with an increase in latitude (Figure 2.2), although there was also a slight tendency for roost size to increase in a westward

direction (Figure 2.3). While small roosts were found at all latitudes, extremely large roosts, containing ≥ 1000 swifts, were only observed at latitudes above 45°N .

In the best-fit negative binomial model, swift roost size was negatively associated with the months of June through September compared to the month of May (Table 2.2). Overall, swift roosts were largest in May and June (during spring migration) and smallest in July (middle of breeding season) and September (autumn migration; Figure 2.4).

DISCUSSION

We found a geographical gradient in maximum swift roost size, where the largest roosts occurred at greater latitudes within the swift's range in Ontario and Quebec. There was also a slight tendency for roosts to be larger in a westward direction. Extremely large roosts, comprised of 1000 birds or more, only occurred at latitudes above 45°N . Although this pattern supports our predictions about latitude, it does not support the hypothesis that roosts are larger where habitat is limiting, as we found no statistically significant relationship between roost size and human population density.

We expected that roost size would vary with human population density because swifts rely on anthropogenic structures and thus human population density could act as a proxy for available roosting chimneys. However, this hypothesis was not supported by our findings. An alternative, but untested, explanation is that roost size may be influenced by specific roost characteristics, such as the size or type of chimney, that are not necessarily linked to human population density (or the abundance of chimneys). For example, colonies of cliff swallows (*Petrochelidon pyrrhonota*) were found to be larger

on substrate types that provided the most area for nesting (Brown et al. 2013). The area available to swifts inside the chimney may limit group size (i.e., larger chimneys can physically support more individuals). In cavity roosting bats, group size was positively correlated with the volume available for roosting (Olson & Barclay 2013). Recent evidence suggests that nesting swifts select chimneys with greater internal areas (Fitzgerald et al. 2014) and larger diameter trees in natural habitat (Zanchetta et al. 2014). Thus, larger structures may attract more swifts.

Another possible factor contributing to the observed latitudinal gradient in roost size may be ambient air temperature. It is possible that swifts could collectively reduce their thermoregulatory demands by forming larger aggregations at more northerly latitudes where mean ambient temperatures are cooler (Montgomery 2006). Larger groups can effectively reduce heat loss by huddling close together to minimize their surface area to volume ratio (Chaplin 1982; McKechnie & Lovegrove 2001; Gilbert et al. 2010), as well as increase the temperature of the roost cavity (Willis & Brigham 2007). This may be an important energy conservation strategy for swifts, especially during migration when overnight temperatures are the lowest.

Roost size varied throughout the breeding season and was greatest during the months of May and June. During May and early June, swifts are migrating northwards and are known to gather in large numbers at roosts (Steeves et al. 2014). The smallest roost sizes were observed in July, when breeding birds disperse from roosting chimneys to nesting chimneys, leaving behind the non-breeding individuals at roost sites (Steeves et al. 2014). Roost size increased slightly in August, as swifts gather at roost sites again during the southward autumn migration. During the autumn migration, swifts depart the

most northerly locations first and have largely vacated Ontario and Quebec by the end of September, accounting for the smaller roost sizes observed during this time (David 1996; COSEWIC 2007).

The observed pattern of increasing roost size and latitude provides an interesting parallel to Bergmann's Rule, where individual body size is known to increase for many species of endotherms when they occur at higher latitudes (reviewed in: Ashton 2002; Meiri 2011). Our study is one of the few studies to identify a similar pattern in groups of social animals. A positive relationship between animal group size and latitude has been found to exist in eusocial insects, such as ants, where fasting endurance has been suggested as an explanation for larger northern colonies compared to tropical colonies (Kaspari & Vargo 1995). Alternatively, in Greenland, the trend for increasing colony size with latitude in thick-billed murre (*Uria lomvia*) colonies was linked to predictable food blooms that occurred as sea ice retreated (Laidre et al. 2008). It is possible that prey availability (i.e. flying insect concentrations) could influence roost size. The factors behind increasing group size for swifts at more northerly latitudes needs further exploration, particularly in terms of thermoregulation and how swifts position themselves in the roost (sensu Chapter 3).

There is still much to be learned about swift roost size that is not explained by this study. For example, why we observed that small roosts can occur in the north and also that large roosts can occur in the south remains unresolved. Nonetheless, the identified patterns in roost size have important conservation and management implications for swifts. Swifts that use large roosts are arguably more at risk from adverse stochastic events than those in small roosts, due to the large proportion of the swift population that

these roosts support. Indeed, the number of swifts at the six large roosts (>1000 swifts/roost) in this study account for 38% of the estimated swift population of Canada (COSEWIC 2007). The largest roost in our study accounted for 9.5% of the total estimated Canadian swift population. Thus, the removal or closure of a single large roost could have strong negative effects on regional and national swift populations. To date conservation measures for swifts have focused largely on supplying artificial structures for swifts to nest within, however these have failed to attract swifts at the northern edge of their range (Finity & Nocera 2012). Artificial roosting structures have been much less prevalent, but have been attempted with variable success (Nocera unpublished data). The opportunistic placement of these structures may be a factor in their limited use by swifts at the northern edge of their range, as they are often placed in areas that are logistically convenient rather than in areas where large numbers of swifts are found or where habitat may be limiting.

The results of this study could be used to a) more effectively place artificial swift roosting habitat (e.g., where roosts are sparsest) and to b) identify roosts in need of conservation (e.g., large roosts where a disproportionate amount of swifts could be adversely affected). Specifically, we have identified 6 roost sites (Rolphton, ON, Sault Ste. Marie, ON, Mont-Laurier, QC, Pembroke, ON, Saint-Georges, QC, and North Bay, ON) that are in need of immediate protection and conservation as they are used by a large proportion of the Canadian swift population.

FIGURES AND TABLES

Figure 2.1 Map of chimney swift roosting sites showing maximum size across Ontario and Quebec, Canada (n = 209). Derived from data collected by Bird Studies Canada and Canadian Wildlife Services between 1998 and 2013. Roosts are defined as a site used by 9 or more swifts.

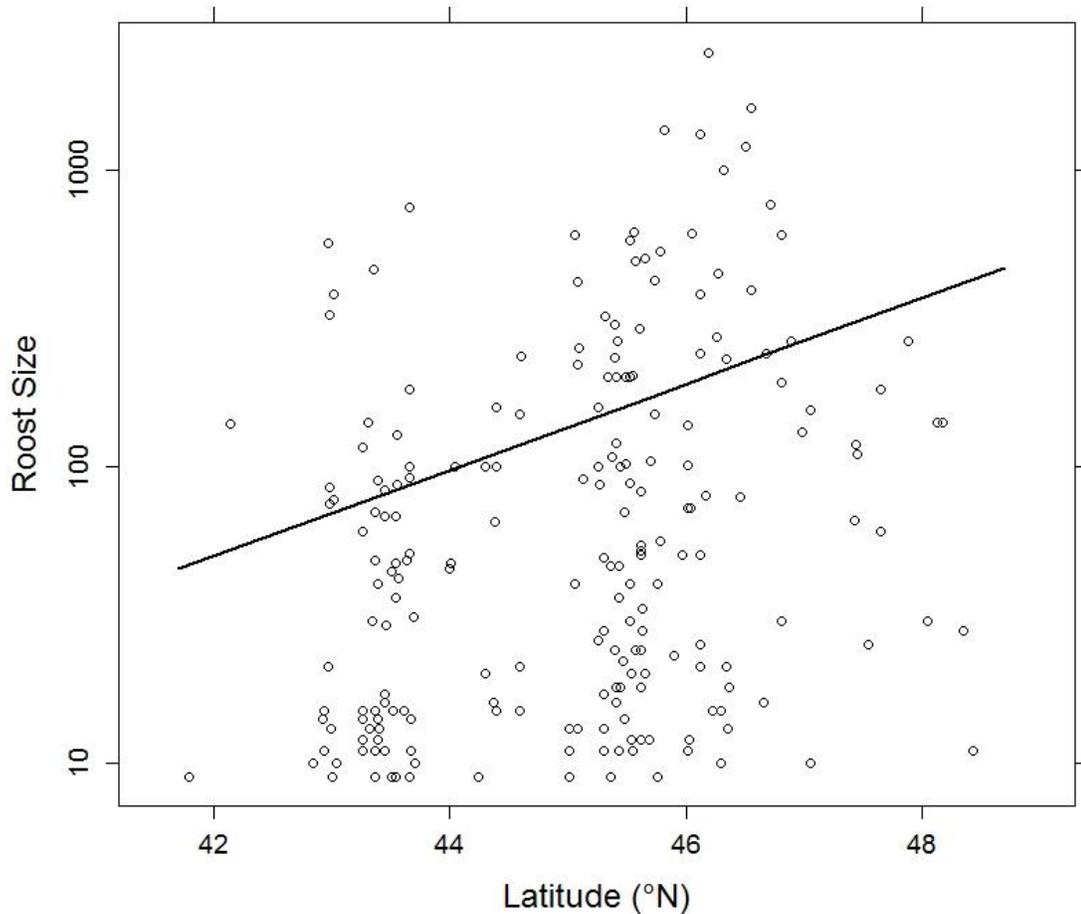


Figure 2.2 Maximum number of chimney swifts counted at each roost site (n = 209) compared to the latitudinal position of the roost. Roost size is shown on a log-scale for visual representation although raw data were used in analyses. The line represents the relationship between maximum roost size and latitude using a negative binomial regression. Data were collected from across Ontario and Quebec between 1998 and 2013.

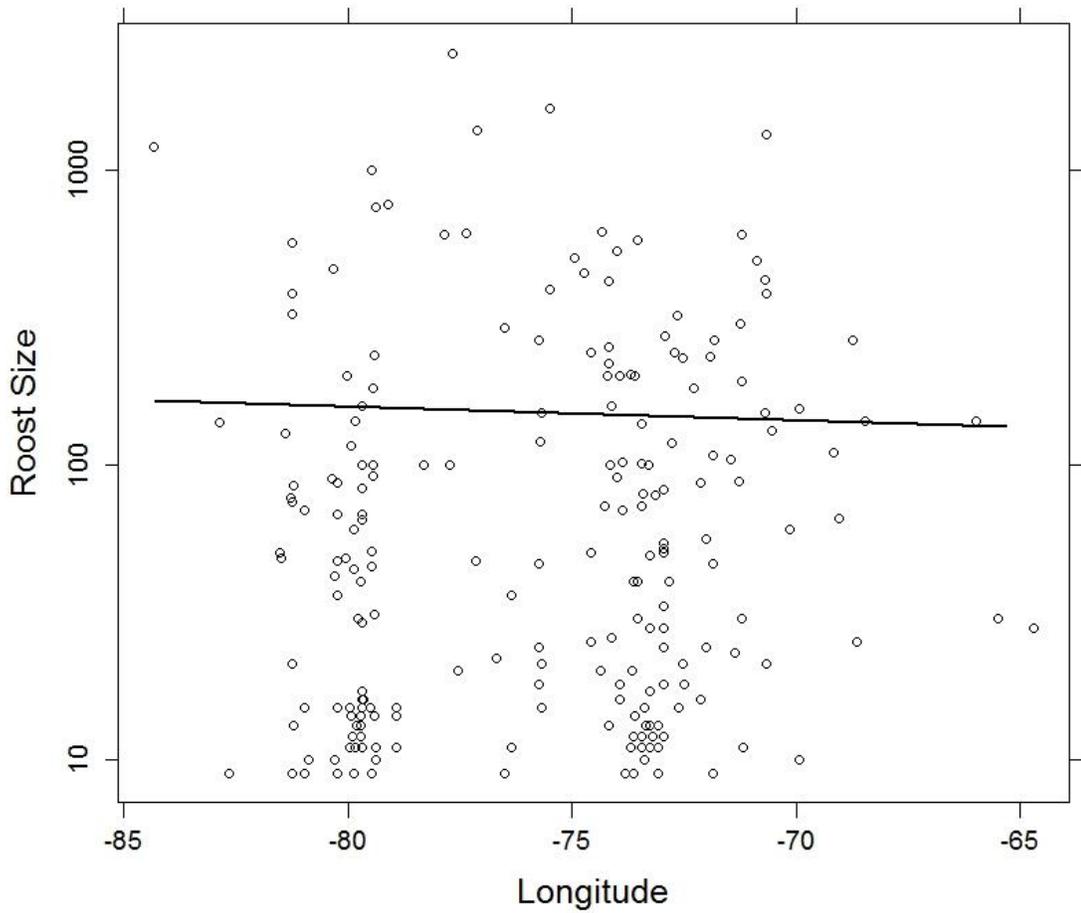


Figure 2.3 Maximum number of chimney swifts counted at each roost site ($n = 209$) compared to the longitudinal position of the roost. Roost size is shown on a log-scale for visual representation although raw data were used in analyses. The negative binomial regression line is shown for the relationship between maximum roost size and longitude. Data were collected from across Ontario and Quebec between 1998 and 2013.

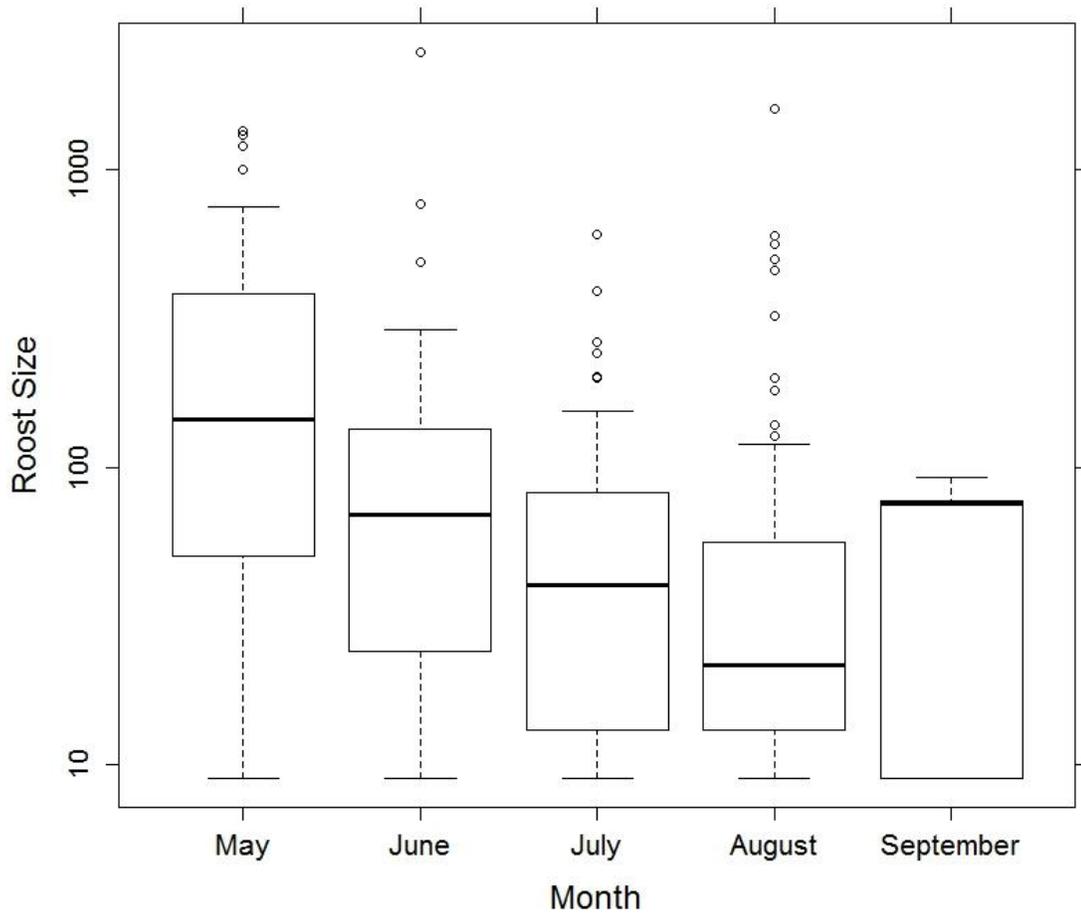


Figure 2.4 The maximum number of chimney swifts recorded for each roost in Ontario and Quebec by month (May: $n = 52$; June: $n = 40$; July: $n = 42$; August: $n = 70$; September: $n = 5$). Roost size is shown on a log-scale for visual representation although raw data were used in analyses. Boxes represent the quantiles and median and circles fall outside the 95th percentile.

Table 2.1 Parameter estimates and standard errors (SE) for the predictive variables of chimney swift roost size in Ontario and Quebec between 1998 and 2013 for the global negative binomial regression model (* indicates significance at $\alpha < 0.05$).

Parameter	Estimate	SE	Z statistic	P-value
Latitude	5.67	3.30	1.72	0.0857
Latitude²	-0.0567	0.0365	-1.51	0.132
Longitude	-0.0206	0.0402	-5.14	<0.001*
May	-183	83.5	-2.19	0.0287*
June	-0.699	0.235	-2.97	0.003 *
July	-1.30	0.238	-5.47	<0.001*
August	-0.913	0.215	-4.24	<0.001*
September	-1.06	0.556	-1.91	0.0561
Pop. Density	-0.00004	0.00007	-0.528	0.597
Year	0.0143	0.0215	0.666	0.506

Table 2.2 Parameter estimates and standard errors (SE) for the predictive variables of chimney swift roost size in Ontario and Quebec between 1998 and 2013 for the best fit negative binomial regression model (* indicates significance at $\alpha < 0.05$).

Parameter	Estimate	SE	Z statistic	P-value
Latitude	0.715	0.110	6.49	<0.001 *
Longitude	- 0.205	0.0384	-5.34	<0.001 *
May	- 42.2	7.61	-5.55	<0.001 *
June	- 0.656	0.232	-2.82	0.005 *
July	- 1.36	0.230	-5.93	<0.001 *
August	- 0.964	0.206	-4.67	<0.001 *
September	- 1.20	0.539	-2.22	0.026 *

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CHAPTER 3:

Fine-scale spatial patterns of chimney swift aggregations inside a roost

ABSTRACT

One of the proposed advantages of communal roosting in birds is a reduction in the costs of thermoregulation. As thermoregulatory benefits are directly linked to the distance between roosting birds, we examined whether temperature is related to inter-bird spacing in roosting chimney swifts (*Chaetura pelagica*) in northeastern Ontario. To test the hypothesis that huddling is used to reduce the costs of thermoregulation, we predicted that swifts would cluster more at colder temperatures. We mounted an all-weather camera atop a 61 m tall industrial masonry chimney, one of the largest swift roosts in the Ontario. We deployed temperature loggers inside the chimney and obtained ambient air temperature from a nearby weather station. From 16 May – 24 July 2013, we captured hourly images of the positions of roosting swifts at night. We used image analysis software to mark the angular positions of all roosting swifts, and calculated mean angles of orientation (preferred direction) inside the roost and the circular variance (i.e., the concentration of swifts around the mean angle). We used a Gamma regression to relate temperature inside and outside the roost to the clustering of swifts around the mean angle for 3 time periods (pre-nesting, nesting, and post-nesting). Converse to our prediction, swifts were closer together when ambient air temperatures were warmer in all periods (pre-nesting ($p < 0.001$, $n = 168$), nesting ($p < 0.001$, $n = 224$), and post-nesting ($p < 0.001$, $n = 135$)). Our findings suggest that swifts do not increase clustering intensity in response to colder temperatures, but instead they increase clustering intensity in response to

warmer ambient temperatures. We suggest clustering may be used by chimney swifts as an energy saving mechanism during periods of lowered food availability, as flying insect concentrations are dependent on ambient air temperature.

INTRODUCTION

It is energetically costly for animals to maintain a constant body temperature over a range of environmental temperatures, especially at low ambient temperatures or during periods of inactivity (McKechnie & Lovegrove 2002). Thermoregulatory costs are particularly high for small endotherms, that must balance metabolic heat production with relatively rapid heat loss due to a larger surface area-to-volume ratio (Merola-Zwartjes 1998; McKechnie & Lovegrove 2002). Alternative physiological strategies, such as torpor, can conserve energy by downregulating metabolism and thus body temperature in response to low ambient air temperatures or decreased energy availability (McKechnie & Lovegrove 2002; Geiser 2004). However, these strategies require inactivity and reduced responsiveness which means animals cannot allocate energy to other fitness-enhancing behaviors, such as vigilance or social interactions, and may be more susceptible to predation (Gilbert et al. 2010; Carr & Lima 2013).

Animals may also modify their behaviour to minimize heat loss, such as selecting sheltered sites that provide favourable microclimates (i.e., milder temperatures and protection from rain/wind) during periods of rest. Sheltered sites reduce radiative heat loss by decreasing the temperature gradient between ambient air and body temperature, and reduce forced convective heat loss from wind (Bakken 1990; Walsberg 1990; Hayes et al. 1992; Walsberg 1996). Social animals can further reduce the costs of thermoregulation by huddling together to reduce their collective surface area available for heat loss (Contreras 1984; Vickery & Millar 1984; Canals et al. 1997; Gilbert et al. 2010). Groups of huddling individuals have been shown to maintain higher body

temperatures and reduce energy expenditure relative to single individuals (DuPlessis & Williams 1994; Ancel et al. 1997; McKechnie et al. 2006; Gilbert et al. 2007; Gilbert, Blanc, et al. 2008; Chappell et al. 2016). A classic example of huddling is observed in breeding male emperor penguins (*Aptenodytes forsteri*) that cluster in large groups to survive the extreme Antarctic winter (Ancel et al. 1997; Gilbert, Blanc, et al. 2008). Emperor penguins involved in huddles can reduce energy expenditure by 17% compared to individuals not involved in huddles (Ancel et al. 1997). Even in less extreme climates, white-backed mousebirds (*Colius colius*) at 15°C can reduce their resting energy expenditure by 50% when involved in a huddle compared to single birds (McKechnie & Lovegrove 2001). Metabolic heat production from huddling individuals can also warm the local environment, resulting in greater energy savings by decreasing the difference between ambient air temperature and body temperature (Walsberg 1990; Hayes et al. 1992; DuPlessis et al. 1994; Willis & Brigham 2007). For example, huddled big brown bats (*Eptesicus fuscus*) in tree cavities raised the cavity temperature by 7°C (Willis & Brigham 2007). In short-tailed field voles (*Microtus agrestis*) local heating accounted for 25-50% of the energy savings in huddles compared to single individuals (Hayes et al. 1992).

Reducing thermoregulatory costs is one of the proposed advantages of communal roosting in birds (Walsberg 1990; DuPlessis et al. 1994; DuPlessis & Williams 1994; Beauchamp 1999). Communal roosts can facilitate energy savings through social thermoregulation (i.e., huddling and local heating), as well as provide a sheltered microclimate in cavity-roosting species (DuPlessis et al. 1994; Douglas et al. 2017). At 5°C, cavity-roosting green woodhoopoes (*Phoeniculus purpureus*) reduced their energy

expenditure by 31% over singly roosting birds which resulted in increased overwinter survival (DuPlessis & Williams 1994). The degree of energy savings conferred from huddling are related to ambient temperature and the intensity of huddling (Canals et al. 1997; Gilbert, Robertson, et al. 2008). Most studies have assessed roosting in birds at broad spatial scales in terms of roost-site selection; however, few studies have examined *how* birds use these roosts in terms of density or intensity of huddling behaviour. Gilbert *et al.* (2008) observed that the frequency of huddling in emperor penguins increased with lower ambient temperatures and higher wind speeds, but the intensity of huddling (i.e., how tightly birds clustered together) increased only with decreasing ambient temperature. Similarly, house sparrows (*Passer domesticus*) decreased inter-individual distance and formed tighter huddles as ambient temperature decreased (Beal 1978; Burns et al. 2013). This suggests the formation of communal roosts in social birds may serve a thermoregulatory benefit.

The chimney swift (*Chaetura pelagica*; hereafter, swift), a small aerial insectivore, forms large communal roosts in vertical hollows throughout its breeding range in North America (Steeves et al. 2014). Swifts roost almost exclusively in anthropogenic structures, predominately masonry chimneys. Although this synanthropic relationship makes swifts readily available for study, and our knowledge of habitat selection is improving, little is known about the roosting behaviour of swifts and how they distribute themselves within roosts. Roost sites are likely important for survival as swifts do not roost in the open, and it has been suggested that roost site selection may be influenced by roost temperature (COSEWIC 2007). The behaviour of diurnal insectivores is energetically costly, especially for swifts that spend most of the day foraging while in

flight (Walsberg 1983; Steeves et al. 2014). Moreover, the abundance of flying insect prey can be highly variable, as it can be affected by small changes in weather conditions, such as temperature and wind speed (Glick 1939; Glick 1957; Taylor 1963; Winkler et al. 2013). Therefore, for swifts that budget energy daily, roost site selection and roosting behavior of swifts may be important energy conservation strategies affecting fitness and survival. While huddling behaviour has been observed in some other swift species, it has not been quantitatively described for chimney swifts (McNab & Bonaccorso 1995). Swifts have been experiencing steep population declines in recent decades (COSEWIC 2007). Thus, if roost structures represent critical habitat for swifts, a thorough understanding of how swifts select and use roost sites is crucial for their recovery and conservation.

We examined huddling behaviour in relation to ambient air temperature and temperature inside a communal roost of swifts in northeastern Ontario, Canada. We tested the hypotheses that communal roosts of swifts provide thermoregulatory benefits through a) the provision of a favourable microclimate and b) huddling with conspecifics. We predicted roost temperature should be warmer than ambient air temperature, thus lowering the gradient between body temperature and the environment to reduce heat loss. We predicted that swifts would cluster closer together as both ambient air temperature and internal roost temperature decreased to minimize the total surface area exposed to the environment for heat loss.

We also examined if swifts preferred to roost in a particular orientation/direction inside the roost.

METHODS

a) Study site

The study was conducted at a swift roost located in a large industrial chimney in Renfrew County, Ontario, Canada (46°03'12.0"N 77°21'53.9"W). This is one of the largest known roosts in Canada as up to 600 swifts roost nightly in this chimney between May and August each year (Chapter 2). The roosting site is a 61m tall cylindrical stack with a 1.07m diameter opening at the top. The stack is composed of two layers, an inner brick lining (13.1 cm thick) and a concrete exterior (15 cm thick), separated by an air space (7.5 cm thick). The stack is currently operational and has a constant air flow of approximately 3.0 m³/s (velocity: 4.0 m/s). The stack is located approximately 200 m from the Ottawa River, and is surrounded by a 50 ha industrially developed area (~ 70 buildings), beyond which is primarily mixed forest and wetlands.

b) Video and temperature collection

We mounted an outdoor network security camera (D-Link™, DCS-7110) at the opening of the swift roost from May to July, 2013. The camera recorded 24 hours a day to a network video recorder (D-Link™, DNS-726-4) secured to the base of the stack. Video footage was downloaded daily via a laptop and stored on external hard drives. We hung HOBO pendant® temperature loggers (UA-001-08, ±0.47°C) inside one side of the stack at depths of 5m and 10m to record hourly roost temperature. However, for our analyses we used temperature data only from the 5m depth as swifts were not observed roosting below this depth at this roost site. Hourly local ambient air temperatures were collected from a local weather station (~2 km from the roost site) at an altitude of 60m.

c) Image analysis

We selected still frames of the video taken on the hour between 22:00 and 05:00 (for a maximum of 8 images/night) between May 16 and July 24, 2013. Although swifts occupied the roost outside of these hours, we selected these times based on the period in which the camera's infra-red light illuminated the inside of the roost so all images were of comparable brightness and quality. Additionally, we never observed birds entering the roost after 22:00 or exiting before 05:00. We excluded images in which heavy rain or condensation on the camera lens obscured the images. For each image we marked the angular position (i.e., direction) of each individual swift relative to the middle of the roost using Tracker Video Analysis and Modelling Tool (v.4.8.3; Brown 2013).

d) Statistical analysis

To examine the thermal microclimate of the roost, we used a linear regression to model the relationship between overnight ambient air temperature and the temperature difference between roost temperature and overnight ambient air temperature. Positive temperature differentials indicated that roost temperature was greater than ambient air temperature and negative values indicated that roost temperature was less than ambient air temperature.

We visually examined the relationship between Julian day and the mean number of swifts occupying the roost and identified three distinct periods based on the variation in the number of swifts occupying the roost (Figure 3.1). The pre-nesting period (16 May – 6 June) was categorized by the high degree of variability in the number of swifts occupying the roosts each night and corresponded with the spring migration period. A

relatively constant number of swifts occupied the roost during the nesting period (7 June – 6 July), as resident non-breeding swifts remained at the roost and breeding swifts dispersed to nest. The post-nesting period (7 July – 24 July) was marked by a steady increase in the number of swifts at the roost as the breeding swifts returned before beginning the autumn migration. To control for possible behavioral and group composition differences associated with each period, we analyzed each period separately.

We calculated the mean angle of orientation, mean vector length (r) and circular variance ($1-r$) for each hour according to Batschelet (1981). The circular variance is a measure of dispersion around the mean angle of orientation, and varies between 0 and 1 (Mardia 1972; Batschelet 1981; Jammalamadaka & SenGupta 2001). As the circular variance approaches 0, swifts are increasingly concentrated around the mean angle (i.e., more clustered around the preferred direction), and conversely a circular variance of 1 indicates swifts are uniformly distributed around the walls of the roost (i.e., there is no preferred direction for roosting). Thus, circular variance acts as a proxy for huddling intensity. We used Raleigh's test of significance to determine if the mean angle varied from a uniform distribution during the pre-nesting, nesting, and post-nesting periods (Batschelet 1981; Jammalamadaka & SenGupta 2001).

To test for an effect of ambient and/or roost temperature on huddling intensity (i.e. circular variance) in roosting swifts, we used a generalized linear model (GLM) due to non-normality (Nelder & Wedderburn 1972). Specifically, we used a gamma GLM with a log link to model circular variance as a function of internal roost temperature and ambient air temperature at 60m during the pre-nesting, nesting, and post-nesting periods. The distribution of our response variable, circular variance, cannot be negative and was

not significantly different from a gamma distribution in all time periods (Kolmogorov-Smirnov test; pre-nesting: $D = 0.0782$, $p = 0.2557$; nesting: $D = 0.0718$, $p = 0.183$; post-nesting: $D = 0.1159$, $p = 0.0661$), thus making the gamma GLM an appropriate choice to model this relationship (Faraway 2006).

All statistical analyses were done using R, version 3.0.1 (R Core Team 2013) with packages CircStats (Lund & Agostinelli 2012), circular (Agostinelli & Lund 2013) and MASS (Venables & Ripley 2002).

RESULTS

Roost and ambient air temperatures

During the study period, internal roost temperature never fell below 18.6°C nor exceeded 26.8°C , and had a mean temperature of 23.5°C . Overnight ambient air temperature at 60m was much more variable, ranging from 3.7°C to 27.7°C , with a mean of 15.8°C . Mean ambient air and roost temperatures were lowest during the pre-nesting period, and increased in the nesting and post-nesting periods (Table 3.1). On average, roost temperature was 9.5°C , 7.4°C , and 6.1°C warmer than ambient air temperature during the pre-nesting, nesting, and post nesting periods respectively. There was a significant tendency for the temperature differential to increase with decreasing ambient air temperature ($n = 527$, $R^2 = 0.8375$, $p < 0.001$; Figure 3.2).

Angle of Orientation

The mean angle of orientation (where true north is 0°) ranged from $123^{\circ} - 230^{\circ}$ during the pre-nesting period, $147^{\circ} - 225^{\circ}$ during the nesting period, and $159^{\circ} - 224^{\circ}$

during the post-nesting period. We found that swifts showed a strong preference for roosting on the south wall of the roost in all periods (pre-nesting: $r = 0.934$, $p < 0.001$; nesting: $r = 0.972$, $p < 0.001$; post-nesting: $r = 0.985$, $p < 0.001$; Figure 3.3).

Huddling intensity

Ambient air temperature was a significant predictor of variance around the mean angle of orientation in the pre-nesting, nesting and post-nesting periods (Table 3.2). In all three time periods, warmer ambient air temperatures were associated with a decrease in variance around the mean angle of orientation (Figure 3.4). Swifts were more clustered around the mean angle of orientation as the ambient air temperature increased. Roost temperature was not a significant predictor of clustering around the mean angle of orientation during the nesting period, but was significantly associated with clustering during the pre-nesting and post-nesting periods (Table 3.2, Figure 3.5). In the pre-nesting period, higher roost temperatures were associated with more variance around the mean angle (i.e., swifts were less clustered), while in the post-nesting period higher roost temperatures were associated with less variance around the mean angle (i.e., swifts were more clustered; Figure 3.5).

DISCUSSION

We found that our study roost provided a thermally stable microclimate that buffered against both low and high temperatures, and that swifts tended to aggregate on the inner south wall of the roost. We also found that swifts were more closely huddled as ambient temperatures outside the roost increased, which is contrary to what we predicted.

Our results do not support our hypothesis that swifts huddle purely for thermoregulatory benefits. To our knowledge, no previous study has examined the intensity of huddling of a species that also roosts within cavities in relation to temperature.

Roost temperature

Ambient temperature influences the rate of energy expenditure, as the amount of heat lost depends on the difference between ambient temperature and body temperature (Reinertsen 1983). The roost in our study provided a thermal environment that was more stable than ambient air temperature; the temperature recorded in the roost was warmer and varied much less. The difference between ambient air temperature and roost temperature decreased as ambient air temperature increased until approximately 25°C, at which point roost temperature was lower than ambient air temperature (Figure 3.2). This observation warrants further investigation into possible lower and upper temperature limits influencing roost site selection by swifts. The stable temperature recorded in the roost is similar to what has been reported for natural tree cavities, which have been shown to buffer daily temperature fluctuations and produce a lag in temperature oscillations inside the cavity relative to ambient air temperature (Wiebe 2001; Coombs et al. 2010; Gruebler et al. 2014). Several species that are secondary users of cavities select roost sites that provide thermally favourable environments resulting in energy savings and increased fitness (Kendeigh 1961; DuPlessis & Williams 1994; Sedgeley 2001). For instance, when cavity sites were not limiting, tree swallows (*Tachycineta bicolor*) exhibited a preference for east and south-facing locations, which were also the warmest (Ardia et al. 2006). Cooper (1999) found the nocturnal energy savings of mountain chickadees (*Poecile gambeli*) and juniper titmice (*Baeolophus griseus*) roosting in

cavities ranged from 23.8 – 37.6%, and these energy savings increased fasting endurance. Similarly, acorn woodpeckers (*Melanerpes formicivorus*) that nested in warmer cavities increased reproductive success (Hooge et al. 1999).

We can draw only modest conclusions from our single study roost site, as the thermal properties of cavities can vary with size, insular properties, and solar rays (Clement & Castleberry 2013). We suggest that swifts may find masonry chimneys attractive for roosting because they offer more stable thermal environments due to the thermal properties of the chimney materials. Masonry materials, such as brick and concrete, have a high heat capacity, that can store heat energy well and release it slowly over time (Kontoleon et al. 2013). Thermal properties of masonry materials vary with thickness and density, where thicker walls increase thermal inertia (Kontoleon et al. 2013). Swifts may find our study roost particularly attractive due to the insulating double-layered wall and the constant flow of warm air. That our study roost is among the largest known roost sites in Canada (Chapter 2) lends support to the hypothesis that swifts seek out roosts with favourable microclimates. However, further investigation of the thermal characteristics of occupied and unoccupied roost sites is needed to determine if swifts select roosts based on microclimate.

Preferred Direction for Roosting

The strong preference for swifts to cluster on the south wall of the roost suggests there is a thermoregulatory benefit associated with this behaviour. In the northern hemisphere, the south-facing sides of tree trunks have been measured to be up to 12°C warmer than the north-facing sides (Derby & Gates 1966). Therefore, swifts roosting on the south wall of a roost potentially incur thermal benefits through conductive heat

transfer of stored heat through the wall of the roost. Although we did not measure temperature at different locations in our study roost, the air cavity between the outer concrete and inner brick wall should allow heat to dissipate evenly, and it seems unlikely that local heating would occur on the innermost walls. Despite this, swifts in our roost showed a strong directional preference for roosting on the south wall of the roost. We speculate that roosting on the south wall may be derived from when swifts historically roosted in natural habitat that would be subject to local heating from sun exposure. Because swifts may not always roost at the same site and change roosts frequently during migration, it would be beneficial to always roost on the warmest wall. Heating by solar radiation may be an important factor determining selection of roost sites, as swifts preferentially selected nesting chimneys that extended higher above rooflines providing a larger area to be heated (Fitzgerald et al. 2014). To our knowledge, no other study has examined roosting direction preference; however, our findings are similar to studies of other cavity users, such as tree swallows (Rendell & Robertson 1994; Ardia et al. 2006), woodpeckers (Inouye 1976), and big brown bats (*Eptesicus fuscus*; Kalcounis & Brigham 1998), that have been observed to show a preference for cavities with south-facing entrances, which have been shown to be warmer (Wiebe 2001).

It is difficult to draw conclusions from one roost, as it is possible there are specific characteristics of our study roost that may have caused swifts to avoid the north-facing wall (e.g., differences in air flow, protection from precipitation). However, Dexter (1969) observed a similar pattern in nesting swifts that showed a preference for building nests on the south and west walls of chimneys, which lends support to a thermoregulatory link to direction preference in swifts. To test the hypothesis that swifts select south-facing

walls due to thermal advantages, it would be necessary to examine the directional preference of swifts inside multiple chimneys in relation to the temperature differences of internal walls. Future studies of nesting swifts could examine the effect of nest orientation on reproductive fitness, by measuring clutch size and/or fledgling success rate.

Degree of huddling

We did not find that swifts huddled more densely in response to cooler temperatures as expected if swifts used huddling only to conserve heat. Instead, swifts were more closely huddled at warmer ambient air temperatures during all periods. While there was a slight trend for swifts to huddle more closely with decreasing roost temperature during the pre-nesting period, this was not observed in any other period. This seemingly counter-intuitive relationship with roost temperature may be an artefact of low variability and range in temperatures we observed inside the roost. The internal temperature of our roost never dropped below 18.6°C, which may not have presented a substantial enough thermoregulatory challenge to influence the degree of huddling.

However, we did find that huddling intensity increased with increasing ambient air temperature in all periods. While huddling can provide thermoregulatory benefits at low ambient temperatures, it can also provide other energetic benefits (Gilbert et al. 2010). One such benefit is that huddling can reduce energy expenditure during periods of lowered food availability through the reduction of metabolic rates, resulting in a decrease in overnight mass loss and increased survival (McKechnie et al. 2006; Hatchwell et al. 2009; Gilbert et al. 2010; Burns et al. 2013). Therefore, swifts may increase huddling to conserve energy in response to lowered flying insect abundance, which is largely

influenced by weather conditions, such as temperature and wind speed (Glick 1939; Glick 1957; Winkler et al. 2013). One study found flying insect abundance reached a maximum at 25°C, with fewer airborne insects occurring above and below this temperature (Glick 1939; Glick 1957). In a more recent study in Ithaca NY, maximum flying insect abundance was observed at 18.5°C (Winkler et al. 2013). At our study roost, ambient temperatures ranged from 3.7- 27.7°C, around which there would be substantial variation in airborne insect availability. Thus, as ambient air temperature increased above the local maximum of flying insect abundance, prey availability would decrease and huddling would become more prevalent to conserve energy. The link between ambient temperature and prey availability is further supported by the observation that the time between feeding visits of adult swifts to their young increased with warmer temperatures, suggesting insects were harder to find as ambient temperature increased (Zammuto et al. 1981).

Restricted food availability has been shown to initiate torpor as an energy conservation strategy in many bird species (McKechnie & Lovegrove 2002; Ben-Hamo et al. 2010). However, torpor may incur other costs, such as rewarming time and increased predation risk, so huddling may be a preferred strategy in social birds (Carr & Lima 2013; Wojciechowski et al. 2011). For example, food-deprived speckled mousebirds (*Colius striatis*) maintained a higher rest-phase body temperature if they huddled compared to single individuals (McKechnie et al. 2006). Swifts have been observed to show a heterothermic response to decreasing ambient temperatures and enter torpor when held at ambient temperatures of 5°C (Ramsey 1970). Therefore, based on Ramsey's (1970) observations, temperatures in our study roost never declined to a point

where complete torpor would be employed as a thermoregulatory mechanism by swifts. However, within a group of roosting swifts thermoregulatory strategies may vary depending on factors such as environmental conditions, food availability, body condition, and/or life cycle stage as seen in some birds (Wojciechowski et al. 2011; Shipley et al. 2015) and Australian sugar gliders (*Petaurus breviceps*).

We also observed that the huddling intensity of swifts was lowest during the pre-nesting period, and greatest during the nesting and post-nesting periods. During these latter periods, not only were mean ambient temperatures higher, but it is likely that the roost would be composed of a higher proportion of juveniles. Juveniles may receive greater benefits from huddling to compensate for lack of foraging experience. For example, in speckled mousebirds, juveniles were observed to huddle more often than adults (McKechnie et al. 2006). It is also possible that huddling plays a social role. For example, in Siberian flying squirrels (*Pteromys volans*) huddling was linked to subsequent mating, rather than reducing the costs of thermoregulation (Selonen et al. 2014).

Our results are seemingly contrary to what has been observed in other species that huddle, however few studies have examined the intensity of huddling in relation to ambient temperature in natural conditions. House sparrows, tree swallows, and common bushtits (*Psaltriparus minimus*) decreased individual distance and formed tighter huddles as ambient temperature decreased (Smith 1972; Grubb 1973; Beal 1978; Burns et al. 2013). Similarly, Emperor penguins formed huddles more frequently and increased huddling intensity at lower ambient temperatures (Gilbert et al. 2008), and little brown bats were more likely to cluster at lower ambient temperatures (Kurta & Smith 2014).

Conclusions

The ability to thermoregulate effectively can affect fitness and survival; consequently, some animals may use behavioral strategies to minimize heat loss and conserve energy during rest and/or low ambient temperatures (McKechnie et al. 2006). An ideal microclimate has been suggested for the preference of endotherms for some roost or nest sites over others (Wiebe 2001). We found that swifts exhibited a preference for southerly facets of a roost; a preference that would have likely provided a thermal benefit in most natural roost cavities. We also found, within the narrow temperature range at our study site, that the huddling density of swifts varied with relation ambient air temperature. We suggest this may be linked to the availability of flying insects outside the roost; on days where flying insects were presumably less available, we saw greater density in huddling swifts. Roosting structures may contribute to the fitness and survival of swifts, as swifts are very rarely found roosting in the open.

Swifts primarily use anthropogenic structures for roosting, which are becoming increasingly uncommon in parts of their Canadian range (Rioux et al. 2010). In addition to habitat loss, climate change and pesticide use may threaten the population dynamics of the swifts' primary food source, flying insects. We suggest that during periods of presumed lowered food availability, roosts may be essential for the survival of swifts, highlighting the need to protect and conserve roosting structures. To enhance our understanding of roost site selection and behaviour, further studies should focus on identifying preferred roost site characteristics and examining the energy savings associated with communal roosting. Specifically, studies on the ecophysiology of swifts

could examine how huddling influences body temperature, metabolism, and mass and how these might vary with ambient temperature and food availability.

FIGURES AND TABLES

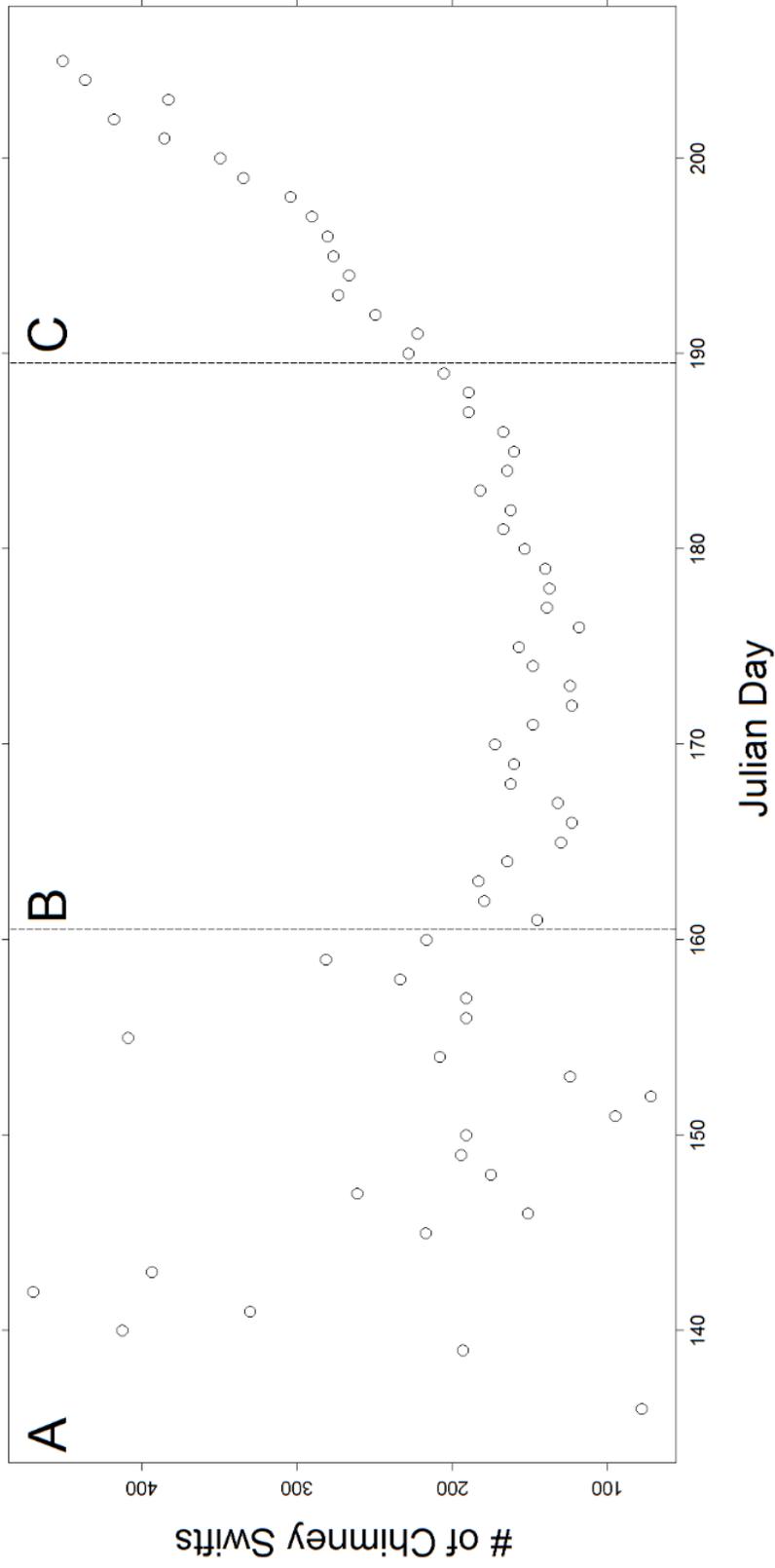


Figure 3.1 Maximum number of chimney swifts recorded inside a single roost each night between 16 May, 2013 and 24 July, 2013 in eastern Ontario. Dashed lines mark A) pre-nesting (16 May – 9 June), B) nesting (10 June – 8 July) and C) post-nesting (9 July – 24 July) periods.

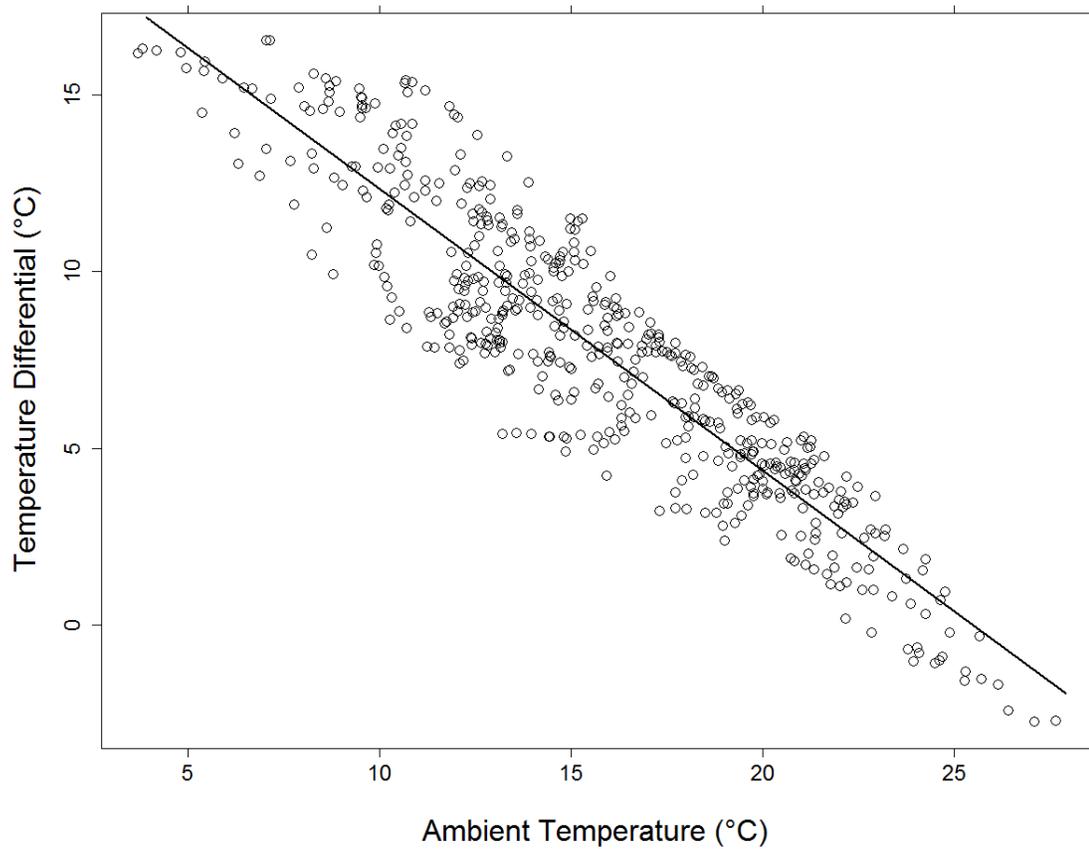


Figure 3.2 Relationship between hourly overnight ambient air temperature at 60m (recorded at a weather station ~2km away) and the temperature differential (roost temperature – ambient temperature) from 16 May – 24 July, 2013. The relationship is represented by the linear equation $y = -0.80x + 20.28$ ($R^2 = 0.8375$, $p < 0.001$)

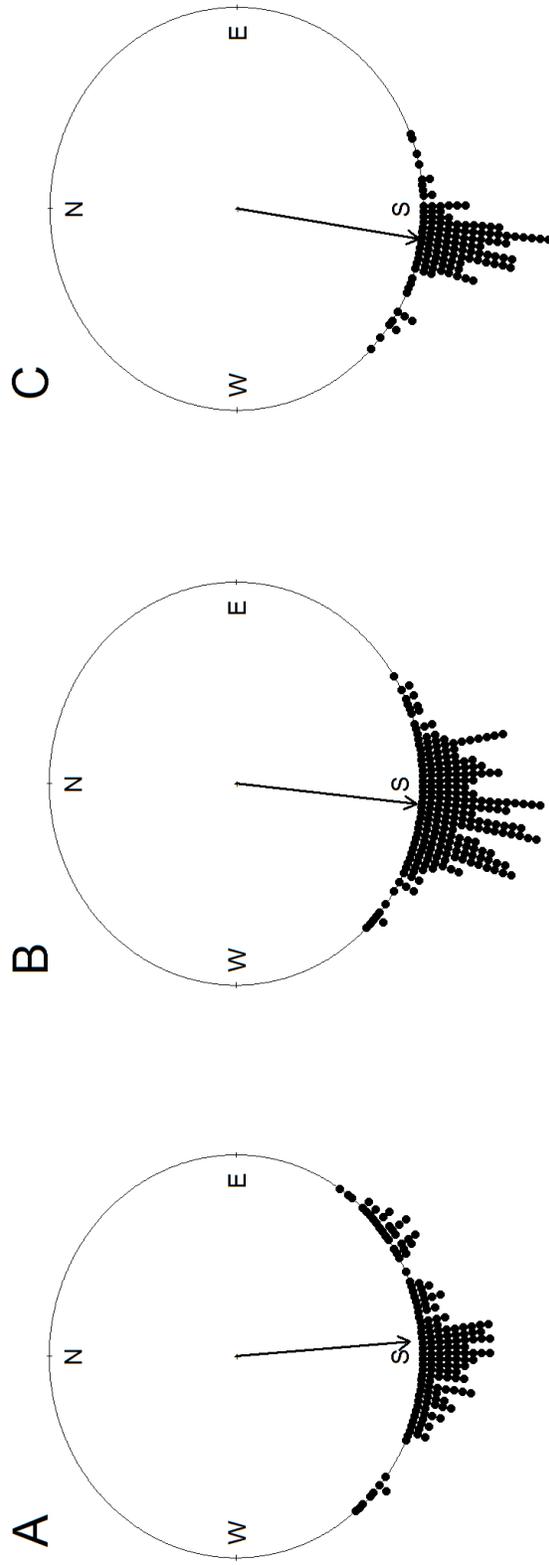


Figure 3.3 Hourly mean angles of orientation (preferred direction) of chimney swifts inside a single roost during A) Pre-nesting period (16 May – 9 June; $n = 168$), B) Nesting period (10 June – 8 July; $n = 232$) and C) Post-nesting period (9 July – 24 July; $n = 127$). The overall mean angle of orientation for each period is indicated by the arrow.

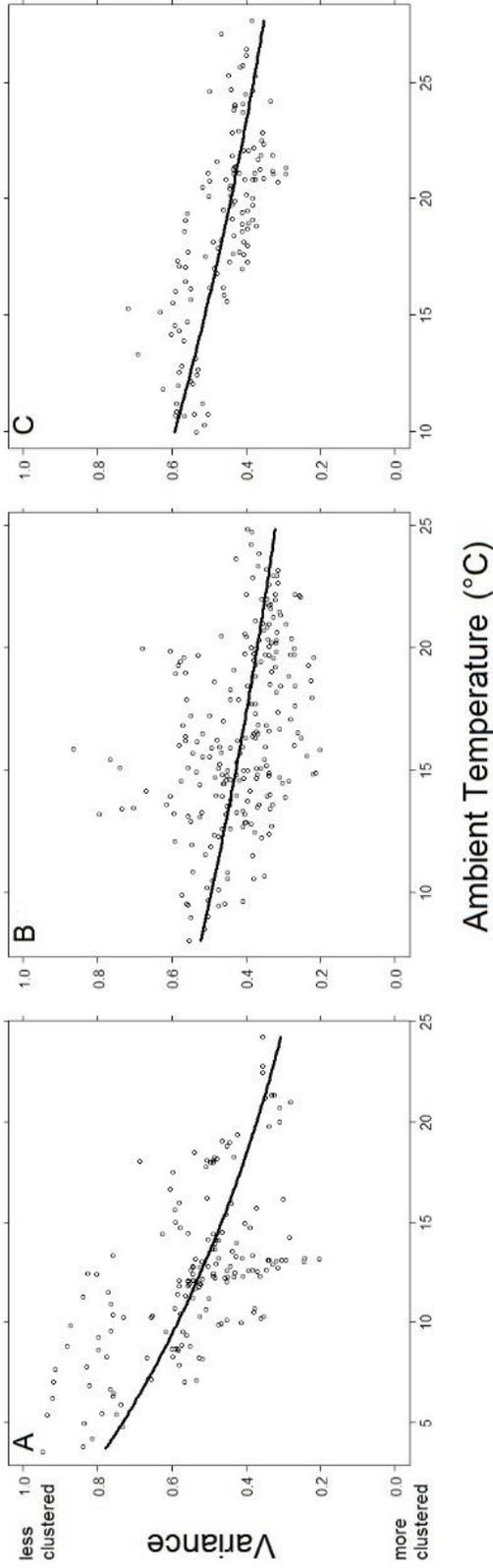


Figure 3.4 Ambient air temperature at 60m and the variance around the mean angle of orientation for chimney swifts during A) pre-nesting (16 May – 9 June), B) nesting (10 June – 8 July), and C) post-nesting (9 July – 24 July) periods inside a roost in eastern Ontario in 2013. Swifts are more clustered around the mean angle as the variance approaches 0, and more dispersed as variance approaches a value of 1. Ambient temperature was significant in all time periods.

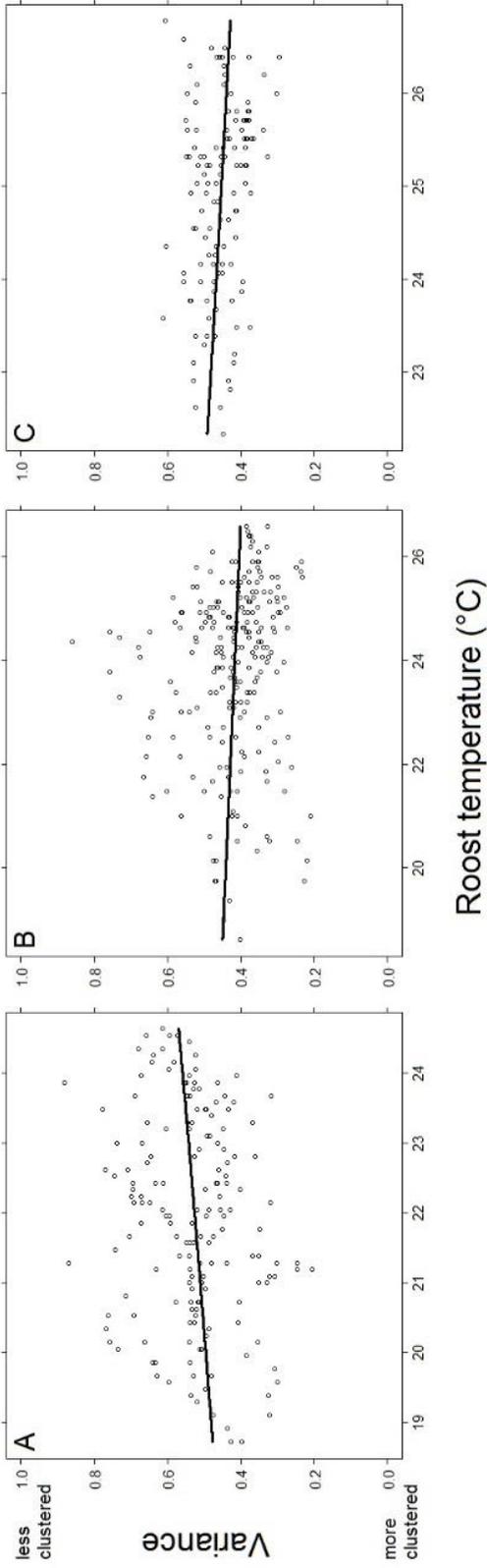


Figure 3.5 Roost temperature and the variance around the mean angle of orientation for chimney swifts during A) pre-nesting (16 May – 9 June), B) nesting (10 June – 8 July), and C) post-nesting (9 July – 24 July periods inside a roost in eastern Ontario in 2013. Swifts are more clustered around the mean angle as the variance approaches 0, and more dispersed as variance approaches 1. Roost temperature was significant in the pre-nesting and post-nesting periods.

Table 3.1 Hourly overnight (23:00 – 5:00) temperatures recorded inside a chimney swift roost at a depth of 5m compared to ambient air temperature at a height of 60m in 2013 for the pre-nesting (16 May – 9 June, $n = 168$), nesting (10 June – 8 July, $n = 232$), and post-nesting (9 July – 24 July, $n = 127$) periods.

Period	Internal roost temperature (°C)		Ambient air temperature (°C)	
	Mean (\pm SE)	Range	Mean (\pm SE)	Range
Pre-nesting	21.9 (\pm 0.115)	18.71 – 24.64	12.4 (\pm 0.313)	3.68 – 24.24
Nesting	23.8 (\pm 0.111)	18.62 – 25.80	16.4 (\pm 0.250)	8.02 - 24.87
Post-nesting	25.0 (\pm 0.087)	22.33 – 26.78	18.8 (\pm 0.353)	9.95 – 27.65

Table 3.2 Gamma GLM parameter estimates for the predictive variables of variance around the mean angle of orientation of chimney swifts roosting inside an industrial chimney during the pre-nesting (16 May – 9 June, $n = 168$), nesting (10 June – 8 July, $n = 232$), and post-nesting (9 July – 24 July, $n = 127$) periods in 2013 (* indicates significance at $\alpha < 0.05$).

Period	Model Variable	$\beta \pm SE$	t	p
Pre-nesting	Intercept	-0.745 ± 0.274	-2.717	<0.00729*
	Roost Temperature	0.030 ± 0.0134	2.236	0.0267*
	Ambient Temperature	-0.045 ± 0.005	-9.109	<0.001*
Nesting	Intercept	-0.067 ± 0.230	-0.293	0.770
	Roost Temperature	-0.014 ± 0.010	-1.396	0.164
	Ambient Temperature	-0.029 ± 0.005	-6.196	<0.001*
Post-nesting	Intercept	0.546 ± 0.333	1.638	0.00749*
	Roost Temperature	-0.031 ± 0.012	-2.458	0.0153*
	Ambient Temperature	-0.029 ± 0.003	-9.686	<0.001*

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CHAPTER 4:

General Conclusion

This thesis explored patterns in how chimney swifts use roosting structures at the northern edge of their range. On a large spatial scale, using data largely collected by citizen science, I examined whether latitude, longitude, and/or human population density could explain the maximum number of chimney swifts occupying roosts in Quebec and Ontario. Because chimney swifts predominantly roost in large chimneys associated with industry and infrastructure, human population density was used as a proxy for available roosting sites. On a much smaller spatial scale, I also examined how chimney swifts position themselves within a roost to investigate the thermoregulatory role of roosts via the relative ambient and/or internal roost temperature.

In Chapter 2, I showed that roost size tended to increase with latitude. In fact, roosts reported to contain >1000 birds only occurred north of 45°N. A weaker relationship was evident with longitude, so that the largest roosts identified occurred in the northwest quadrant of the study area. I had hypothesized that roost size would be larger in areas of lower human density, as there would be fewer chimneys. The lack of a relationship between human population density and maximum roost size does not support the hypothesis that roost availability is a factor contributing to roost size. Instead, other factors such as interior area available for roosting, or quality of surrounding foraging habitat may be more important in determining roost size. However, the latitudinal gradient observed in roost size lends some support to a link between ambient temperature

and maximum roost size. In areas with lower ambient temperatures the costs of thermoregulation could be mitigated by forming larger groups as groups of roosting animals can raise the ambient air temperature and decrease the area available for heat exchange by huddling together. This function of roosts may be especially important to chimney swifts during their spring and autumn migrations when ambient temperatures are most variable, and it is exactly during these times when we observe the largest number of chimney swifts at a roost. Not only do these roosts at northerly latitudes comprise a large proportion of the overall chimney swift population, but these roosts may be critical for chimney swift survival.

If the communal roosting of chimney swifts serves a thermoregulatory role, positioning of chimney swifts inside the roost may be influenced by ambient and roost temperatures. In Chapter 3, I showed that chimney swifts grouped themselves more tightly as ambient temperature increased; the opposite of what is expected if huddling served purely as a heat conservation measure. Nonetheless, these results do still suggest that chimney swifts may select a position inside the roost to gain thermal benefits as they showed a strong preference for clinging to the south facing wall of the roost, presumably the warmest wall of most roosting structures in the Northern hemisphere.

The lack of support for the hypothesis that chimney swifts group more tightly as temperature decreases may be due to the nature of my study site. Although one of the largest roosts in Ontario, my study roost was an active exhaust stack that may have more constant temperature than a typical roost. It is possible that temperatures inside the roost were not cold enough to warrant a strong huddling response, but my observation of increased huddling at higher ambient temperatures is intriguing. A potential explanation

for this pattern is that chimney swifts use huddling to conserve energy during periods of lowered food availability. A reduction in food availability has been shown to trigger energy conservation strategies in many species (Reinertsen & Haftorn 1986; McKechnie & Lovegrove 2002; Gilbert et al. 2010), and huddling individuals can lower metabolic rates, allowing them to conserve mass and increase survival (McKechnie et al. 2006; Gilbert et al. 2010; Burns et al. 2013) Pesticide use, agriculture intensification, and climate change have all been linked to changes in flying insect distributions/availability that are in turn linked to the wide-spread decline in aerial insectivore populations (Evans et al. 2007; Nocera et al. 2012; Mineau & Whiteside 2013; Paquette et al. 2013).

Given the unique characteristics of my study roost, future studies could focus on the thermal profiles of occupied and unoccupied roost sites in chimneys with greater temperature variation, to determine if chimney swifts select sites based on the specific microclimate of the roost. In occupied roosts, similar positional studies can be conducted to determine if chimney swifts follow the same organizational patterns in all roosts, which would then lend support to whether this is a universal behaviour or instead linked the individual properties of each roost. If food availability is a driver of behavior within a roost, it would be worthwhile to investigate and model the importance of variables known to affect insect populations, such as cloud cover, wind speed, and land use (Grüebler et al. 2008). Although my study was a useful first step, further learning of how chimney swifts select and use roosts can inform management decisions and can contribute a more effective design of artificial habitat.

Through this study, I have identified geographic areas that contain a significant portion of the Canadian chimney swift population. Based on the estimated chimney swift

population of Canada from the COSEWIC assessment report (2007), a large roost may contain up to 9.5% of the overall Canadian chimney swift population at a given time (especially during migration). Thus, any removal, closure, or modification that would render one of these roosts unusable to chimney swifts would be detrimental to the recovery of the species due the large number of chimney swifts it would displace. As of the writing of this thesis, the federal recovery strategy for the chimney swift has yet to be released, and thus critical habitat has not been formally defined. However, it can be foreseen that identifying anthropogenic habitat as critical habitat for a species presents several management challenges, especially when aging structures (e.g., old masonry chimneys) pose a human safety risk. In fact, a recent review of critical habitat identification in completed Canadian recovery strategies indicated that only 11.8% of recovery strategies listed comprehensive definitions of critical habitat, despite loss of habitat being identified as a major threat for most of the species assessed (Bird & Hodges 2017).

Conservation methods for species that use anthropogenic habitat such as barn swallows (*Hirundo rustica*) and chimney swifts, have focused largely on stewardship and the provision of supplementary habitat with limited levels of success (Heagy et al. 2014; MCSI, 2015). In chimney swifts, the provision of nesting towers has experienced moderate success in the United States in attracting successful breeding pairs, but the same design has yet to attain any success in Canada. These towers may be unsuccessful due to the thermal properties, poor placement of the towers, or the fact that suitable nesting sites are not limiting yet (Finity & Nocera 2012; Fitzgerald et al. 2014). These towers are built for nesting purposes and are not large enough to hold the number of birds congregating at

roosting sites. The provision of specific roosting towers is a much larger endeavor, has been much less common, and has met with varying success across Canada and the United States (Farquhar, unpublished data). However, cases in which a building containing a chimney occupied by swifts was demolished and the original roosting structure was retained and/or augmented (e.g., Robie Tufts Nature Centre in Wolfville, Nova Scotia) appear to have been more successful in keeping and attracting roosting chimney swifts. Further understanding of roost microclimate and how chimney swifts use roosts can aid in the development of towers that are well suited for chimney swifts at the northern edge of the range and increase their effectiveness.

My study has highlighted the importance of roosting structures for chimney swifts at the northern edge of their range. My results can also provide guidance on managing areas that are important to protect for a disproportionately large number of birds and also provides insight into where the placement of artificial roosting or nesting structures may be more successful (i.e., areas where large roosts currently occur). With increasing effects of climate change and changes in flying insect availability, the presumed energetic benefits that swifts receive from suitable roosting structures may become increasingly crucial to the survival of chimney swifts.

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