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Article

High ambient temperatures induce aggregations of chimney swifts *Chaetura pelagica* inside a roost

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One proposed advantage 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*. 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 study region. 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 the warmest ambient temperatures. This likely a metabolic response to reduced prey availability at higher temperatures and/or an attempt to reduce evaporative water loss. We suggest clustering may be used by chimney swifts as an energy saving mechanism during periods of lowered food availability.

Keywords: chimney swifts, roosting, huddling

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 and Lovegrove 2002). Thermoregulatory costs are particularly high for small endotherms that must balance metabolic heat production



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with relatively rapid heat loss due to a larger surface area-to-volume ratio (Merola-Zwartjes 1998, McKechnie and Lovegrove 2002). Alternative physiological strategies, such as torpor, can conserve energy by down-regulating metabolism, and thus body temperature, in response to low ambient air temperatures or decreased energy availability (McKechnie and 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 and 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, 1996, Hayes et al. 1992). 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 and Millar 1984, Canals et al. 1997, Gilbert et al. 2010). Groups of huddling individuals can maintain higher body temperatures and reduce energy expenditure relative to single individuals (DuPlessis and Williams 1994, Ancel et al. 1997, McKechnie et al. 2006, Gilbert et al. 2007, 2008a, 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 et al. 2008a). 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 and 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 and Brigham 2007). For example, huddled big brown bats *Eptesicus fuscus* in tree cavities raised the cavity temperature by 7°C (Willis and 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 and Williams 1994, DuPlessis et al. 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 and 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 et al. 2008b). 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. (2008a) 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) is a small aerial insectivore with a large breeding range in North America (Steeves et al. 2014). During the breeding season, one nesting pair of swifts will occupy a single vertical hollow. However, swifts also form communal roosts in large vertical hollows, which in spring and fall is comprised of migratory birds and in summer is comprised of non-breeders and members of breeding pairs that are not incubating that night. 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, 1957, Taylor 1963, Winkler et al. 2013). Therefore, although the thermo-neutral zone of swifts has not been quantified, it is likely that roost site selection and roosting behavior of swifts represent 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 and 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.

The full thermo-metabolic profiles of swifts have not been described; upper and lower critical thresholds remain

unquantified. However, Ramsey (1970) documented a positive linear relationship between body temperature of swifts and ambient temperature, with the birds entering torpor at temperatures $< 5^{\circ}\text{C}$. Bartholomew et al. (1957) showed that a closely related species, white-throated swifts *Aeronautes saxatalis*, could not tolerate body temperatures $< 20^{\circ}\text{C}$, which the equation derived by Ramsey (1970) predicts would be reached by chimney swifts at $\sim 5^{\circ}\text{C}$ ambient temperature. Given these knowledge gaps, we examined huddling behavior of chimney swifts 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 further 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

Study site

The study was conducted at a swift roost located in a large industrial chimney in Renfrew County, ON, Canada ($46^{\circ}03'12.0''\text{N}$, $77^{\circ}21'53.9''\text{W}$). 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 (Farquhar 2017). At this site, northward migrating swifts generally begin arriving in the second week of May. The roosting site is a 61 m tall cylindrical chimney with a 1.07 m diameter opening at the top. The chimney 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 chimney is currently operational and has a constant air flow of $1.747\text{ m}^3\text{ s}^{-1}$ (velocity: 3.8 m s^{-1}). The chimney is located approximately 300 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.

Historical data from Environment and Climate Change Canada (2018) show that ambient temperatures at the site during spring migration (16 May–9 June) reach an average high of 19°C and an average low of 6.1°C , thus nighttime temperatures in this period could represent periods of cold stress for swifts. During the nesting period (10 June–8 July), ambient temperatures at the site reach an average high of 23.7°C and an average low of 11.2°C ; the average low is almost double that seen in May. During the post-nesting period (9 July–24 July), ambient temperatures at the site reach an average high of 26.1°C and an average low of

13.9°C . Average monthly rainfall at the site varies little across our study period (80 mm in May, 88 mm in June, 87 mm in July).

Video and temperature monitoring

We mounted an outdoor network security camera (D-LinkTM, DCS-7110) at the opening of the swift roost from May to July 2013. The camera recorded continuously to a network video recorder (D-LinkTM, DNS-726-4) secured to the base of the chimney. Video footage was downloaded daily via a laptop and stored on external hard drives. We hung HOBO pendant[®] temperature loggers (UA-001-08, $\pm 0.47^{\circ}\text{C}$) on the inside of the chimney at depths of 5 and 10 m to record hourly roost temperature. However, for our analyses we used temperature data only from the 5 m 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 ($\sim 2\text{ km}$ from the roost site) at an altitude of 60 m.

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 16 May and 24 July 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 (ver. 4.8.3; Brown 2013).

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 (Fig. 1). The pre-nesting period (16 May–6 June) was categorized by the high degree of variability in the number of swifts occupying the roost each night and corresponded with the spring migration period. A relatively constant number of swifts occupied

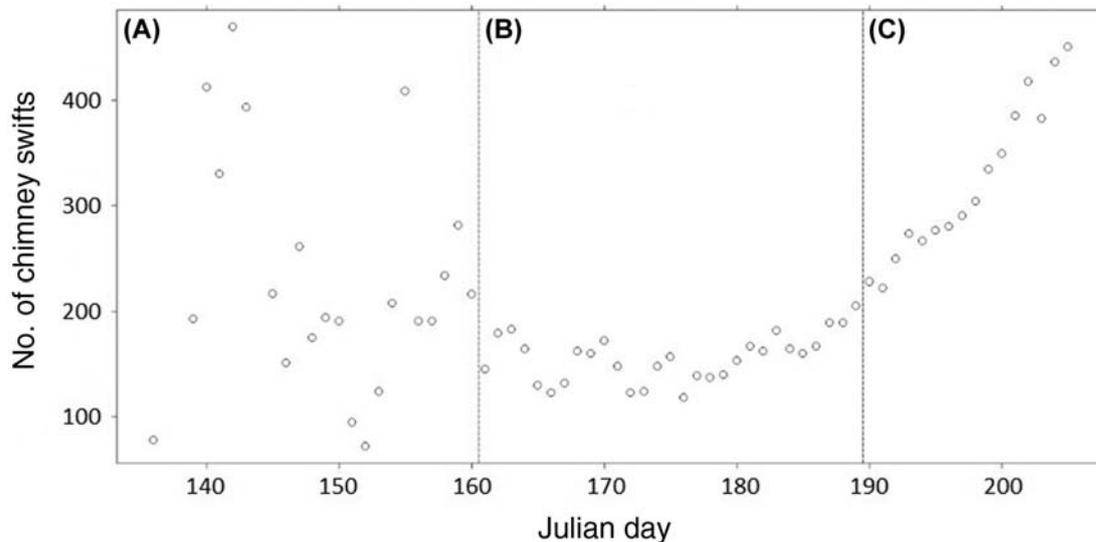


Figure 1. Maximum number of chimney swifts recorded inside a single roost each night between 16 May and 24 July 2013 in eastern Ontario. Dashed lines mark (A) pre-nesting (16 May–9 June), (B) nesting (10 June–8 July) and (C) post-nesting (9 July–24 July) periods.

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 and 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 and 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 and 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 60 m 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).

Analyses were conducted in R statistical software ver. 3.0.1. (R Core Team), with packages CircStats (Lund and Agostinelli 2012), circular (Agostinelli and Lund 2013), and MASS (Venables and Ripley 2002). For all tests, we assumed statistical significance at $\alpha \leq 0.05$.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.ss0j12k>> (Farquhar et al. 2018).

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 60 m 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 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 ($n=527$, $R^2=0.8375$, $p < 0.001$; Fig. 2). 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

Table 1. Hourly overnight (23:00–5:00) temperatures recorded at a depth of 5 m inside a chimney swift roost compared to ambient air temperature at a height of 60 m 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 (± SE)	Range	Mean (± SE)	Range
Pre-nesting	21.9 (± 0.115)	18.71–24.64	12.4 (± 0.313)	3.68–24.24
Nesting	23.8 (± 0.111)	18.62–25.80	16.4 (± 0.250)	8.02–24.87
Post-nesting	25.0 (± 0.087)	22.33–26.78	18.8 (± 0.353)	9.95–27.65

decreased as ambient air temperature increased until approximately 25°C, at which point roost temperature was lower than ambient air temperature (Fig. 2).

Angle of orientation

The mean angle of orientation (where true north is 0°) ranged from 123°–230° during the pre-nesting period, 147°–225° during the nesting period, and 159°–224° 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: $r=0.985$, $p < 0.001$; Fig. 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 2). In all three time periods, warmer ambient air temperatures were associated with a decrease in variance around the mean angle of orientation (Fig. 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 2, Fig. 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; Fig. 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.

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). In our study, the difference in temperature in and out of the roost decreased as ambient air temperature increased until approximately 25°C, at which inside temperature was lower than outside. This suggests a point at which swifts might experience heat stress, although this remains unknown without quantitative studies of swift thermoneutral zones. Therefore, the 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 and Williams 1994, Sedgeley 2001). For instance, when cavity sites were not limiting, tree swallows *Tachycineta bicolor* exhibited a

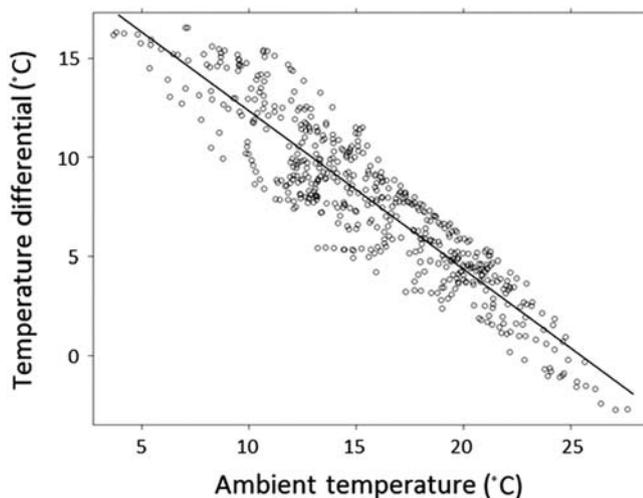


Figure 2. Relationship between hourly overnight ambient air temperature at 60 m (recorded at a weather station ~2 km away) and the temperature differential (roost temperature–ambient temperature) from 16 May–24 July 2013. The relationship is represented by the linear equation $y = -0.80x + 20.28$ ($R^2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

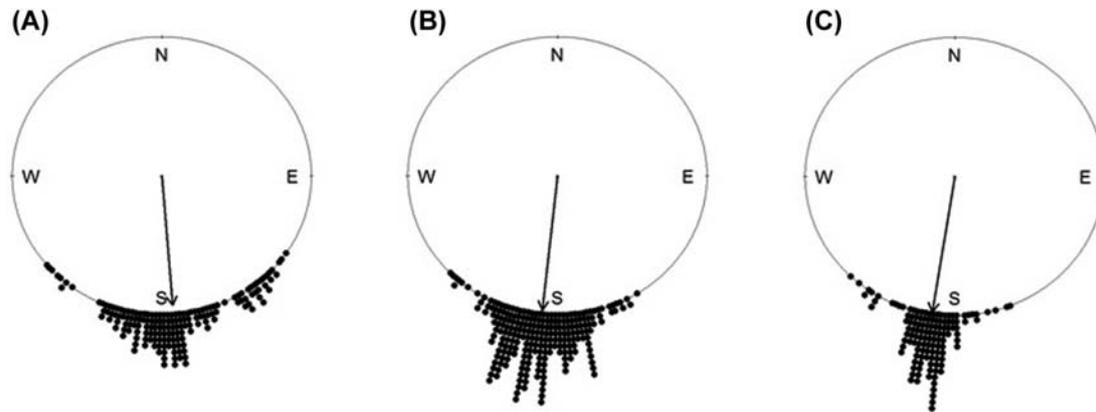


Figure 3. Hourly mean angles of orientation (preferred direction) of chimney swifts inside a single roost during (A) pre-nesting period (16 May–9 June; $n = 168$), (B) nesting period (10 June–8 July; $n = 232$) and (C) post-nesting period (9 July–24 July; $n = 127$). The overall mean angle of orientation for each period is indicated by the arrow.

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 experienced 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 and 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 (Farquhar 2017) 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.

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 and 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

Table 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 $\alpha \leq 0.05$).

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*

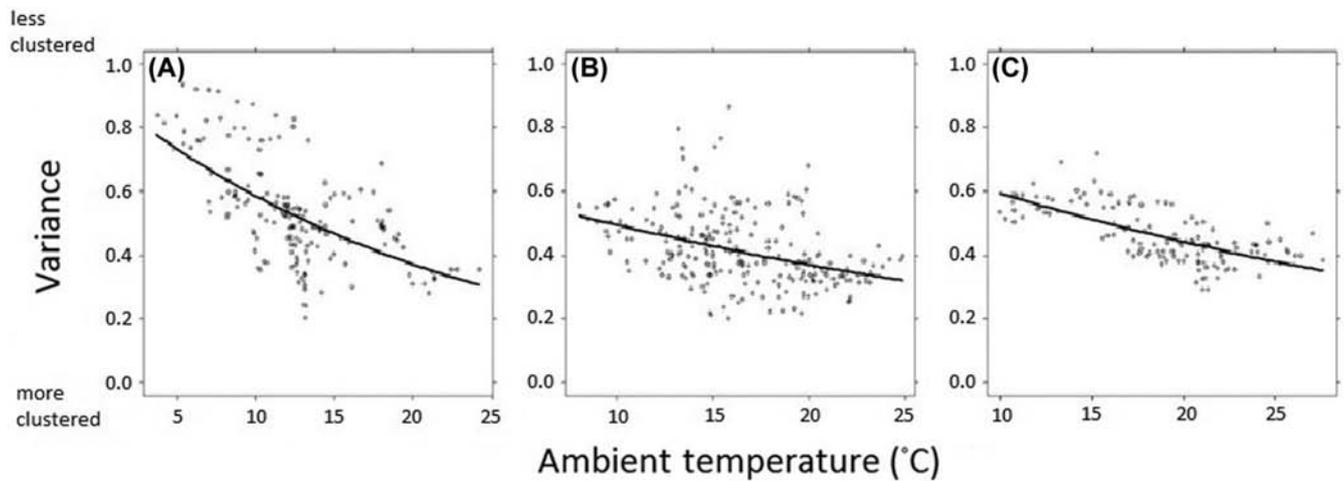


Figure 4. Ambient air temperature at 60 m and the variance around the mean angle of orientation for chimney swifts during (A) pre-nesting (16 May–9 June), (B) nesting (10 June–8 July), and (C) post-nesting (9 July–24 July) periods inside a roost in eastern Ontario in 2013. Swifts are more clustered around the mean angle as the variance approaches 0, and more dispersed as variance approaches a value of 1. The relationship between variance and ambient temperature was significant in all time periods.

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 and Robertson 1994, Ardia et al. 2006), woodpeckers (Inouye 1976), and big brown bats (Kalcounis and 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 constructing 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.

We did not find that swifts huddled more densely in response to cooler temperatures as we would have 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

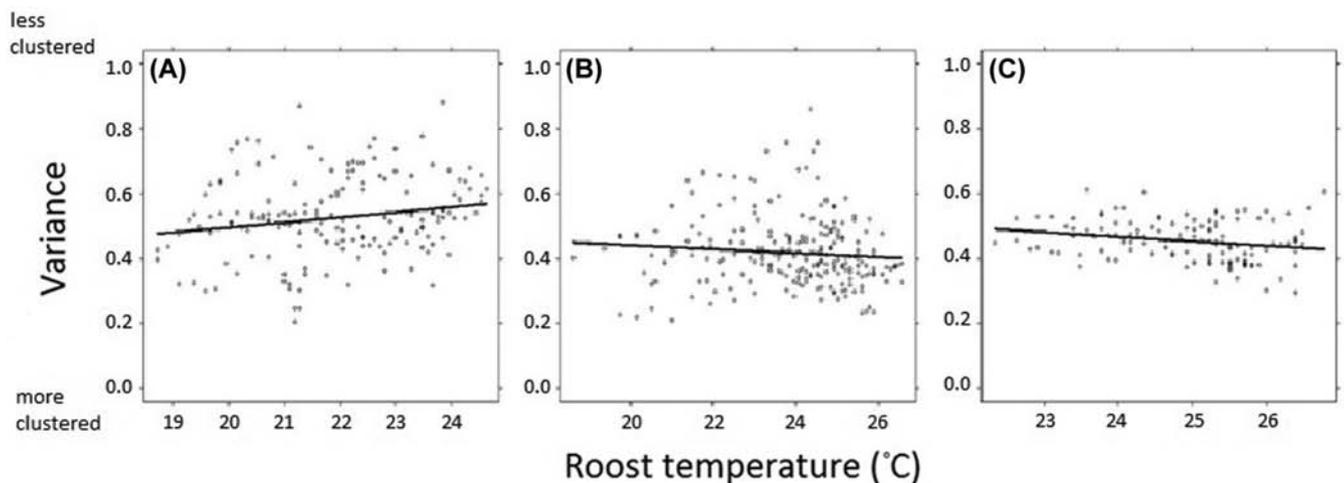


Figure 5. Roost temperature and the variance around the mean angle of orientation for chimney swifts during (A) pre-nesting (16 May–9 June), (B) nesting (10 June–8 July), and (C) post-nesting (9 July–24 July) periods inside a roost in eastern Ontario in 2013. Swifts are more clustered around the mean angle as the variance approaches 0, and more dispersed as variance approaches 1.

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). The closer huddling we observed at higher ambient temperatures could be a function of swifts trying to reduce evaporative water loss. At higher temperatures, the use of sheltered roosts (Bakken et al. 1991) and huddling have been observed to reduce evaporative water loss in many taxa (Tauson et al. 2006, Boratynski et al. 2015). However, we did not measure water balances in swifts and this remains an area worth exploring in further study. Another possibility 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, 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, 1957). In a more recent study, 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 and 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 (Wojciechowski et al. 2011, Carr and Lima 2013). For example, food-deprived speckled mousebirds 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 Australian sugar gliders *Petaurus breviceps* and several bird species (Wojciechowski et al. 2011, Shipley et al. 2015).

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. 2008a), and little brown bats were more likely to cluster at lower ambient temperatures (Kurta and Smith 2014).

Conclusion

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, the huddling density of swifts varied with 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.

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