Ambient temperature preferences of chimney swifts (*Chaetura pelagica*) for Nest Site Selection ☆

Courtney E. le Roux[a,*], Laura A. McFarlane Tranquilla[b], Joseph J. Nocera[a]

[a] *University of New Brunswick, 3 Bailey Drive, Fredericton, New Brunswick, Canada E3B 5A3*
[b] *Bird Studies Canada, 17 Waterfowl Lane, Sackville, New Brunswick, Canada E4L 1G6*

A B S T R A C T

Chimney swift (*Chaetura pelagica*) populations are declining rapidly, with no clear indication as to why. Reduced availability of nesting habitat (chimneys) was thought to be a limiting factor for this threatened species, but data from Ontario, Canada did not support this hypothesis. If availability is not limiting, then perhaps habitat quality may play a role. We examined the thermal aspect of chimneys that are used by nesting swifts. To do so, we identified upper and lower thermal limits influencing the selection of chimneys for nesting. Across Nova Scotia and New Brunswick, we deployed temperature loggers in 19 chimneys, 11 of which contained chimney swift nests and 8 that were deemed suitable for nesting but were not occupied. Temperature readings were recorded at 30-min intervals from 23 June to 15 September 2017. We found that chimney occupancy by swifts was negatively correlated with maximum and mean chimney temperature. We did not find a relationship between occupancy and minimum temperature, temperature fluctuations, or chimney material. These results indicate that chimney swifts are preferentially selecting cooler chimneys for nesting.

1. Introduction

Incubation is a costly activity for birds that needs to be balanced with the energetic costs of self-maintenance (Williams, 1996; Tinberg, Williams, 2002). This trade-off occurs between the energetic self-maintenance of the incubating adult and the thermoregulatory requirements of the developing embryos (Walsberg, 1986; Gilbert et al., 2009; Grüebler et al., 2014; Robertson, 2009). Extended time away from nests spent in self-maintenance feeding can have detrimental effects on developing embryos (Ardia et al., 2010) including higher embryonic mortality (Yildirim and Yetisir, 2004), reduced mass (Basso and Richner, 2015), and longer incubation times (Bueno-Enciso et al., 2017). Nest site selection is one aspect of incubation that can have important consequences for both adults and the development of young (Huey, 1991; Amat-Valero et al., 2014). By preferentially choosing nest sites that have a warm microclimate, adults require less energy for thermoregulation via metabolic heat production, allowing more to be allocated to self-maintenance without the need for extensive feeding bouts away from the nest (Huey, 1991; Clement and Castleberry, 2013).

Nesting in enclosed spaces, such as cavities or enclosed man-made structures, provides a potentially more stable environment that can limit the cost of thermoregulation by protecting the nest from changes in temperature and exposure to wind and rain (Walsberg, 1986; Rhodes et al., 2009). By roosting within an enclosed space, barn owls (*Tyto alba*) conserved up to 26% of their metabolic energy requirements (McCafferty et al., 2001), and green woodhoopoes (*Phoeniculus purpureus*) saved up to 30% of energy otherwise diverted to thermoregulation (Du Plessis and Williams, 1994). Some species, such as the mountain chickadee (*Poecile gambeli*) and blue tit (*Cyanistes caeruleus*), preferentially nest in cavities with an internal temperature higher than the external ambient temperature resulting in energy savings up to 35% (Yomtov and Wright, 1993; Wachob, 1996). Nesting in cavities that have an internal temperature greater than the ambient temperature can also have positive reproductive effects such as larger clutch sizes (D'Alba et al., 2009; Wiebe, 2001), greater reproductive success (Hooge et al., 1999), higher fledging rates, and more successful second brooding attempts (Reid et al., 2000). However, there are also risks associated with nesting in structures with higher internal temperatures than the external ambient temperature, such as lower nestling body mass and dehydration (Salaberria et al., 2014), reduced hatching rates (Reyna and Burggren, 2017), heat stress, and water loss (Farquhar et al., 2018).

The relationship between microclimate at enclosed nesting sites and site selection is especially important in species with high energetic

demands. Chimney swifts (*Chaetura pelagica*) are a threatened species (in Canada; COSEWIC, 2007) of aerial insectivore that requires enclosed spaces for nesting (COSEWIC, 2007). Chimney swifts historically nested in the hollows of large trees (COSEWIC, 2007; Zanchetta et al., 2014). As the availability of suitable trees diminished in North America with an increase in logging activities following European settlement (Steeves et al., 2014), swifts adopted chimneys for nesting. Because of the chimney swifts' highly aerial life history, they experience high metabolic demands and must compensate for this high energetic cost of aerial foraging when nesting (Ramsey, 1970).

By studying a species with high energetic demands, we sought to identify a profile of the thermal environment that contributes to the selection of nest sites. To do this, we investigated the temperature profiles of chimneys used as nest sites compared to chimneys that, despite being deemed suitable (uncapped and lined with a porous material), were not used by swifts. This allows us to assess the trade off between nesting in environments with higher or lower internal temperatures than ambient temperature.

2. Methods

2.1. Study sites

We collected temperature data during the incubation and nestling period at 19 chimneys throughout southern New Brunswick and western Nova Scotia, Canada, from 23 June to 15 September of 2017. The chimneys we sampled were attached to residences (n = 11) and commercial properties (n = 8). Because we sought to compare occupied and unoccupied chimneys, we selected 11 study chimneys known to be used for nesting within the past three years by Bird Studies Canada's SwiftWatch Program (Bird Studies Canada, unpublished data). We verified occupancy in 2017 using Bird Studies Canada's SwiftWatch protocol which involves arriving at the site 30 min prior to sunset, observing the putative nest chimney until 15 min after the last swift enters, or until it has become too dark to observe (Bird Studies Canada, 2017). We also chose 8 control sites which had no record of chimney swift presence but were within 1 km of a known roost site and whose chimney was open to allow access, with interior walls made of porous material.

2.2. Site characteristics

We recorded the total width, height, and length of the external portion of the chimney above roofline. We measured total chimney height from the chimney base where there was no obstruction within the chimney. In cases where an obstruction was present (e.g., insulation), we recorded total height as height above the obstruction. We also documented the materials from which the flue and external surface of the chimney were made. All chimneys were confirmed not to be in use for heating purposes during the study.

We monitored the internal temperature (T_i) (at 30-min intervals) of both used an unused chimney by placing a Hobo® temperature data-logger (Pendant® Temperature Data Logger UA-001-xx) in each of the selected chimneys. Loggers were placed against the interior wall of the chimney, away from nesting birds. In five chimneys that could be accessed from the rooftop, we placed loggers within 3 m of the top of the chimney because nests are typically found in the upper third of the chimney (Steeves et al., 2014). For 14 chimneys, rooftop access was not possible due to steep pitches; in those cases, we placed loggers at various heights within the structure where access could be gained from below. To account for variation caused by logger placement in these 14 chimneys, we used a correction factor to estimate temperature in the upper 3 m of the chimney (see Section 2.3). To generate this correction factor, we suspended temperature loggers at various heights within these chimneys to calculate temperature change in relation to height. We used data from the nearest Environment Canada weather station

(maximum 10 km from site) to obtain ambient temperature (T_a) measurements.

2.3. Temperature calculations

In the 14 cases where we could not deploy temperature loggers in the upper 3 m of the chimney, we corrected for alternative placements. Using the five locations that had more than one temperature logger per chimney, we calculated a temperature change of + 0.36 °C/m from the base of the chimney to the top by dividing the temperature difference between loggers by distance between loggers. We assumed that temperature changed uniformly with height between chimneys. As we had differential amounts of access to the internal portion of the chimneys studied, we were unable to place loggers at discreet locations within chimneys to calculate non-linear variation.

2.4. Statistical analysis

We tested for independence between T_a and T_i using a Pearson Correlation test. We then used Welch's *t*-test to test whether chimneys buffered against maximum, minimum, and mean T_a, as well as the standard deviation of T_a. We considered buffering to be a significant difference between T_a and internal chimney temperatures. Chimneys were then classified binomially as either occupied or unoccupied by swifts. Thus, we used a logistic regression (using glm function in R) to model occupancy with the fixed factors of maximum temperature (T_{max}), minimum temperature (T_{min}), mean temperature (T_{mean}), and temperature variability (standard deviation, which has been used as a proxy for temperature variation in other studies (e.g., Hepp et al., 2005)) both with daily and seasonal temperature data. All temperature data we used in the regression were from the actual or calculated measurements in the upper 3 m of the chimney. A saturated model was impossible to run as it failed to converge due to multi-collinearity (Graham, 2003) in the data (i.e., all temperature data are integrated), therefore we fit four non-nested single-term models (therefore amounting to four instances of single-term stepwise forward model building from the null model). We identified whether each model was better than the null model by assessing whether the overall deviance (χ^2) was significantly reduced with the addition of a variable to the null model (Chi-square test, $P > 0.05$). Using Cook's Distance criterion, we detected two outliers and eliminated them as they exhibited excessive leverage and influence on parameter estimates (i.e., $D_i > 1$). We used the program R (version 3.4.2, standard statistical package; R Core Team, 2017) for all statistical tests. For all analyses, we set $\alpha = 0.05$, and for descriptive statistics we report means ± SD.

3. Results

We monitored 11 occupied chimneys in New Brunswick (n = 7) and Nova Scotia (n = 4), and 8 unoccupied chimneys in New Brunswick. We collected temperature data for 84 days at each site, resulting in 76,608 temperature logs. T_i and T_a were not correlated, based on the Pearson Correlation test (r < 0.44). Chimneys did seem to buffer T_a, resulting in lower T_{max} (p = 0.012, t = 2.75, df = 22.41) and fluctuations (p < 0.00001, t = 16.75, df = 24.90), and higher T_{mean} (p < 0.0001, t = -4.70, df = 21.02) and T_{min} (p < 0.00001, t = -15.36, df = 19.84).

Within occupied chimneys, T_{max} varied from 21.6 to 31.7°C, and T_{min} varied from 9.3 to 23.2 °C (Table 1). Unoccupied chimneys were on average 3 °C warmer than occupied chimneys, with T_{max} between 21.8 and 35.4 °C and T_{min} between 20.7 and 26 °C. The mean difference between T_{max} and T_{min} in occupied chimneys was 6.8 °C, and 10.6 °C in unoccupied chimneys (Table 1).

Logistic regression of seasonal internal chimney temperatures indicated that chimney occupancy is influenced by T_{max} (p = 0.05, df = 16, z = 1.89, β = 0.67 ± 0.36SE) (Fig. 1), and T_{mean} (p = 0.01, df =

Table 1

Temperature parameters including maximum (Max), minimum (Min), mean, difference between maximum and minimum (Diff), and standard deviation (St. Dev.) from chimneys that were occupied (n = 11) and unoccupied (n = 8) by chimney swifts during the summer of 2017, throughout New Brunswick (NB) and Nova Scotia (NS), Canada.

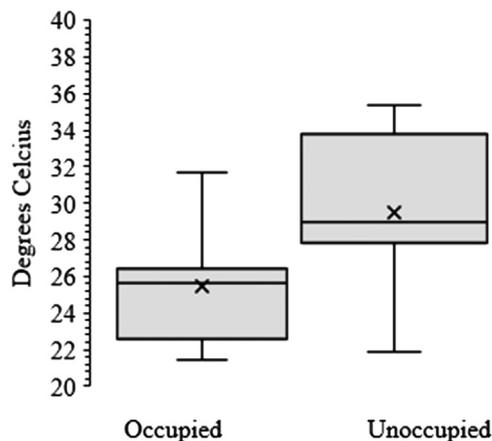| Occupied						Unoccupied					
Prov.	Max	Min	Mean	Diff.	St. Dev.	Prov.	Max	Min	Mean	Diff.	St. Dev
NB	21.6	20.0	20.8	1.6	3.6	NB	29.2	19.6	24.2	9.6	1.8
NB	22.6	15.3	18.9	7.3	1.3	NB	28.5	20.5	21.8	8.0	0.6
NB	25.7	21.9	22.8	3.8	0.4	NB	21.8	19.0	20.7	2.8	0.7
NB	21.5	9.7	20.0	12.2	0.9	NB	29.1	19.8	24.7	9.3	1.8
NB	25.7	23.2	24.3	2.5	0.5	NB	27.6	22.2	24.9	5.4	4.2
NB	25.5	16.6	21.4	8.9	1.7	NB	35.3	15.6	23.0	19.7	3.2
NS	31.7	11.7	21.1	20.0	3.3	NB	35.4	11.8	23.5	23.6	4.3
NS	28.3	16.0	23.7	12.3	2.3	NB	28.9	22.2	26.0	6.7	1.7
NS	26.4	17.7	22.3	8.7	1.6						
NS	26.3	18.5	21.3	7.8	0.9						
NS	25.4	22.9	24.1	2.5	0.5						

Fig. 1. Maximum temperatures of chimneys occupied (n = 11) and unoccupied (n = 8) by chimney swifts during the 2017 breeding season in New Brunswick and Nova Scotia, Canada. From top to bottom, the lines represent the maximum, 75th percentile, median, 25th percentile, and minimum values. The 'x' represents the mean value.
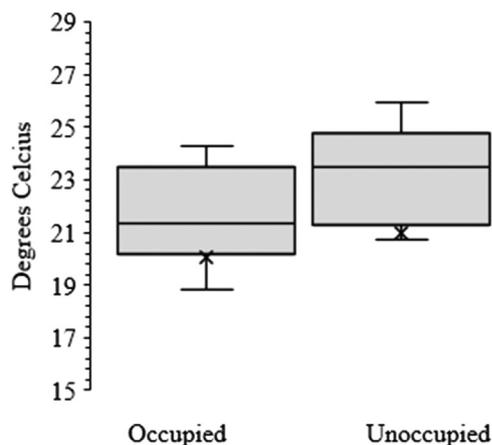

Fig. 2. Mean temperatures of chimneys occupied (n = 11) and unoccupied (n = 8) by chimney swifts during the 2017 breeding season in New Brunswick and Nova Scotia, Canada. From top to bottom, the lines represent the maximum, 75th percentile, median, 25th percentile, and minimum values. The 'x' represents the mean value.

16, z = 2.05, β = 0.94 ± 0.46SE) (Fig. 2). There was no relationship between occupancy and T_{min} (p = 0.53, df = 16, z = -0.80, β = 0.08 ± 0.13SE) or standard deviation (p = 0.24, df = 16, z = -

1.21, β = -0.11 ± 0.09SE) in seasonal temperatures. There was also no significant relationship between occupancy and T_{max} (p = 0.11, z = -1.59, β = -0.28 ± 0.17SE), T_{min} (p = 0.23, z = -1.20, β = -0.29 ± 0.24SE), T_{mean} (p = 0.14, z = -1.50, β = -0.72 ± 0.78SE), or standard deviation (p = 0.27, z = -1.10, β = -0.34 ± 0.31SE) in logistic regressions on daily internal chimney temperature data. Our logistic regressions also suggested no relationship between occupancy and chimney characteristics of internal area (p = 0.57, t = -0.52, β = -0.01 ± 0.03SE), height (p = 0.41, t = -0.74, β = -0.03 ± 0.04SE), and construction material (p = 0.14, t = 1.54, β = 0.37 ± 0.24SE).

4. Discussion

We found that chimneys buffered against T_a, and that occupancy by swifts was related to lower maximum and mean temperatures during the breeding season, although swifts did not seem sensitive to daily temperature fluctuations. Nest site selection by chimney swifts appears to be determined, in part, by the ability of the structure to buffer the nest from excess heat. T_{max} in occupied structures were significantly lower (by an average of 3.7 °C) than in unoccupied structures. This relationship was also evident in that T_{mean} was significantly lower in occupied chimneys than unoccupied. Based on our results, we suggest that a T_{max} threshold for breeding site selection in chimney swifts is ca. 32–35 °C, which is consistent with studies in some other non-passerine avian taxa (Mehaisen et al., 2017; Zhu et al., 2017). Similarly, a T_{mean} of ca. 22 °C is associated with the greatest rate of occupancy recorded during this study. However, as there is overlap in T_{max} between occupied and unoccupied chimneys, this T_{max} threshold is not a hard limit. As we collected these data from the northern portion of the chimney swifts' range, it is possible that the maximum threshold is higher in southern portions of their range, or that occupancy is further limited to chimneys that buffer temperatures below this threshold.

We do not know the ideal embryonic development temperature for swifts, though it is generally believed to occur between 37 and 38 °C (White and Kinney, 1974; Drent, 1975; Webb, 1987). A nesting environment that approaches these temperatures may be detrimental. Thus, a threshold of 32–35 °C limits the extent of warming required by the incubating adults without placing the developing embryo at risk of overheating. By nesting in a structure below this ideal temperature, adults can maintain optimal embryo development temperatures through minimal incubation/brooding and shading eggs from radiant light that enters the chimney. This could allow adults the freedom to leave the nest for longer and more frequent bouts of self-maintenance feeding, without risk of the eggs overheating (Nocera unpublished data). A T_{max} threshold may be a trade-off between the risk of overheating, water loss, and minimizing energetic costs of incubation.

We did not find a relationship between chimney occupancy by

swifts and standard deviation of temperature, which we used as a proxy for temperature fluctuations within a chimney. One possible explanation for this result is that the fluctuations observed in our study were not extreme enough to induce a response, which is plausible because temperature stability is one reason that animals choose cavities as breeding sites (Combrink et al., 2017). This is supported by the data showing that occupied chimneys have a lower mean difference between T_{max} and T_{min}, and in that T_i had lower standard deviations than T_a. It has been reported (COSEWIC, 2007) that chimney swifts will preferentially occupy chimneys with stable T_i over those in which temperatures vary more. However, our results suggest that a stable microclimate may not be as important a factor as previously thought in determining suitable nesting habitat for chimney swifts. As developing eggs have been shown to tolerate both low and varied temperatures without developmental disadvantages (Zerba and Morton, 1983), it appears that temperature fluctuation (measured by standard deviation) is less important to nest site selection than buffering from heat.

Swifts may be particularly sensitive to evaporative water loss. The intensity of nocturnal huddling in roosting swifts was greatest on warmer days than colder (Farquhar et al., 2018), possibly to reduce water loss. We found a similar relationship where the highest temperatures in potential nesting structures were associated with those structures being unoccupied. Taken together, these patterns indicate that swifts are less tolerant of heat for both nesting and roosting than they are cold. This pattern is not limited to swifts; spotted owls (*Strix occidentalis*) select cooler nest sites to reduce water loss (Ganey, 2004), while owlet-nightjars (*Aegotheles cristatus*) nest in cavities due to their low heat tolerance limit (Talbot et al., 2017).

As regional temperatures increase due to climate change, many species will be forced to alter their nesting behavior to accommodate higher temperatures (La Sorte and Jetz, 2010). One possible response to temperature increase is an earlier commencement of migration and nesting as seen in the collared flycatcher (*Ficedula albicollis*) and the Eastern screen-owl (*Megascops asio*) (Adamík and Král, 2008; Gehlbach, 2012). Increasing ambient temperatures may also force swifts to nest further down inside of chimneys where temperatures are lower. We coarsely estimated a temperature change of $+ 0.36\,°C/m$ in chimneys, from which we can infer that, by nesting lower in the chimney, swifts may be able to offset small increases in temperature. Lastly, should temperatures increase beyond the structure's ability to buffer the heat, it is possible that swifts will migrate increasingly further north to find cooler nesting sites (La Sorte and Jetz, 2010).

Given our data, we are unable to determine whether/how swifts anticipate if a structure will sufficiently buffer from temperature extremes later in the season. The variables we addressed (chimney size, construction material, location) were not significantly related to occupancy by swifts. Thus, if swifts are using structural cues to determine thermal suitability, these cues were not among the variables we measured. It is likely that previous breeders had experience with certain chimneys to help them predict future habitat states, but whether/how first-time breeders do this remains unknown.

Our results indicate that swifts preferentially select nest sites that buffer from heat rather than those with temperatures approaching the theoretical optimal incubation temperature. The risks of overheating appear to be greater than the risks associated with cooler nest temperatures. Though many species living in hot climates have adapted to heat stress and water loss over long time periods (Smith et al., 2015; O'Connor et al., 2017), temperate species may need to alter their nesting behavior much more quickly as regional temperatures increase due to climate change.
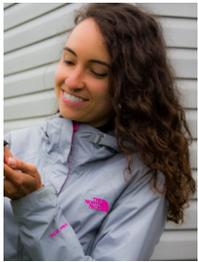
Acknowledgements

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Dr. Laura A. McFarlane Tranquilla is Atlantic Regional Program Manager for Bird Studies Canada in Sackville, New Brunswick. A seabird ecologist by training, her work currently focuses on multiple species of conservation concern in Atlantic Canada. Her professional interest in birds began with New Brunswick's forest songbirds and has since expanded to include seabirds such as auklets, murres and petrels, Piping Plover, Bicknell's Thrush, owls, wetland birds, Chimney Swifts and other aerial insectivores, many of which are focal species for Bird Studies Canada's Atlantic programs.

Dr. Joseph J. Nocera is an Associate Professor of wildlife ecology at the University of New Brunswick, in the Faculty of Forestry and Environmental Management. His research program focuses on habitat selection and movement ecology of species-at-risk, especially aerial insectivores. He has led many studies of *Chaetura* swift species, ranging from historical dietary profiles of Chimney and Vaux's Swifts to patterns of huddling in roosts.

Courtney E. le Roux is a MSc student at the University of New Brunswick, Canada. She is using radio-telemetry to determine nest-site selection of chimney swifts (*Chaetura pelagica*) breeding in wilderness areas. Her research aims to contribute to the definition of what constitutes 'critical habitat' for the Threatened species. Courtney will also be using the MOTUS network to provide the first real-time documentation of chimney swift migration routes.