NESTING ECOLOGY OF THE BARN SWALLOW ON AGRICULTURAL LANDS IN YUKON

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ABSTRACT: Since the 1980s, the abundance of the Barn Swallow (*Hirundo rustica*) in North America, including the far north, has declined. To better understand the species' biology north of 60° N, near the northern limit of its range, and in a region of expanding agriculture, we studied its nesting ecology on farms in southern Yukon Territory, Canada, in 2019 and 2020. We followed 21 attempted nests in 2019, 20 in 2020, of which 52% and 60%, respectively, were inside buildings with permanently open entrances. Other nests were built on the outside of buildings. In both years we inferred successful double brooding by three pairs, which is rarely reported north of 60°N latitude. We found the swallows' reproductive output to be similar to that at temperate latitudes: first clutches ranged from three to six eggs (mean 4.8 in 2019; 4.2 in 2020); second clutches may have averaged marginally smaller ($n = 6$). The mean number of fledglings per nest was 3.3 in 2019 and 3.0 in 2020. Twenty-one percent of nests failed, either by falling off a vertical substrate or because of predation by deer mice (*Peromyscus* spp.), Black-billed Magpies (*Pica hudsonia*), or domestic cats. We also compared the air temperatures at nests, usually near building roofs, to ambient temperatures, finding them on average 1.6°C warmer than temperatures outside buildings. We set out 33 platforms and 20 wooden cups designed for Barn Swallow nesting but over the two years of our study the birds did not use any of them.

The decline of North American avifauna is well documented, and this loss is prominent among passerines (Rosenberg et al. 2019). Nebel et al. (2010) reported that the probability of decline of aerial insectivores was higher than that of passerines with other feeding strategies. Like that of other aerial insectivores, the population of the Barn Swallow (*Hirundo rustica*) has declined across North America since the 1980s (Nebel et al. 2010, Smith et al. 2015). Limited Breeding Bird Survey data from Yukon suggest a substantial population decline since 1970 (with some stabilization since 2000), but the level of confidence in the data is low (Smith et al. 2020, COSEWIC 2021). Suggested causes of the North American decline include the loss of nesting habitat, loss of foraging habitat, reduced availability of insect prey, degradation of the winter range, and periods of inclement weather that inhibit foraging, especially in the nesting season (Nebel et al. 2010, COSEWIC 2011, 2021, Spiller and Dettmers 2019). The replacement of older structures (e.g., wooden barns) by newer ones that provide fewer suitable nesting sites is thought to degrade nesting habitat (COSEWIC 2011). Various factors are implicated in the decline of insect populations, including the use of agro-chemicals and the frequency of severe storms increasing with climate change (Sánchez-Bayo and Wyckhuys 2019, Brown and Brown 2020).

Up until the mid-1900s, the population increase and range expansion of the Barn Swallow in North America were facilitated by the clearing of land and construction of buildings suitable for nesting, often on farms. In Yukon Territory, situated north of 60°N, the increase in human-made structures and the expansion of agricultural lands are more recent than in southern Canada, with the greatest expansion of agriculture in Yukon occurring since 1990 (Hill et al. 2000). Therefore, the population increase seen up to the mid-1900s in the Canadian provinces was probably not as pronounced in Yukon. Conversion of wildlands to agricultural fields continues; from 2013 to 2017, when the extent of agriculture exceeded 15,500 ha, the government of Yukon approved 23 applications for agricultural land and issued 45 agricultural titles (Government of Yukon 2018).

In contrast to most parts of North America south of 60°N, and many parts of Europe, in Yukon data on the nesting ecology of the Barn Swallow are limited (Sinclair et al. 2003, Brown and Brown 2020, COSEWIC 2021), motivating us to undertake a field study of the species' nesting ecology there.

In many birds, warmer temperatures can enhance nestlings' growth, as long as ambient temperatures are below or within the thermal neutral zone for provisioning adults or nestlings (Sauve et al. 2021). Ambient temperatures above the thermal neutral zone may constrain chicks' growth through overheating and dehydration (Tapper et al. 2020, Sauve et al. 2021). Grüebler et al. (2010) suggested that the higher temperature and more constant microclimate in livestock barns allow nestlings to allocate more energy to growth and less to thermoregulation. We hypothesized that in the subarctic Yukon, Barn Swallows should choose nesting sites with warmer than ambient temperatures to buffer the chicks against the relatively cold temperatures.

Deployment of nest boxes to benefit aerial insectivores initially targeted cavity nesters (Jedlicka et al. 2011, Norris et al. 2018, Dulisz et al. 2021). Deployment of structures such as nest platforms and wooden cups for birds that do not nest in cavities is more recent. Nest platforms and nest cups for the Barn Swallow are promoted on websites, in guidelines for best practices, and through outreach events (www.nrcs.usda.gov/wps/portal/nrcs/detail//?cid=nrcs142p2_008682, OMNRF 2016, Lamoureux and Dion 2019). However, published studies on their utility in North America are few (Campomizzi et al. 2019).

In our field study we aimed to (1) document the Barn Swallow's nesting ecology (nest locations, nesting phenology, nesting success) on agricultural lands near the northern limit of its breeding range, (2) determine whether Barn Swallows gain a thermal advantage in their choice of nest sites, and (3) assess the Barn Swallow's use of supplementary nest structures we provided. We also augmented our data with data on nest locations, nesting phenology, and productivity from https://ebird.org.

METHODS

Study Area

Our study area encompassed ~5400 km^2 (Figure 1) within 170 km of Whitehorse, Yukon (60.721° N, 135.057° W). Here undeveloped valley bottoms are covered with boreal forest, dominated by white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*), and aspen (*Populus tremuloides*) and interspersed with wetlands, rivers, and lakes. Farmlands are concentrated in a

Figure 1. Area where Barn Swallow nests were monitored in 2019 and 2020 in Yukon.

few valleys, alongside rivers and lakes, where soils are arable (Government of Yukon 2018). Structures on which Barn Swallows nest are situated on farms and adjacent to croplands, including fallow fields, hay or grain fields, pasture with livestock, and vegetable gardens.

Nesting Ecology

To access Barn Swallow nests on agricultural lands, in spring 2019 we asked the Yukon Agricultural Association and Growers of Organic Food Yukon to notify their members of our study and request that volunteers contact us. Word of mouth drew additional participation. We tracked nests on all the rural properties whose owners expressed interest. Thus our sample of nests was not chosen systematically so may not be representative of southern Yukon as a whole. Nevertheless, we surveyed 30 properties for Barn Swallows and found nests at 13 farms. Nests were located in and on a variety of structures, including metal and wooden shelters with and without livestock (Table 1).

In 2019 and 2020, we visited each nest weekly throughout the breeding

Table 1 Situation of Barn Swallow Nests on Agricultural Properties in Southern Yukon in 2019 and 2020

Year and site	Description of nest site	Height (m)
2019		
A	atop metal bar clamps just below ceiling of SeaCan	2 to 3
B1	on corner of bamboo window blind on outside of house; west exposure	2 to 3
B2	atop light fixture inside wooden goat barn	2 to 3
C	on window frame under eaves of house; southeast exposure	4 to 5
D	on side of metal roof support inside large metal barn	>6
E1	on side of wood support under roof of upper deck of house	>6
E2	atop wood support on underside of deck	<1
E3	on wood wall under roof of covered deck	2 to 3
F	on wood rafter by light fixture inside carport	2 to 3
G	on light fixture by upper corner of small goat shed	2 to 3
H	on side of wood roof rafter inside pig barn	3 to 4
I1	on siding on outside of house under eaves; north exposure	4 to 5
I2	on wood support close to roof inside hay barn	3 to 4
J	adhered to metal roof support inside small Quonset for feeding cattle	1 to 2
K1	on wood wall halfway up corner inside garage beneath loft	2 to 3
K2	inside wood wall of garage	3 to 4
K3	on painted siding of house under eaves; west exposure	2 to 3
K4	on window frame outside of house under eaves; north exposure	2 to 3
K5	on light fixture above door under eaves; south exposure	2 to 3
K6	above window of house under eaves; south exposure	2 to 3
L	on side of metal roof support inside large metal storage building	>6
2020		
A	atop tubular metal frame inside a portable garage	2 to 3
B1	atop wood shelf above window outside; west exposure	2 to 3
B2	on ceiling joists in goat barn (1st nest)	2 to 3
	atop light fixture in goat barn (2nd nest)	
B3	atop wood support above feeding trough inside barn	2 to 3
C	on window frame under eaves of house; southeast exposure	4 to 5
E1	on wood frame of house outside	>6
E2	atop wood support on underside of deck	<1
E3	on wood wall under roof of covered deck	2 to 3
E4	on wood wall under roof of cabin porch	2 to 3
F	on wood rafter inside carport	2 to 3
G	on light fixture by upper corner of small goat shed	2 to 3
K1	on wood wall halfway up corner inside garage beneath loft (1st nest)	1 to 2
	on wood rafter in garage (2nd nest)	3 to 4
K2	on wood ceiling joist in shed (1st nest)	2 to 3
	on wood wall in shed (2nd nest)	
K3	atop wood loft in generator building (1st nest)	2 to 3
	atop breaker box in generator building (2nd nest)	1 to 2
K4	on siding, inner corner of house under eaves; southeast exposure	2 to 3
L	on side of metal roof support inside large metal storage building	>6
M	on metal frame under transport truck trailer	<1

season (May to September). During each visit, we counted the number of eggs or nestlings, and photographed nest contents by aiming a camera at a hand-held mirror positioned above the nest. We used binoculars to estimate the number of hatchlings at nests to which we could not get close enough to use a mirror. We did not capture or mark any birds for individual recognition.

To record activity at nests between our visits, we installed Bushnell "Trophy Cam" cameras (model 119537) that recorded 10 seconds of digital video when triggered by an infrared motion sensor. The sensor delayed a minimum of 1 second before it could trigger the camera to take the next clip. Farmers and property owners supplemented our efforts with their observations.

When our visits to a nest did not coincide with egg laying or hatching, we estimated the start of incubation and the date of hatching on the basis of (1) the 15-day average length of incubation in British Columbia (Campbell et al. 1997), (2) a guide to the age of nestling Barn Swallows by day (Fernaz et al. 2012), (3) the onset of the adults' provisioning of hatchlings, as observed on camera recordings, and (4) ~12 days as the age at which nestlings begin defecating independently rather than the adults removing fecal sacs, as observed on camera recordings (Fernaz et al. 2012). Backdating to estimate initiation of laying was based on the apparent age of the most developed nestling. The number of nestlings approaching fledging and the date of fledging were based on site visits and camera recordings.

We report reproductive output per nest as the mean number of eggs, hatch success (percentage of nests hatching at least one egg), nest success (percentage of nests fledging at least one chick), rate of predation (percentage of nests at which predation was video-recorded or the entire clutch was lost), and mean number of young fledged. Following McClenaghan et al. (2019), we consider the number of young at the nest on or after day 16 after hatching as a count of number of fledglings. We inferred that a nest represented a second attempt in a season when a pair's first attempt failed and they renested close by, and for some nests started after 15 July.

Double brooding is defined as the laying of a second clutch of eggs after fledging of young from the first clutch (Munroe et al. 2008). To assess double brooding in this unmarked set of birds, we relied on our nearly continuous record of numbers of adult Barn Swallows at a property and the date of occupation of specific nests. At sites with only one pair of adults, we inferred double brooding when that pair either built a second nest or reoccupied the first nest after the first brood had fully fledged, then laid a second clutch of eggs. At sites with more than one pair of adults, we inferred double brooding only if the second clutch was laid in the same nest or in one within a few meters of the first. We address attempted second nests separately from first nests because second nests are not fully independent from first nests with respect to the pair's choice of site and conditions at the nest.

To develop a regional understanding of the Barn Swallow's nesting ecology, we searched eBird (https://ebird.org/science/use-ebird-data/download-ebird-data-products) for Yukon records of Barn Swallows clearly occupying one or more nests whose supporting structure the observer noted. This supplemented our data on nest locations and timing of nesting. Some eBird observers provided data on numbers of eggs, nestlings, or fledglings from which we could estimate productivity.

Temperature at Nest Sites

To assess a possible relationship between nest-site occupation and air temperature, in 2020 we installed data loggers (Thermochron iButton DS1921G-F5) to measure temperatures at nests and outside ambient temperatures. Where possible, to reduce heat absorption from direct sunlight, we placed outdoor data loggers on the building's outside north face. For nests inside buildings, we added the comparison of nest-site temperature with indoor ambient temperature, measured with an additional logger installed inside the building. Loggers were set at 1.5 m above ground level in accordance with World Meteorological Organization (2018) guidelines. To measure the temperature near a nest, we placed the logger within 30 cm of the nest and at the same height. We installed loggers either during egg laying or incubation. Loggers recorded temperatures hourly for 40 days. To compare temperatures at the nest with ambient temperatures we used the nonparametric Wilcoxon signed-rank test for difference in medians, a paired test (Zar 1999), because the data did not meet the criterion of normality for parametric tests. The sample size for a site equaled the number of simultaneous hourly readings of ambient temperature and nest-site temperatures and ranged from 961 to 973. From the hourly temperature data, we calculated the means for nest-site temperature, indoor ambient temperature, and outdoor ambient temperature. For statistical analyses we used NCSS8 (Hintze 2012) or followed Zar (1999), accepting statistical significance at $P < 0.05$.

Artificial Nest Platforms and Nest Cups

We tested two types of artificial nesting structures. A "nest platform" consisted of a horizontal platform with sides and roof to support a nest, and a "nest cup" mimicked the shape of a Barn Swallow nest, consisting of a semicircular cup-shaped wooden structure mounted on a wooden backboard (Figure 2). Dimensions for nest platforms are available at https://nestwatch.org/wp-content/themes/nestwatch/birdhouses/american-robin.pdf and http://www.nrcs.usda.gov/wps/portal/nrcs/detail//?cid=nrcs142p2_008682, among other sites. Dimensions for nest cups are in OMNRF (2016).

Between 19 April and 16 May 2019, we placed 33 nest platforms across 26 properties. Barn Swallows had nested at 13 of these properties during the previous five years. We placed two platforms at seven farms and a single platform at the remaining 19 properties. Six platforms were placed inside buildings and 27 were placed on the exterior of buildings. Three platforms were removed before April 2020; we continued to monitor the remaining 30 platforms in 2020.

Between 4 May and 12 May 2020, we installed 20 wooden nest cups manufactured by the Bird House Nature Company (Orillia, Ontario, Canada) and built to OMNRF (2016) specifications. These we monitored in 2020. We placed nest cups at 15 properties where nest platforms had been installed the previous year and at two additional properties where swallows had nested in 2019. Three properties had two nest cups each and the remainder had one nest cup each. Thirteen of the nest cups were installed inside buildings or in shelters; seven were placed on the exterior of buildings.

FIGURE 2. Wooden cup deployed as a prospective nest site for Barn Swallows in southern Yukon in 2020. This example has the beginnings of a Barn Swallow nest.

Photo by Maria Leung

RESULTS

Nesting Ecology

Location. In 2019, we tracked Barn Swallow nests at 12 farms (Figure 3, Tables 1 and 2). Eight farms had a single active nest, two had two nests, one had three nests, and one had at least six nests, comprising 20 initial nesting attempts and one second attempt. At least four pairs reoccupied a nest built in a previous year.

In 2020, we tracked Barn Swallow nests at nine farms (eight being the same as in 2019). Six farms had one nest, one had three nests, and two farms had four nests, comprising 16 initial nesting attempts and four second attempts (Figure 3). At least six pairs used a nest that was built the previous year. No birds were marked so we do not know whether the same pairs reoccupied sites, whether fledglings from previous years reoccupied sites, or whether subsequent use was by pairs with no previous affiliation with the sites.

We inferred double brooding by three pairs each year (Figure 3, Tables 1 and 2). In 2019, one pair began building a second nest when their first brood had almost fledged, but then reverted to using the original nest when their first brood vacated it. Another pair raised their second brood in the same nest used for the first brood. The third pair built a new nest for their second clutch. In 2020, one pair built a new nest while their fledglings were still begging for food. Another pair began reusing their first nest, laid 5 eggs and abandoned

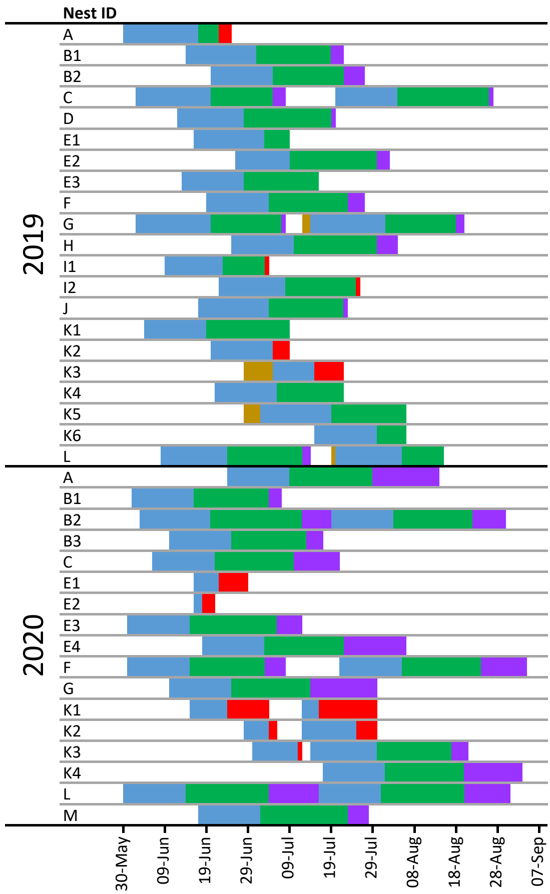

FIGURE 3. Phenology of Barn Swallow nests in southern Yukon. See Table 1 for identification of nests. Brown, nest building; blue, incubation; green, nestlings; purple, fledglings; red, nest failure (e.g., predation, abandonment). K2 and K3 in 2019 and E1 and K2 in 2020 are rough estimates, derived from one or two observations.

the clutch, then laid 4 eggs in a different pre-existing nest within 2 m of the first and raised this brood. The third pair raised young in a pre-existing nest that was within the same room as its first nest. Unlike the other pairs, the third pair was on a property with two other pairs, but each pair used separate dwellings or separate rooms with separate exits.

Of the 21 initial nests in 2019, 11 (52%) were constructed inside buildings, each with a permanently open side or open door (Table 1). Of the 20 initial nests in 2020, 12 (60%) were inside buildings (Table 1). The nests were built on and in a wide variety of buildings and structures, and at a wide variety of heights (Table 1). Only 3 of 12 properties had large barns or sheds (total of 5

Table 2 Nesting Phenology of the Barn Swallow in Yukon

	n^a	Median	Range
Field study, 2019–2020			
First broods			
2019			
Onset of incubation[b]	18	16 Jun	31 May–6 Jul
Hatch date	18	3 Jul	18 Jun–20 Jul
Fledging date	10	22 Jul	6 Jul–1 Aug
2020			
Onset of incubation[b]	11	7 Jun	2–25 Jun
Hatch date	11	22 Jun	17 Jun–10 Jul
Fledging date	11	13 Jul	5–24 Jul
Second broods			
2019			
Onset of incubation	3	21 Jul	15–21 Jul
Hatch date	3	5 Aug	2–6 Aug
Fledging date	2	23 Aug	18–27 Aug
2020			
Onset of incubation	3	20 Jul	17–22 Jul
Hatch date	3	4 Aug	1–6 Aug
Fledging date	3	23 Aug	21–24 Aug
eBird, 1975–2021			
Incubation period	4		17 Jun–30 Jul
Nestling period	8		25 Jun–3 Aug
Fledglings at nest	13		8 Jul–4 Sep

[a]Number of nests.

[b]Second nests attempted after a failure excluded.

buildings) more than 4 m high. Barn Swallows nested in two of those in 2019, and one in 2020, and Cliff Swallows (*Petrochelidon pyrrhonota*) nested in three of the five in both years. Cliff Swallows were nesting, mostly colonially, at five of the 12 properties with Barn Swallows. Livestock were kept in four of the buildings with nests: two held goats, one had pigs, and one had young cows. The permanent building materials forming the roof above nests were made of wood (64%), metal (22%), or plastic (14%).

No active nests were closer together than 30 m. All but one were in or on separate buildings, even on properties with multiple nesting pairs. The exception, in 2020, was of two nests within the same building but in different rooms with different exits.

The eBird data (1975–2021) had records of 76 occupied nests at 67 locations at least 50 m apart. Most locations (88%) had single nests, but 10% had two nests and 2% had three nests close to each other. Only nine nests (12%) were on farm buildings like those on which we focused our field study. The majority of nests (53%) were on rural buildings away from agricultural lands, while 18% were on buildings within a townsite, 16% were on rural bridges, and one was in a culvert. Nests were commonly close to open water.

Phenology and reproductive output. Table 2 summarizes the phenology data, and Table 3 summarizes reproductive-success data from our field study and eBird data combined. The period of reproductive activity at nests, not

Table 3 Reproductive Output of Barn Swallows in Southern Yukon

	No. Nests	Hatch success (%)	Nest success (%)	Depredation rate (%)	No. eggs[a]	No. hatch-lings[a]	No. fledged[a]
Field study, 2019–2020							
2019	24	92	71	17	4.6 ± 0.21 (17)		3.3 ± 0.47 (21)
First brood[b]	21	90	67	19	4.8 ± 0.20 (15)		3.3 ± 0.52 (19)
Second brood	3	100	100	0	3.5 ± 0.50 (2)		3.5 ± 0.50 (2)
2020	23	70	70	26	4.2 ± 0.19 (22)		3.0 ± 0.45 (23)
First brood[b]	20	65	65	30	4.2 ± 0.21 (19)		2.9 ± 0.52 (19)
Second brood	3	100	100	0	4.0 ± 0.58 (3)		4.0 ± 0.58 (3)
Totals	47	81	70	21	4.4 ± 0.15 (39)		3.2 ± 0.32 (44)
eBird, 1975–2021							
Incubation	4				3.6 ± 0.40		
Hatchlings	8					3.4 ± 0.26	
Fledglings	13						3.9 ± 0.23

[a]Numbers of eggs, hatchlings, and young fledged are means with standard errors of the mean, and sample sizes of nests.

[b]First broods include second nestings after failed first attempts (1 in 2019, 3 in 2020).

including nest building, was similar for both data sets and lasted more than three months, suggesting more than one nesting cycle for some pairs. In our field study, the onset of incubation for first broods extended from late May to early July, hatching extended from mid-June to mid-July, and most young fledged in July. In 2020, two pairs successfully fledged young after their first broods were depredated. They began incubation around 15 July and 17 July, eventually raising 5 and 4 fledglings.

In 2019, two of the second broods were successful, with all young fledging by 27 August (Table 2, Figure 3). Two second clutches were smaller than first clutches: three compared to six, and four compared to five. We were not able to see into the nest of the third second clutch. In 2020, the second clutches were the same size as the first: 3, 4, and 5 eggs (Figure 3). That year, all three pairs raised their second broods in a nest different from the first brood. Two of these nests pre-existed and the third was newly built. Of the three pairs of Barn Swallows that likely raised a second brood in 2020, one occupied the same site as a pair that had raised a second brood in 2019; the others were at sites not previously recorded to have second broods. Recently fledged juveniles continued to occupy nests as late as 4 September, even though they had taken their first flight at least 10 days earlier (26 August).

The interval between initiation of first and presumptive second clutches was 41, 41, and 47 days for the three pairs in 2019, and 45, 47, and 51 days for three pairs in 2020. Both years combined, the mean was 45 days (SD = 3.9). The pair that took 51 days had laid a clutch of 5 eggs after raising their first brood, abandoned the 5 eggs, and then laid another clutch of 4 eggs, which they raised.

For our full data set, hatching success was 81%, nest success was 70%, and 21% of nests were depredated (Table 3). Hatching success in 2019 and 2020 differed because of a greater rate of egg predation in 2020 (Table 3). Mean clutch size was 4.4 eggs, and mean number of young fledged was 3.2 (Table 3).

Nest failures. Over the two years, we recorded 12 nest failures: 10 for first attempts, and 2 for second attempts (both in 2020). The primary cause of failure was confirmed or likely predation (10 nests). One nest fell off the outside wall to which it had been attached and another was pulled off a rafter by a domestic cat that then consumed all five nestlings. Eggs in two other nests at one site were likely lost to predators. Black-billed Magpies (*Pica hudsonia*) nested at one farm, and video confirmed that they removed and consumed eggs at four nests. One pair of swallows lost all 3 eggs to deer mice (*Peromyscus* sp.), as attested by video of a mouse feeding in the nest on three successive nights.

Nest Temperature

We recorded data on nest temperature at 19 nests (including second broods and failed nests) across 16 sites in 2020. In all 13 comparisons, the temperature at the nest was significantly greater than the indoor ambient temperature ($P < 0.0001$, $n = 961$ to 973; Table 4), averaging 1.7° C higher. Among 19 comparisons between temperature at the nest and outside ambient temperature, in 16 the nest temperature was significantly higher (P ranging from 0.028 to <0.0001, $n = 961$ to 971), in one there was no difference ($P = 0.912$, $n = 973$), and in two the nest temperature was significantly lower ($P < 0.0001$, $n = 732$ to 972). Overall, nest temperature averaged 1.6°C higher than outside ambient temperature. The one nest site with no significant temperature difference was built inside a portable garage consisting of a metal frame and PVC fabric cover.

Across all sites except one, the median daily temperatures at nests varied from 12° C to 17° C. The exception was a nest in a generator shed where the median temperature was above 22°C (Figure 4). The highest nest-site temperature was 42°C, which lasted 2 hours. The top of this nest was within 15 cm of a metal roof with a western exposure. The median temperature during the development of a pair's second brood was slightly lower than during that of its first brood (Figure 4: nests B2, F, and L).

Artificial Nest Platforms and Nest Cups

None of the nest platforms was occupied by swallows. Neither were any nests completed in the cups provided.

DISCUSSION

We found that in Yukon Barn Swallows nest in and on a wide diversity of man-made structures. No birds nested colonially. Our observations on nesting phenology expand the range of dates for the incubation and nestling phases beyond those reported for Yukon by Sinclair et al. (2003) (3 June–8 July and 4 July–8 August, respectively) and in eBird (see Table 2). Our ob-

Table 4 Comparisons of Temperatures (°C) Measured at Barn Swallow Nests with Ambient Temperatures in Yukon in 2020

		At nest (T_n)		Indoor ambient temperature (T_i)[a]			Outside ambient temperature (T_o)		
Nest	n[b]	Mean	SE[c]	Mean	SE[c]	Z[d] (T_n:T_i)	Mean	SE[c]	Z[d](T_n:T_o)
A	973	13.9	0.18	12.9	0.16	21.407[e]	13.9	0.18	0.111[f]
B1	961	16.5	0.24	—	—	—	13.8	0.15	23.241[e]
B2 (1st)	961	16.1	0.21	14.5	0.13	13.030[e]	13.8	0.15	21.560[e]
B2 (2nd)	961	14.9	0.19	14.1	0.12	6.347[e]	13.1	0.14	21.351[e]
B3	961	16.9	0.21	15.4	0.14	14.813[e]	13.8	0.15	23.806[e]
C	972	15.8	0.15	—	—	—	14.7	0.19	11.492[e]
E1	972	15.5	0.16	—	—	—	13.0	0.15	26.120[e]
E2	972	14.1	0.14	—	—	—	13.0	0.15	18.713[e]
E3	972	14.8	0.14	14.4	0.16	9.065[e]	13.0	0.15	24.927[e]
E4	972	14.2	0.15	—	—	—	13.0	0.15	20.533[e]
F (1st)	972	16.5	0.25	13.0	0.14	22.523[e]	14.0	0.16	20.793[e]
F (2nd)	961	14.5	0.24	12.0	0.15	20.558[e]	12.6	0.17	21.424[e]
G	961	14.2	0.12	13.0	0.13	26.426[e]	13.9	0.20	2.196[e]
K1	972	13.1	0.06	12.5	0.06	27.854[e]	15.6	0.16	15.052[g]
K3	971	21.6	0.13	19.0	0.10	27.035[e]	15.8	0.17	26.026[e]
K4	971	17.4	0.15	15.9	0.11	23.530[e]	15.8	0.17	13.198[e]
L (1st)	961	15.8	0.16	13.4	0.08	17.103[e]	13.9	0.13	24.474[e]
L (2nd)	961	16.0	0.16	13.2	0.08	24.046[e]	13.3	0.12	26.908[e]
M	732	13.9	0.15	—	—	—	14.3	0.14	8.303[g]

[a]Measured if the nest was in a building or other shelter.
[b]Number of simultaneous hourly temperature records.
[c]SE, standard error.
[d]From Wilcoxon signed-rank test for difference in medians
[e]Temperature at nest was significantly warmer ($P < 0.05$).
[f]No significant difference.
[g]Temperature at nest was significantly colder ($P < 0.05$).

servations of earliest onset of incubation (31 May) and latest fledglings at nests (4 September) correspond closely with the range of dates of nest occupancy elsewhere in Yukon (26 May–4 September; eBird), and in the adjacent Northern Boreal Mountains Ecoprovince of British Columbia (late May–late August; Campbell et al. 1997).

On the basis of clutch size, the Barn Swallow's potential productivity in Yukon is similar to that in other parts of North America. Sinclair et al. (2003) reported a mean clutch size in Yukon of 5.0 ($n = 5$), whereas we found 4.3, data from all nests combined (Table 3). In British Columbia, Campbell et al. (1997) reported clutch sizes ranging from 1 to 10, with 84% of nests having 3 to 5 eggs. Studies in Kansas and West Virginia found that first clutches averaged 4.6 eggs, second clutches 4.1 eggs (Samuel 1971, Anthony and Ely 1976). In two years of study in Ontario, first clutches had 4.6 or 4.7 eggs, second clutches 3.9 or 4.4 eggs (McClenaghan et al. 2019).

Campbell et al. (1997) noted that in British Columbia "first clutches were significantly larger than second clutches." In only two of the five cases in

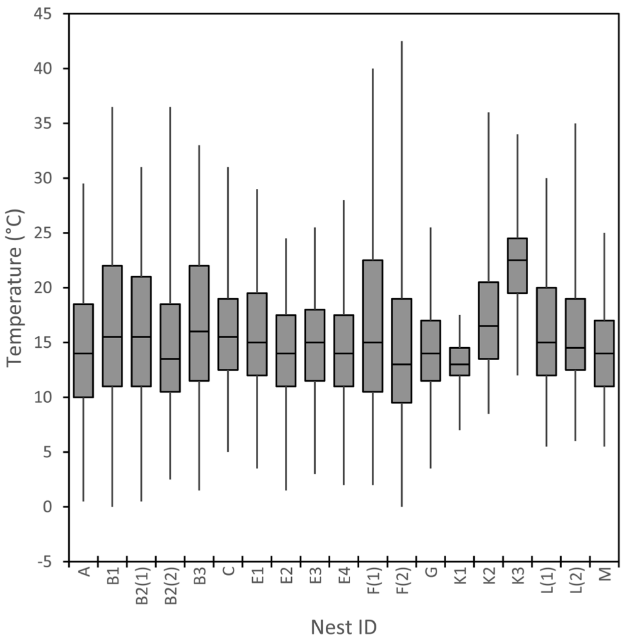

Figure 4. Box-and-whisker plot of temperature at Barn Swallow nesting sites in 2020 in southern Yukon. Numbers in parentheses after the nest identifier distinguish first and second broods. Horizontal line in each box is median temperature. The lower border of the box is the median of the lower half of temperatures, and the upper border is the median of the upper half of temperatures. Whiskers indicate minimum and maximum recorded temperatures.

which we could ascertain the size of the second clutch was it smaller than the first. Yukon data on clutch size are still limited but do not suggest that in the north clutches are larger. This does not fit with the general increase in clutch size with latitude in many passerines (Lack 1947, Kulesza 1990) but may be explained by Lack's (1947) food-limitation hypothesis if in this area the Barn Swallows experience substantial competition (e.g., from Cliff Swallows) for food.

The overall nest success we observed (70%) was lower than the 80.1% reported by McClenaghan et al. (2019) for southern Ontario, largely because of a higher rate of nest predation (21% vs. 15.7%). In our study nest predation was heavily influenced by one farm with resident Black-billed Magpies. Our mean number of young fledged per nest (3.2 ± standard error 0.32) was slightly less than but not significantly different from the 3.4 ± 0.12 reported by McClenaghan et al. (2019) ($t = 0.42$, d.f. 56, $P > 0.50$). It appears that this species largely compensates for the extra cost of migrating farther north but does not increase its reproductive output.

Several studies have addressed double brooding in songbirds north of 60°N in North America (Custer and Pitelka 1977, Jamieson 2011, Hussell et al. 2014, Ringgenberg and Winker 2015), but most present indirect evidence. Hussell et al. (2014) reported double brooding of the Northern Wheatear (*Oenanthe oenanthe*) on Baffin Island but were unable to determine whether the young of the second brood fledged. Custer and Pitelka (1977) recorded a very late nesting attempt by Lapland Longspurs (*Calcarius lapponicus*) and assumed it followed an earlier successful nesting. Fledging was not confirmed. Ringgenberg and Winker (2015) suggested that the long period during which Common Redpolls (*Acanthis flammea*) are reproductively active (late April to late August) in Alaska is evidence for double brooding. Our evidence for double brooding by several pairs in both years was not conclusive (because birds were not marked), yet we did confirm successful fledging of later broods.

The time between initiation of first and second clutches appears shorter in Yukon than farther south in British Columbia. In a British Columbia study of 135 nesting pairs over 10 years, 37% laid a second clutch (Campbell et al. 1997). These second clutches may have included ones that followed a failed first attempt. The authors noted a period of about 51 days between the initiation of a successful first clutch and initiation of the second clutch. The interval in our study was shorter (mean = 45 days, SD = 3.9).

Possible reasons for a more compressed nesting cycle at northern latitudes include the longer daylight hours during which swallows can feed and a greater abundance of insect prey. Turner et al. (2017) suggested that the greater availability of prey farther north allows American Robins (*Turdus migratorius*) to forage and provide food to young for longer periods each day. Insect availability also changes with weather and farming practices. On the basis of study in the United Kingdom, Facey et al. (2020) considered the effects of weather on nestlings' body mass to be a result of how temperature, rainfall, and wind speed interactively affect prey availability and influence the nest's microclimate. In Denmark, Møller (2019) reported the rate at which Barn Swallows feed nestlings to increase with increasing insect abundance. We lack data on prey abundance, so cannot explore this further.

We documented nest failure because of predation and failed adhesion of the nest to a vertical substrate during brooding. The predators that Campbell et al. (1997) listed—the Common Raven (*Corvus corax*), Black-billed Magpie, Red Squirrel (*Tamiasciurus hudsonicus*), and domestic cat—are similar to ours, but our evidence of egg predation by a deer mouse is new. Brown and Brown (2020) noted that nests frequently fall from the substrate they are built on. Other cited causes of death include entanglement in monofilament fish line (Bartel 1984) and horse hair (Knight and Ryan 1980) incorporated in the structure of the nest. We did observe a Cliff Swallow strangled by horse hair.

Ambrosini and Saino (2010) suggested that the warmer temperatures and higher air humidity associated with rooms with livestock buffer developing embryos against the stress imposed by cool temperatures. Although few of our nesting sites were within rooms with livestock, nests built inside buildings or shelters were significantly warmer than ambient indoor temperature. With few exceptions, nest sites indoors and outdoors were significantly warmer than ambient outdoor temperatures. The two exceptions were nests in unusual places. One was on the metal frame under the trailer of a transport truck about 1 m from the ground. Another was halfway up the inside permanently shaded wall of a garage. Cliff Swallows pre-empting other nest sites or high risk of predation by the Black-billed Magpie likely influenced where these nests were built.

Although warmth often favors nesting Barn Swallows, COSEWIC (2011) suggested that nests built under metal-roofed barns are at risk of overheating. Imlay et al. (2019) found the survival rate and body mass of nestling Cliff Swallows to be lower under metal than under wooden roofs. We observed the highest temperatures at a nest site built under a metal roof. Unlike the adults at other nests, those at this nest often perched beside it instead of sitting on eggs or young. Smith and Montgomerie (1992) noted that the amount of time that adult Barn Swallows devoted to incubation was negatively correlated with nest temperature. In many birds, the need to buffer the eggs against the cold declines with increasing ambient temperature (Sauve et al. 2021).

The nest platforms and nest cups we installed were not used, likely for several reasons. First, the distance between the ceiling of the building and floor of the platform (20 cm) may have been too great. Brown and Brown (2020) stated that the gap between most nests and the ceiling above them is 2.5 to 6 cm, and nests are about 13 cm high (i.e., total of 15.5 to 19 cm). Unlike platforms, cups can be placed closer to an overhanging roof. Second, returning Barn Swallows may prefer to use old nests from previous years. We found reuse of existing nests to be common. Third, the swallows may have preferred sites more sheltered than those where we placed the platforms and cups. Fourth, we monitored the structures no more than two years. Over time, and with changes in the individual swallows prospecting for nest sites, use of structures may increase. Teglhøj (2018) observed this in Denmark, finding that the number of broods raised in artificial nest cups increased from 16% in 2012 to 52% in 2016.

Despite the birds not nesting in the structures we provided, in 2020 a pair of Barn Swallows did construct a nest on a wood shelf provided by landowners, following removal of the 2019 nest. Mercadante and Stanback (2011) also demonstrated that removal of old nests encourages use of artificial nest structures. They attained an occupancy rate of 23% to 46% in wooden nesting cups at a Barn Swallow colony in North Carolina. As they removed the option of reuse of old nests and experimented at an established colony, their rate of nest-cup occupancy is not comparable to ours.

Our study is the first to address the Barn Swallow's nesting ecology in Yukon and may serve as a basis for future investigations and monitoring of this species at subarctic latitudes. Our data suggest that in this area the swallow's clutch size and nest success are similar to those farther south. Our temperature data suggest that Barn Swallows choose relatively warm microsites for nesting. Future studies could explore the role of changing prey availability (influenced by weather and pesticide applications) in nesting success, competition with Cliff Swallows for nest sites and prey, and the value of retaining known nest sites for returning birds, as our and other data suggest high site fidelity (COSEWIC 2021).

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