

Nesting ecology and reuse of nest burrows by Bank Swallow (*Riparia riparia*) in southern Yukon

PAMELA H. SINCLAIR^{1*}, MARTY D. MOSSOP¹, and SHANNON A. STOTYN¹

¹Canadian Wildlife Service, Environment and Climate Change Canada, 91780 Alaska Highway, Whitehorse, Yukon Y1A 5X7 Canada

*Corresponding author: pam.sinclair@canada.ca

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Abstract

Bank Swallow (*Riparia riparia*) is a declining insectivorous bird that nests colonially in near-vertical surfaces, including natural banks along waterways as well as those created by industrial excavation. Several threats are likely contributing to the population decline, conservation measures have been recommended, and monitoring methods have been developed. However, little is known of this species in the extensive boreal portion of its breeding range. To assess whether recommendations developed in southern areas are likely to be effective in a more northerly region, we investigated aspects of the nesting ecology of Bank Swallow in southern Yukon during 2013–2017. Nesting activity occurred between 20 May and 21 August. We found an exceptional abundance of nest burrows in natural riverbanks along 46 km of the Yukon River near Whitehorse (326 burrows/km), but relatively low percent burrow occupancy in both natural and artificial habitats compared to studies from other regions. Year-to-year persistence of nest burrows and rates of reuse of burrows were high compared to other studies. We highlight the potential importance of the boreal region for recovery of Bank Swallow in Canada, and the importance of using region-specific estimates of percent occupancy when monitoring Bank Swallow using burrow counts. Further study is needed to determine whether unoccupied burrows contribute to nesting success, and whether there are situations in which Bank Swallow burrows should be protected year-round instead of only during nesting.

Key words: Bank Swallow; *Riparia riparia*; nesting ecology; Yukon; colony occupancy; burrow reuse; nesting phenology; aerial insectivore; Species at Risk; boreal region

Introduction

Bank Swallow (*Riparia riparia*) is a colonial breeder. Each nest is in a long, narrow, horizontal burrow (a few centimetres in diameter, with average length ranging from 59 to 90 cm; Garrison 1999) that the birds excavate. Historically, Bank Swallow had centres of abundance in areas where natural banks of friable material occur along rivers and on lake and ocean shores. However, increasing human settlement has provided nesting habitat in other areas, in the form of road cuts and sand and gravel quarries (Erskine 1979). The proportion of the population that nests in naturally, versus artificially-created, substrates varies among regions (Erskine 1979; Garrison 1999).

Louis Bishop (1900: 88), surveying birds along the entire Canadian portion of the Yukon River in 1899, ranked Bank Swallow among the region's most abundant species and noted:

We were entirely unprepared for the great abundance of this species on Fifty-Mile River above Miles Canyon. There almost every bank was

honeycombed with their holes. Along the rest of the Yukon as far as Circle [Alaska] bank swallows were common and often abundant...

Although still a common species in Yukon, Bank Swallow is now listed as Threatened under Canada's federal *Species at Risk Act* (SARA), due to nationwide population declines (SARA Registry 2020). Bank Swallow is widely distributed in North America, and the breeding range includes the boreal region from Alaska to Labrador, extending well beyond areas surveyed by the North American Breeding Bird Survey (BBS; Environment and Climate Change Canada 2019). Little is known of its abundance, trends, habitat use, or breeding biology in northern areas (but see Hickman 1979; Bols 2017). In Yukon, data from the BBS show a steep decline in Bank Swallow numbers (long-term change –90.8% during 1972–2017, short-term change –15.6% during 2007–2017; Smith *et al.* 2019). However, the BBS is conducted along roads, and it is unknown whether this dramatic decline reflects the overall status of the Yukon population or tracks the effect

of changing road construction practices on the portion of the population that nests near roads.

Several threats may be driving the Canadian decline of Bank Swallow, which is a long-distance migrant that winters in South America (Garrison and Turner 2020). These include loss of nesting habitat through erosion control and flood control projects that make natural banks unsuitable for nesting, management of sand and gravel quarries, decreased abundance of flying insects due to pesticide use, and poorly-understood threats related to climate change (COSEWIC 2013). Threats specific to Bank Swallows that nest in Yukon are unknown. Recommendations for recovery of Bank Swallow populations have been developed (Falconer *et al.* 2016), along with management recommendations for quarry operations (OSSGA 2013; Environment Canada 2016), and methods for monitoring populations (Bird Studies Canada 2010). Avoiding nesting colony disturbance is recommended during the nesting season, and habitat regulation has been suggested for colonies that have been occupied within the last three breeding seasons (Falconer *et al.* 2016). Burrow counts can be used for monitoring, and an assumption that 50% of burrows are occupied by nesting swallows is recommended for general use, unless local data are available (Cadman and Lebrun-Southcott 2013). Reported percent occupancy of burrows ranges from 63% for lakeshore colonies in Ontario (Burke 2017) to 35.3% for colonies in southern Yukon (Bols 2017).

Yukon Territory is predominantly mountainous, but with wide river valleys. Although a large portion of the territory adjacent to Alaska has been unglaciated for three million years, other regions of the territory feature deep glacial deposits from recent glaciations, including deep deposits in the Whitehorse area from glacial Lake Champagne (Smith *et al.* 2004). Tall riverbanks are found along parts of several major rivers in the territory, including the Yukon, Teslin, Takhini, and Nisutlin rivers in the south, the Liard and Hyland rivers in the southeast, the Stewart River in central Yukon, and the Porcupine and Peel rivers in the north. The human footprint in Yukon is relatively small, with a population of 35 874 (Statistics Canada 2017), although the road system is fairly extensive compared to some northern regions. In a compilation of Yukon Territory bird observations from 1861 to 1998, 78 of 90 (87%) Bank Swallow colonies were in natural banks adjacent to rivers or lakes, while 12 (13%) were in roadside cut banks ("road cuts") or gravel pits (Sinclair *et al.* 2003). This is in contrast to regions such as southern Ontario, Quebec, and British Columbia, where the majority of Bank Swallows nest in artificial habitats (Erskine 1979; Falconer *et al.* 2016).

Bank Swallow is protected in Canada under the federal *Migratory Birds Convention Act* and *Migratory Birds Regulations* (1994), and SARA, which prohibit destruction of nests. However, under SARA the nest burrow is protected only while the birds are actively nesting (Government of Canada 2019). Bank Swallows can excavate new nest burrows each year or occupy old burrows excavated in previous years (Hickman 1979; Garrison *et al.* 1989). In some regions, few burrows persist over winter (Garrison *et al.* 1989; Cadman and Lebrun-Southcott 2013). It is speculated that Bank Swallows may avoid old burrows due to the persistence of ectoparasites from the previous year's nest (Garrison 1999; Cadman and Lebrun-Southcott 2013; Falconer *et al.* 2016). Range-wide, there is little documented information on year-to-year burrow persistence, or reuse frequency of existing burrows. Therefore, it is unknown how the use of nest burrows excavated in previous years contributes to nest success.

Our goal was to assess whether recommendations for management and monitoring, developed in southern areas, are likely to be effective in a more northerly region. To do so, we collected five years of data on: (1) nesting phenology, to inform optimal timing of monitoring as well as avoidance guidelines for industry, (2) percent occupancy of burrows to inform monitoring methods, and (3) persistence and reuse of nest burrows to inform management recommendations regarding protection of burrows in the non-breeding season.

Methods

Study area

Our study was conducted in and near Whitehorse, Yukon, Canada (60.72°N, 135.05°W), located on the section of the Yukon River that was historically known as the "Fifty-Mile River" (Yukon Department of Tourism and Culture 2013). It is in the Yukon Southern Lakes ecoregion, within the Boreal Cordillera ecozone, a mountainous region with major river valleys characterised by deep glacial deposits rich in silt and clay from the most recent McConnell glaciation (Smith *et al.* 2004). Here, the river is typically 100–200 m wide, although it occasionally narrows to <50 m or widens to >500 m. Land adjacent to the river is predominantly forested, but also includes residential, urban, and industrial developments near the city.

Selection of survey sites

To survey Bank Swallow colonies, we boated down two segments of the Yukon River: (A) from the Yukon River Bridge (southeast of Whitehorse on the Alaska Highway) to Schwatka Lake (27.7 river km; Figure 1), and (B) from Shipyards Park in downtown Whitehorse to the Takhini River Bridge north

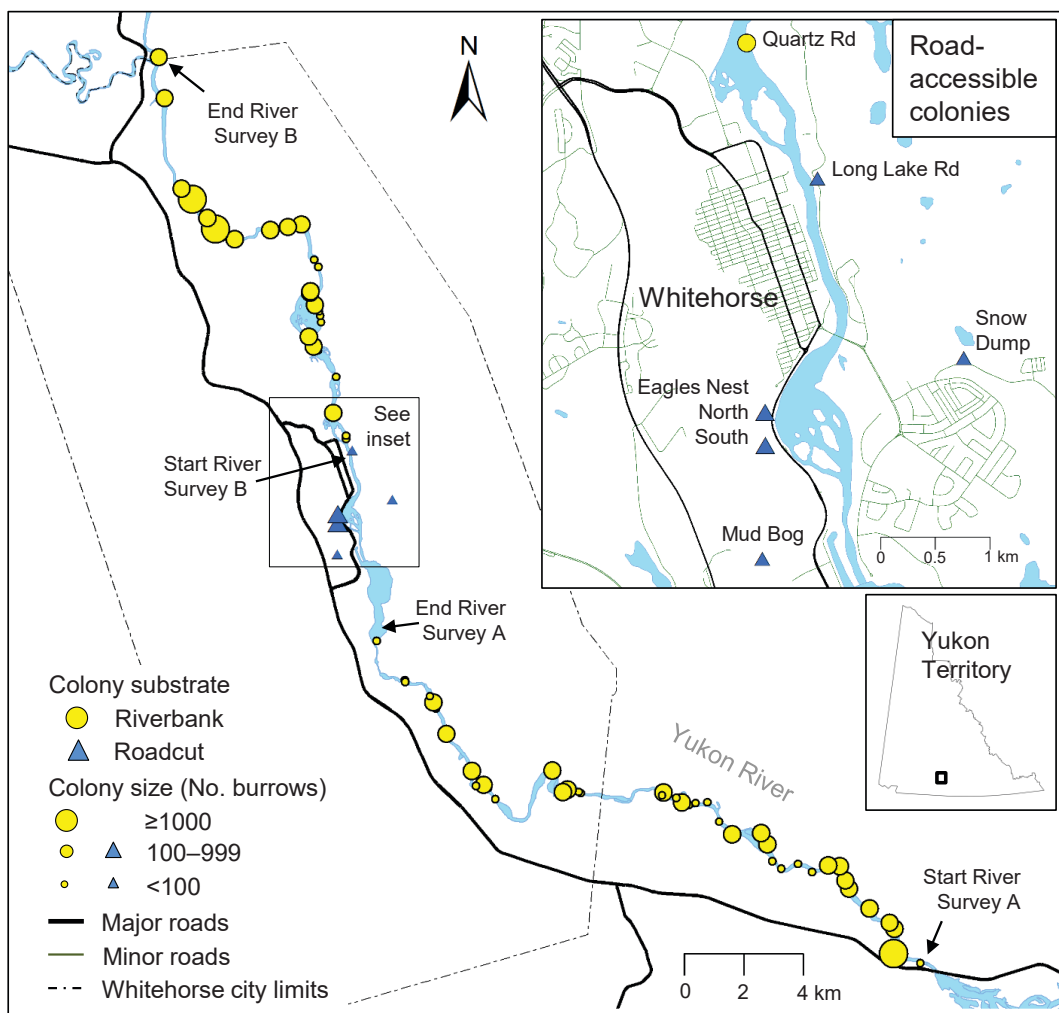


FIGURE 1. Locations of Bank Swallow (*Riparia riparia*) colonies surveyed in the vicinity of Whitehorse, Yukon, Canada.

of Whitehorse (18.3 river km; Figure 1). Both banks of the river were easily visible from its middle, except at three points where the river widens substantially.

In addition to our river survey, we also located Bank Swallow colonies that were visible from public roads within the limits of the City of Whitehorse, for more detailed study. These road-accessible colonies were located by visiting colony sites previously known to the authors and local birders, as well as by searching additional potential habitat. All occupied road-accessible colonies found that could be safely observed and were close enough to obtain clear video footage (i.e., within about 250 m) were included in the study; one colony was excluded because it was too far away (across a lake), and two colonies in active quarries were excluded due to access and safety

issues. As a result, we included six road-accessible colonies in the study: five colonies in old road cuts, and one colony in a riverbank which was part of the river survey route described above but could also be observed from land. Road-accessible sites were selected in May 2013, with no new sites added later in the study.

River surveys

River surveys, using two observers, were conducted twice each year from 2013 to 2016: once during 17–26 June and once during 6–17 July. Each river survey was conducted over a two-day period, with segments (A) and (B) each conducted on a separate day. During the first survey in June 2013, a global positioning system (GPS) unit was used to mark the approximate upstream limit of every Bank Swallow col-

ony encountered and we noted on which side of the river the colony occurred. A colony was defined as a group of burrows ≥ 100 m from other burrows. In June and July of each year (2013–2016) except July 2013, we counted the number of burrows at each colony (by ones, 10s, and 100s depending on the size of the colony), the number of Bank Swallows observed, and the number of occupied burrows. We also noted evidence of nesting stage such as excavation, nestlings visible in burrow entrances, or adults carrying faecal sacs. In July 2013, the first survey year, data collection was limited to the number of Bank Swallows observed and whether the colony was present and occupied. Visits were brief (1–5 min duration at each colony), with shorter visits at smaller colonies with immediate evidence of activity, and longer visits at larger colonies or where activity was not immediately evident. Observations were mostly made with a single pass as we moved down the river, although occasionally, for large colonies, we immediately made a second pass to ensure our counts were correct. Our priorities were counting the total number of burrows and determining whether each colony was occupied. Counts of numbers of birds and occupied burrows were not considered complete, as most swallows presumably remained inside nest burrows or were away foraging. If a new colony was encountered, it was added to the survey and marked with a GPS waypoint. A colony was considered occupied if ≥ 1 burrow was occupied. A burrow was considered occupied if ≥ 1 Bank Swallow was seen to enter or exit the burrow or was visible inside the burrow entrance. If a colony was observed to be occupied in ≥ 1 survey (i.e., June or July), it was considered to be occupied that year.

Road-based surveys

We visited the six road-accessible colonies for more detailed observation between 3 May and 18 July, 2013–2017 (Figure 2). We used photographs to count the total number of burrows, and also to track persistence of individual burrows. At each site we photographed the entire colony at least twice each year (in May before arrival of the birds, and in July when excavation was presumed to be complete, and usually also in June). A complete burrow count was made at each colony 2–9 times per year. We numbered and tracked individual burrows, noting presence or absence of each burrow in each photograph, including newly-excavated burrows as they appeared. At smaller colonies (<100 burrows; $n = 3$), all burrows were tracked this way. At larger colonies (>100 burrows; $n = 3$) we tracked sample sections, including about 20 burrows in each sample, until the samples included about 20% of the colony, as recommended by Bird Studies Canada (2010). The same sample sections

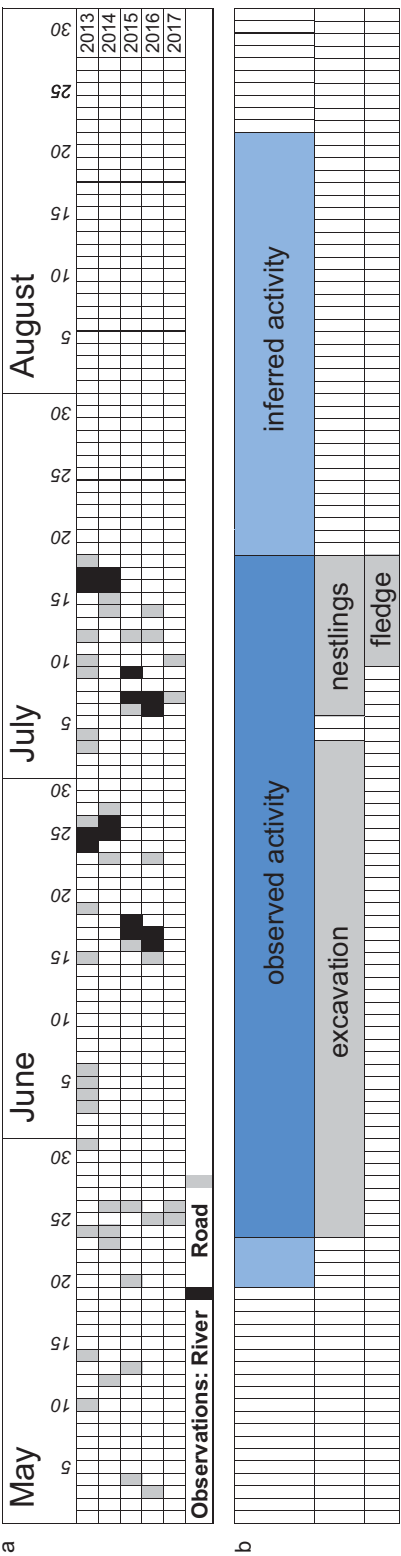


FIGURE 2. Seasonal timing of nesting of Bank Swallows (*Riparia riparia*) near Whitehorse, Yukon, Canada, 2013–2017. a. Survey dates for river (black) and road-accessible (grey) surveys. b. Date ranges of observed and extrapolated nesting activity (dark blue and light blue, respectively), with date range of observed excavation of burrows, nestlings, and fledglings shaded grey.

were used annually, regardless of whether the original burrows remained.

Recording nesting activity

To assess percent occupancy of burrows and track year-to-year reuse of individual burrows, we recorded activity for 20 min by direct observation of the two smallest road-accessible colonies (Long Lake Road and Snow Dump by two observers) and by video recording of sections of the four larger road-accessible colonies (Eagle Nest north and south, Mud Bog, and Quartz Road). Burrow numbers and all entries and exits were recorded along with any additional behaviours indicating nesting stage, such as burrow excavation, adults entering burrows, or nestlings visible in burrows. Video recordings were also made of six river-survey colonies on 16–17 July 2013. For these recordings, a section of burrows was selected which was occupied (i.e., adults entering/exiting burrows) and suitable for recording (i.e., low enough on the bank that the distance and angle allowed a clear image, and in a position where the river current allowed safe landing or steady boating at a distance far enough to avoid disturbing the birds). One to three occupied sections of each colony were thus selected, for a total of nine recordings from six colonies, with 10–15 min long videos.

Data summary and analysis

To calculate linear density of burrows on the river we used mean total burrow counts from six 46-km river surveys (river segments A plus B, completed over a two day period) conducted in June and July 2014–2016. We did not include 2013 data because the June 2013 survey involved a different observer and slightly different technique, and because burrows were not counted in July 2013.

To infer nesting phenology from our observations, we assumed the following: seven days for excavation of burrow (Petersen 1955; Hickman 1979), four days for nest building (Petersen 1955), four days for laying a clutch of four eggs (Hickman 1979) at a rate of one egg per day (Petersen 1955), 14 days incubation (14–15 days in Alaska [Hickman 1979]; 13–15 days in Wisconsin [Petersen 1955]), nestlings moving to the burrow entrance at 15–17 days after hatch (Garrison 1999), fledging (first flight) at 20 days (Petersen 1955; 18–21 days [Beyer 1938]; 18–19 days [Beecher *et al.* 1981]), and fledglings re-entering burrows for up to an additional seven days (Petersen 1955; Beecher *et al.* 1981).

We calculated mean burrow counts for each colony from the six surveys of river colonies (June and July 2014–2016) and the two to nine surveys per road cut colony per year (2013–2017). We used a Wilcoxon Rank Sum test to compare mean colony

size of river ($n = 74$) versus road cut ($n = 5$) colonies and between colonies that were never occupied versus those that were occupied at least once during the study, and also to compare percent occupancy of burrows in river versus road cut colonies. A Chi-square Test was used to compare year-to-year patterns of occupancy of river colonies, and to compare patterns of burrow reuse for different colony types. We used R version 3.1.1 (R Core Team 2014) for statistical analyses. Results are presented as mean \pm SD.

Results

Abundance

We found 74 Bank Swallow colonies along 46 km of the Yukon River, which represented 326 burrows/km (Figure 1). The total number of nest burrows counted on the river averaged 15017 ± 963 over six surveys during 2014–2016. Fifty-one colonies which were occupied in ≥ 1 year of the study accounted for 13947 ± 952 burrows ($n = 6$ surveys; 303 burrows/km), while 23 colonies which were never occupied during the study had a total of 1069 ± 129 burrows ($n = 6$; 23 burrows/km). In a given year, 33–37 colonies were occupied, and occupied colonies had a total of 11624 ± 624 burrows ($n = 6$; 253 burrows/km).

Mean number of burrows per river colony (203 ± 297 , range 1–1670, $n = 74$) was higher but not significantly different than that of road cut colonies (103 ± 49 , range 53–165, $n = 5$; $W = 181$, $P = 0.9438$). Median number of burrows per colony were 95 and 112 for river and road cut, respectively. Colonies that were occupied at least once during the study were larger (259 ± 322 burrows, $n = 56$) than colonies that were never occupied (46 ± 44 , $n = 23$; $W = 200$, $P < 0.001$). Total number of burrows on the river was relatively consistent from year to year (Table 1). However, there was an early-season deficit in the number of burrows in 2016 (presumably from greater-than-usual erosion during the 2015/2016 non-breeding season) compensated for before the July survey (presumably by excavation of new burrows).

Nesting phenology

During river- and road-based surveys, we detected Bank Swallows at colonies between 24 May and 18 July, which was the latest survey date (Figure 2). Specific indications of nesting stage were detected on the following dates: burrow excavation and adults in burrow entrances facing out (“male advertising”; see Garrison 1999) from 24 May to 19 June, birds entering and exiting burrows from 24 May to 18 July, and nestlings visible in burrow entrances and adults carrying faecal sacs from nests during 6–18 July. We observed birds hovering outside burrows without landing during 10–18 July only, which suggests these were fledging juveniles that remain in and around the col-

TABLE 1. Total number of Bank Swallow (*Riparia riparia*) burrows on a 46-km survey of the Yukon River, and percent change between surveys and between years for: all colonies ($n = 72, 74$, and 72 colonies in 2014, 2015, and 2016), colonies that were occupied in ≥ 1 year (“sometimes-occupied” colonies, $n = 51$), colonies that were never occupied during 2013–2016 ($n = 23$), colonies occupied in a given year ($n = 33, 35$, and 37), and colonies unoccupied in a given year ($n = 39, 39$, and 35).

	2014		2015		2016	
	June	July	June	July	June	July
Total burrows in:						
All colonies	14 240	14 959	15 168	16 091	13 643	16 000
Sometimes occupied	13 021	13 783	14 146	14 954	12 754	15 029
Never occupied	1 219	1 176	1 022	1 137	889	971
Occupied this year	10 594	11 198	11 357	11 964	11 258	13 374
Unoccupied this year	3 646	3 761	3 811	4 127	2 385	2 626
Percent change since previous count:						
Sometimes occupied		6	3	6	−15	18
Never occupied		−4	−13	11	−22	9
Occupied this year		6	1	5	−6	19
Unoccupied this year		3	1	8	−42	10
Percent change since previous year, same month:						
Sometimes occupied			9	8	−10	1
Never occupied			−16	−3	−13	−15
Occupied this year			7	7	−1	12
Unoccupied this year			4	10	−37	−36

ony and fly clumsily for several days (Garrison 1999).

Extrapolation from our observations using published information on the duration of Bank Swallow nesting stages (details shown above) indicates the following: clutches were initiated during 2–24 June, hatch occurred between 20 June and 12 July, and juveniles took their first flights during 9–31 July. Excavation of burrows may have started as early as 20 May, and fledglings may have continued to re-enter burrows as late as 7 August. Individual burrows were first occupied (beginning of excavation) between 20 May and 13 June and abandoned for the season between 16 July and 7 August. We had additional incidental observations of later nesting behaviour, including burrow excavation on 3 July 2013 at a small, newly-established road cut colony near the Snow Dump colony, indicating that nesting may extend by two weeks resulting in fledglings potentially continuing to re-enter burrows as late as 21 August. Thus, based on direct observation and inferred nesting activity, the overall period of occupancy of nest burrows in our study was from 20 May to 21 August.

Burrow and colony persistence

Most river colonies (70 of 74; 95%) had burrows present in all four river survey years (2013–2016), while two were newly excavated in the third survey year and still present in the fourth year, and two small never-occupied colonies present for the first three

years had no burrows in the fourth year. Burrows were present at all five road cut colonies in all five years of road-based surveys (2013–2017).

Of 203 individually-tracked burrows present in 2013 at four road-accessible colonies (including three road cut colonies and one river colony), 25% persisted for four years into the 2017 season (Figure 3). Of the three road cut colonies, two were apparently

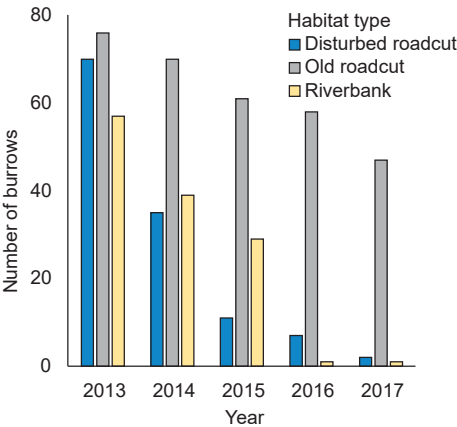


FIGURE 3. Persistence of 203 Bank Swallow (*Riparia riparia*) burrows individually tracked at road-accessible colonies beginning in 2013, for the following four years, for riverbank ($n = 57$ burrows in one colony), old road cut (76 burrows in two colonies), and frequently-disturbed road cut (70 burrows in one colony) substrates near Whitehorse, Yukon.

undisturbed during the study, while we frequently observed human and canine tracks close to nest burrows as well as obvious signs of disturbance from digging at Snow Dump. For this reason, we have summarized the Snow Dump colony separately. Burrows at the two undisturbed road cut colonies persisted longer than burrows at the river colony (road cut: 3.1 ± 1.4 years, $n = 76$ burrows; river: 1.2 ± 0.96 years, $n = 57$ burrows). Burrows at the Snow Dump road cut colony had the lowest rate of persistence (0.79 ± 1.0 years, $n = 70$ burrows). Burrows were not individually tracked at two other road-accessible colonies (Eagles Nest North and South) because many of the photographs and videos at those sites were of poor quality due to poor lighting conditions. Twenty-three river colonies that were unoccupied in all four years retained most (72%) of their burrows, with a total of 1345 burrows in June 2013 declining to 971 burrows in July 2016.

Overwinter persistence of burrows varied among colonies. At the single river colony (Quartz Road), which was also part of the road-based survey and therefore was photographed before the spring arrival of the birds each year, the number of burrows remaining in spring as a percentage of number of burrows present the previous July was on average 47% ($n = 4$ years, range 21–60%); this colony was occupied every year, with a burrow count of 446 ± 75 ($n = 6$ surveys). Two road cut colonies with counts of total burrows each spring and summer had very different rates of persistence of burrows over the winter. The Long Lake Road colony had an average of 94% ($n = 4$ years, range 92–97%) of burrows from the previous July still present the next spring before arrival of the swallows, while the Snow Dump colony, which was often disturbed and damaged by humans and pets, had a mean of 46% ($n = 4$, range 26–61%) of the previous July's burrows still present the following May.

Colony occupancy

Of 74 river colonies, 23 small colonies (31%), which accounted for ~7% of the total burrow count, were never occupied during four survey years and it is uncertain whether they were suitable for occupancy

by Bank Swallows during the study. Of the river colonies that were occupied ≥ 1 year, 45% (23 of 51) were occupied in all four years. Of the five road cut colonies, all were occupied in at least three years and two (40%) were occupied in all five years of the road-based survey.

Considering the 51 river colonies that were occupied at least once and thus known to be suitable for nesting, the year-to-year patterns of occupancy were consistent among consecutive pairs of years (i.e., 2013 to 2014, 2014 to 2015, and 2015 to 2016; $\chi^2_4 = 2.61$, $P = 0.625$; Table 2). There were three instances of river colonies being occupied after at least three years unoccupied, and an additional five instances of colonies being occupied after at least two years unoccupied (Figure 4). Of the 33–37 colonies occupied in a given year, nesting activity was detected on both visits (i.e., June and July) in 74–94% of colonies, only in July for 3–24% of colonies, and only in June for and 0–6% of colonies (Figure 4).

Percent occupancy of burrows

Within colonies, the percent of burrows that were occupied by Bank Swallows was higher for river colonies ($47.7 \pm 21\%$, $n = 32$ video samples from seven colonies over five years) than road cut colonies ($14.5 \pm 13.5\%$, $n = 40$ video and direct observation samples from five colonies over five years; $W = 1169.5$, $P < 0.001$).

Burrow reuse

Of 119 occupied burrows (i.e., active nests) at four road-accessible colonies tracked by video, direct observation, and photographs, 55% were newly-excavated burrows while 45% were reused burrows (32% in burrows occupied the previous year and 13% in burrows present but unoccupied the previous year). This pattern of burrow reuse differed among colony types ($\chi^2_4 = 34.4$, $P < 0.001$). Active nests at the two undisturbed road cut colonies were more frequently in reused burrows, and active nests at the frequently-disturbed Snow Dump colony were more frequently in newly excavated burrows (Figure 5).

TABLE 2. Year-to-year use patterns of Bank Swallow (*Riparia riparia*) colonies on the Yukon River during 2013–2016. For each pair of years, only colonies that were occupied in at least one of the two years are included. Values are numbers of colonies, with percent in parentheses.

Use pattern	Years		
	2013–2014	2014–2015	2015–2016
Occupied colony occupied previous year	27 (63%)	28 (70%)	30 (71%)
Occupied colony unoccupied previous year	6 (14%)	7 (18%)	7 (17%)
Unoccupied colony occupied previous year	10 (23%)	5 (12%)	5 (12%)
Total	43 (100%)	40 (100%)	42 (100%)

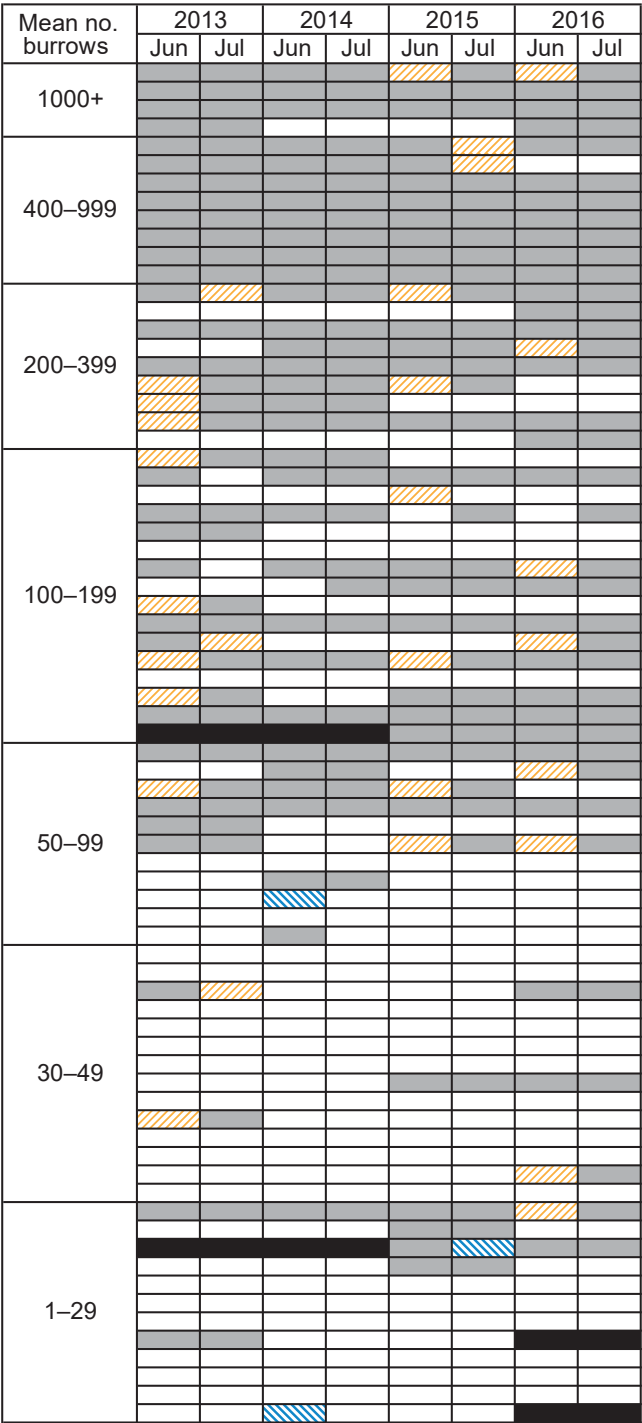


FIGURE 4. Year-to-year occupancy of 74 Bank Swallow (*Riparia riparia*) colonies along the Yukon River, in descending order of colony size (colony size = mean no. burrows from six surveys 2014–2016). Grey = occupied that year, white = unoccupied that year, crosshatching up to right = no evidence of nesting activity during survey but occupied in other survey that year so presumed occupied, crosshatching up to left = unknown, i.e., colony missed on survey; black = no burrows (i.e., no colony at that time).

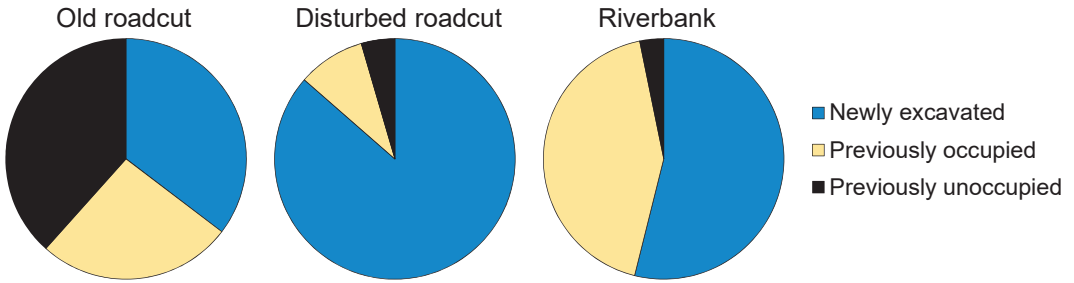


FIGURE 5. Percent of active Bank Swallow (*Riparia riparia*) nests in newly-excavated versus pre-existing burrows (occupied or unoccupied in previous year), in old road cuts (34 nests in Mud Bog and Long Lake Road colonies), a frequently-disturbed road cut (22 nests at Snow Dump colony), and a riverbank (63 nests in two sections of Quartz Road colony); includes 119 active nests from 2014 to 2017 at road-accessible colonies.

Discussion

We found comparatively high densities of nesting Bank Swallows along a 46-km stretch of the Yukon River that suggest northern populations may potentially contribute significantly to the persistence and recovery of this declining species. We documented local nesting phenology, information that is required for designing regional monitoring as well as guidelines to mitigate disturbance by local industry. Low percent occupancy of nest burrows previously found for this region (Bols 2017) is supported by our results, indicating that regional estimates are important for use with burrow counts to estimate local populations. Burrows persisted for much longer than in some other regions, and rates of reuse of nest burrows that have persisted over the winter were higher than in other regions, pointing to the need for further study to determine how old burrows contribute to nest success and whether burrows should be protected year-round in some regions.

Abundance

The abundance of Bank Swallow nesting burrows along the Yukon River near Whitehorse was higher than that along rivers known for high abundance elsewhere in North America. The few published examples include the Sacramento River between Redding and Yolo, estimated to host 80% of California's population of nesting Bank Swallows, with 28 894 burrows along 336 km of river, or 86 burrows/km (Humphrey and Garrison 1987). A three-year study along one of the stretches with highest abundance had 12 000–17 000 burrows along 80 km of river, or 150–212 burrows/km (Garrison *et al.* 1989). In Ontario, a 14.9 km stretch of the Saugeen River had an average of 147 burrows/km, which was considered an exceptionally large population, while other stretches of river in the region had 2.3 to 20.2 burrows/km (Cadman and Lebrun-Southcott 2013). The density of nest burrows that we found

along 46 km of the Yukon River (326 burrows/km) was approximately double these densities recorded elsewhere and considered “high”. Even considering only the 51 colonies that were occupied in some years (303 burrows/km), or only the colonies occupied in a given year (237–268 burrows/km), the density of burrows was higher than reported elsewhere.

Applying our 47.7% occupancy rate to the 11 624 burrows in active colonies along our river survey route yields an estimated 5545 occupied nests, or 11 090 nesting Bank Swallows on the 46 km stretch of river. This amounts to 0.8% of the estimated Canadian population and 7% of that for Yukon (1 400 000 and 160 000 birds, respectively; COSEWIC 2013). Considering that Bank Swallow is likely also abundant along other major rivers within glaciated areas of the territory (for example the Teslin, Takhini, Nisutlin, Liard, Hyland, Stewart, Peel, and Porcupine rivers), this suggests that the Yukon population may be considerably larger than current estimates based on roadside surveys.

Nesting phenology

The inferred beginning of the nesting period in our study (20 May) and the directly observed start date (24 May) are similar to the earliest date from historical Yukon data (28 May; Sinclair *et al.* 2003). In contrast, the inferred end date (21 August) for the nesting period of Bank Swallow in our study is later than the last calendar date of historically observed burrow occupancy in Yukon (8 August; Sinclair *et al.* 2003). This late end date, although inferred from a late observation of excavation of a burrow which may not have successfully produced young, can be used to inform avoidance guidelines for industrial work in the vicinity of Bank Swallow colonies.

In a two-year study of Bank Swallow in Fairbanks, Alaska, nesting dates were also similar; birds were first noted at colonies on 23 May and leaving by 6 August.

One unusually late nesting was noted in which young were ready to fledge on 18 August (Hickman 1979). An observation of a colony near Old Crow, in northern Yukon, on 30–31 July 1970 (Morlan 1972) also fell within the nesting dates inferred from our observations. Our study shows a longer nesting season for Bank Swallow than indicated in the Bird Nesting Calendar Query Tool (28 May–3 August for Yukon; Hussell and Lepage 2015), which is based on a citizen-science database and is designed to inform avoidance periods for industry (Rousseu and Drolet 2017). Nesting in our study area began later than in southern Ontario (earliest clutch initiation 8 May; Burke *et al.* 2019) and British Columbia (earliest clutch initiation 27 April; Campbell *et al.* 1997). The nesting period found in our study falls within the “possible period of occupancy” stated in the SARA Residence Description for Bank Swallow (May to late August; Government of Canada 2019).

Burrow and colony persistence

The high overwinter persistence of river colonies and burrows in our study (47% of burrows at a river colony; 94% and 46% at two road cut colonies) contrasts with results from elsewhere. On the Sacramento River, California, most burrows eroded away between nesting seasons, particularly in wet years (Garrison *et al.* 1989), and the Saugeen River, Ontario, almost all burrows disappeared due to erosion over the winter (e.g., 2.3% of the previous year’s burrows remained in spring one year; Cadman and Lebrun-Southcott 2013). However, a study in Alaska of 11 Bank Swallow colonies at gravel pits found that, on average, 61% of the previous year’s nest burrows persisted into the next season (Hickman 1979), which is within the range of burrow persistence that we found at artificial (road cut) sites.

Colony occupancy

If we omit the 23 small river colonies that were never occupied and may not have been suitable for nesting during our study (~7% of all river burrows counted), the 45% of 51 Yukon River colonies that were occupied in all four survey years was similar to the 43% of Saugeen River colony sites that were occupied in all five survey years in Ontario (Cadman and Lebrun-Southcott 2013). For our small sample of road cut colonies, our result of 40% of colonies occupied in all five survey years was higher than the 32% of 19 southern Ontario aggregate pit colony sites occupied in all three survey years (Burke 2017). In that study, annual occupancy was greater at lakeshore sites, with 100% of 11 lakeshore colony sites occupied in all five survey years (Burke 2017).

Occupancy patterns at Yukon River colonies appeared to differ from those found on the Sacramento

River, where only 40–56% of sites were occupied colonies that had been occupied the previous year and 21–42% were occupied colonies that had been unoccupied the previous year (Garrison *et al.* 1989). This compares with 63–71% and 14–18%, respectively, in our study, suggesting that the Sacramento River had more inter-annual change in locations of occupied colonies, perhaps due to higher erosion rates changing the suitability of sites more often, or avoidance of previously-occupied sites, possibly due to ectoparasite densities. Colony sites may be unoccupied because of major predation events during the previous breeding season (Freer 1979), or when bank erosion makes a site unsuitable (Cadman and Lebrun-Southcott 2013). Other swallow species, such as Cliff Swallow (*Petrochelidon pyrrhonota*), avoid occupying existing nesting colonies with high densities of ectoparasites (Brown and Brown 1986). Our observations of old colonies with highly persistent burrows no longer in use suggest that changes in river course, or vegetation succession, may have slowed erosion to the extent that these sections of riverbanks are no longer suitable for nesting.

Percent occupancy of burrows

Percent occupancy of nest burrows on the Yukon River (mean 47.7%) was similar to published estimates from river colonies elsewhere, while percent occupancy of our road cut colonies (mean 14.5%) was lower. In Sacramento River colonies, percent occupancy determined by directly checking the contents of nest burrows was 56% (Humphrey and Garrison 1987), 46% and 47% (Garrison *et al.* 1989). Burke (2017) found 63% of burrows occupied in lakeshore colonies, and 60% occupancy in aggregate pit colonies in southern Ontario, based on weekly 20 min videos. Cadman and Lebrun-Southcott (2013) considered 50% occupancy to be a good approximation when estimating number of birds from burrow counts, which agrees with our data from Yukon River colonies, but not those at road cuts.

Because our occupancy estimates were based on single visits and videos ranging from 10 to 20 min, they may have been underestimates. However, we used shorter (10 and 15 min) videos only during the nestling stage, when nest visits are frequent. Also, Bird Studies Canada (2010) recommends 15 min videos to assess occupancy of Bank Swallow colonies, although Burke (2017) used the middle 20 min of 30 min video recordings. In a separate study that assessed occupancy of Bank Swallow colonies along the same stretch of the Yukon River, 91% (range 66–100%, $n = 16$ colonies) of occupied burrows were detected within the first 15 min of 30 min videos used to assess occupancy at 16 colonies between 22 June and 7 July 2015 (Bols 2017).

Although the short duration of our video recordings may have resulted in occupancy being underestimated, the fact that we selected occupied sections of colonies (rather than random sections or whole colonies) suggests they are more likely to be overestimates. Bols (2017) used video recordings of 16 entire occupied colonies to assess occupancy along the same stretch of river, thus avoiding this bias, and found a lower mean occupancy rate of 35%. Using that occupancy rate, with our burrow counts from occupied colonies only (i.e., $0.353 \times 11\,624$ burrows) would indicate 4103 active burrows, or 8206 adult Bank Swallows along the 46 km stretch of river. This is equivalent to a 27% occupancy rate for total burrows counted including occupied and unoccupied colonies (i.e., 4103/15017).

The relatively low percent occupancy of road cut colonies in our study area may be partly due to the very high persistence of old burrows, many of which may appear usable while actually being incomplete or obstructed (e.g., by roots or eroded material). In general, estimates of local Bank Swallow populations based on burrow counts should either count only occupied colonies (if occupancy rates are based on occupied colonies), or use a lower occupancy rate that accounts for unoccupied colonies (such as the 27% suggested above for our study area), as appropriate for the region.

Burrow reuse

Our study provides the first evidence of frequent reuse of old nest burrows by Bank Swallows nesting in riverbanks. A study in interior Alaska found that at 11 gravel pit colonies over two years, 76% of active nests were in old burrows from previous years while only 24% had been newly excavated (Hickman 1979). This reuse rate is even higher than we found in old road cuts in the Whitehorse area. For riverbank colonies, there is a lack of information on nest burrow reuse, perhaps because the Sacramento and Saugeen rivers, where most burrows erode away over the winter (Garrison *et al.* 1989; Cadman and Lebrun-Southcott 2013), may be typical and few burrows persist long enough to be available for reuse.

Bird species that nest colonially are more likely to have nests infested with ectoparasites (Poulin 1991). Bank Swallow nests host fleas (*Ceratophyllus* spp. and *Celsus* spp.; Haas *et al.* 1980), blowflies (*Protophormia* spp.; Whitworth and Bennett 1992), mites (Peters 1936), and lice (Stoner 1936; Emerson 1972), and nestling growth has been shown to be slower in ectoparasite-infested nests of this species (Alves 1997). Some swallow species inspect old nests for ectoparasites and avoid reusing nests that are infested (Brown and Brown 1986; Barclay 1988). There has been speculation that Bank Swallows avoid reus-

ing nests because of the risk of ectoparasites (Garrison 1999; Cadman and Lebrun-Southcott 2013; Falconer *et al.* 2016), but no evidence of this has been documented. It is unknown whether overwinter mortality of Bank Swallow ectoparasites is greater in the north, due to colder winters, and whether this allows greater rates of reuse of old burrows. Nevertheless, it is noteworthy that the highest documented rates of reuse of old nest burrows are from cold regions in Alaska (Hickman 1979) and Yukon.

It is also unknown whether excavation of new burrows is hindered by freeze/thaw patterns of some nesting substrates in the north. Nesting dates of Bank Swallow have not advanced with warming climate as they have for other swallow species (Imlay *et al.* 2018), which invites speculation that the well-insulated nature of Bank Swallow nesting substrates may play a role; e.g., if frozen ground limits excavation of burrows in early spring and/or the northern part of the breeding range.

Conclusions

Our study provides new information from the northern boreal region on the nesting ecology of Bank Swallow, a Threatened species. The comparatively high abundance of Bank Swallow in natural habitats away from roads suggests that numbers may be higher, and declines less severe, than indicated from roadside surveys. Variation in percent occupancy estimates point to the need for further standardization of monitoring methods for this species. The longer persistence of burrows, and higher rates of reuse of temporarily unoccupied colonies as well as old nest burrows within colonies, points to the need for further study to determine how old burrows contribute to future nesting success, and whether nest burrows should be protected even when they are not occupied.

Author Contributions

Writing – Original Draft: P.H.S.; Writing – Review & Editing: M.D.M., P.H.S., and S.A.S.; Conceptualization: S.A.S. and P.H.S.; Investigation: M.D.M., P.H.S., and S.A.S.; Methodology: S.A.S. and P.H.S.; Formal Analysis: P.H.S. and M.D.M.

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