

**Final Report to the Nova Scotia Habitat Conservation Fund:
Determining the role of food availability on swallow population declines**

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Background

In the past 40 years, Breeding Bird Surveys documented declines in most species of aerial insectivores (birds that feed in the air, on flying insects) such as swallows, swifts, nightjars and flycatchers (Nebel et al. 2010). These declines are most severe for populations in northeastern North America (Nebel et al. 2010), including Nova Scotia. Although the reason for these declines is unknown, several explanations have been suggested. The leading explanation suggests that declines relate to decreases in aerial insects, the common food source for this group of birds, and/or a mistiming between peak breeding and insect prey availability.

In 2014 and 2015, we examined the role of aerial insect abundance on reproductive success and the timing of breeding activities Barn, Cliff and Tree Swallows in Nova Scotia (NS) and New Brunswick (NB). In addition, we characterized Bank Swallow roosting habitat in order to inform future management of habitat for this species. The project had four main objectives:

1. Determine the relationship between insect abundance during nestling development and the timing of breeding (i.e., clutch initiation dates) and reproduction success (i.e., nestling survival and body condition) for three species of swallows;
2. Determine if the timing of breeding and reproductive success (i.e., clutch size, brood size and nestling survival) has changed over the last 50 years through examining long-term data and determine if changes are correlated with climate;
3. Characterize Bank Swallow roosting habitat at known roosts and unused wetlands; and
4. Identify how Bank Swallow roosting behaviour affects nesting success.

Below, we present the methods used to address these objectives, our preliminary results and next steps in this multi-year project.

Methods

Data collection

We collected 234 insect samples using stationary tow nets (Hussell and Quinney 1987) at four sites throughout the breeding season and measured the dry sample mass. We calculated an index of daily insect abundance based on the biomass collected and the amount of time nets were open (mg/h), hereafter referred to as insect abundance.

We monitored 132 Bank, 103 Barn, 64 Cliff and 115 Tree Swallow nests every 2-3 days during the breeding season. From these frequent checks, we were able to determine the timing of breeding (i.e., clutch initiation and hatching dates) and the breeding success (i.e., clutch size, brood size and chick survival to day 12). We also banded 207 Barn, 117 Cliff and 381 Tree Swallow nestlings at day 9, 10 and 12, respectively. Due to nest structure, we were unable to band Bank Swallow nestlings. At the time of banding, we collected morphological measurements from the young, including mass, tarsus length and head-bill length. To date, we have focused on nestling mass as an index of body condition.

We also compiled long-term data from the Maritime Nest Records Scheme (all species; 1961-present), data from Marty Leonard/Andy Horn/Sherman Boates (Tree Swallows; 1988-2013) and Nat Wheelwright (Tree Swallows; 1987-2010). From these data, we identified clutch size, brood size and nestling survival to day 12 (Table 1) to determine if there were changes in reproductive success since the 1960s.

Finally, we captured adult Bank Swallows with tube traps and mist-nets during the late incubation or early nestling stage of breeding. We selected 44 adults to be tagged with a small radio-transmitter (0.29 g) and the remaining 91 adults captured (22 of which had known nests) were identified as a control group. Swallows were monitored daily for up to 82 days by manual radio-tracking and an automated array of telemetry towers to identify their roosting locations throughout the breeding season and in early migration. Once roost sites were discovered, we compared the size and distance of these sites to other cattail wetlands within 25 km from the colony site. In addition, we conducted 9-11 point counts at each wetland to monitor the roosting behaviour of both tagged and untagged Bank Swallows. During these counts, the number of Bank Swallows roosting in the wetland were recorded for 20 minutes before and after sunset (total of 40 minute observation at each wetland).

Data analysis

Insect abundance and swallow breeding

To determine if food availability during nestling development was higher for earlier breeding swallows, we calculated the Pearson's r correlation coefficient between clutch initiation date and mean insect abundance during the first twelve days of nestling development. We first examined the Pearson's r correlation coefficient for all species and then for each individual species to determine if there were differences in this relationship between species.

Next, to determine if high food availability during nestling development was associated with higher nestling survival, we used a logistic regression to examine the relationship between nestling survival to day 12 and mean insect abundance during the first 12 days of nestling

development. The logistic regression also included species, site, year and brood size as additional explanatory variables. A backwards step-wise approach was used to determine the best-fit model.

Although we were unable to directly measure post-fledgling survival, several studies have demonstrated that nestling body condition can provide an indication of survival after leaving the nest (e.g., Naef-Daenzer et al. 2001). Therefore, to determine if high food availability was associated with higher body condition (and presumably higher post-fledgling survival), we used a generalized linear model to examine the relationship between within-clutch mean nestling mass and mean insect abundance during nestling development (from hatching to banding day). We also used a generalized linear model to determine if high food availability was associated with lower within-clutch variance in nestling mass. These models also included species, site, year and brood size as additional explanatory variables, and a backwards step-wise approach was used to determine the best-fit model.

Long-term trends in breeding

Using long-term data on the timing of breeding (i.e., clutch initiation date) and reproductive success (i.e., clutch size, brood size, and nestling survival to day 12) for all four species of swallows, we determined if reproductive success had changed over the last 50 years. First we compare the timing of breeding and breeding success for all four species from 1962-1972 and 2005-2015 using Wilcoxon-Mann-Whitney tests to determine if there were differences in the clutch initiation date (up to and including the median date), clutch size, brood size (successful nests only) and nestling survival to day 12 (successful nests only) between these two time periods for all four species. We also used a Chi-square test to determine if there were differences in the hatching and fledgling success (i.e., the number of nests that hatched and fledged at least one young, respectively).

Next, we determined if change in breeding were related to climatic conditions (since climate is likely to influence insect abundance). The number of breeding records where we were able to determine at least one variable for the timing of breeding or reproductive success varied considerably by species (Bank: 563, Barn: 2,099, Cliff: 658, and Tree: 4,294 records). Since there was more data for Barn and Tree Swallows, we focused on these species for this analysis. These models examined the relationships between the timing of swallow breeding and spring temperature and spring precipitation. We also used modeled the relationships between reproductive success and spring temperature and precipitation. All these models included species, year, longitude and latitude as additional explanatory variables. Reproductive success models also included clutch initiation date as an explanatory variable even though there are weak relationships between clutch initiation date and mean temperature (Pearson's $r = -0.250$), year (r

= -0.304) and latitude ($r = 0.309$). A backwards stepwise regression was used to determine the best-fit model.

Bank Swallow roosting

We modelled the relationship between the number of tagged birds detected at a roost site to compare the effect of wetland size and distance from the colony along with other potentially significant variables in the following generalized mixed model with a Poisson distribution:
Number at roost \sim wetland size + distance + mean age of young + proportion females + moon phase (% full moon) + standard pressure + dew point + precipitation + wind speed + (1|year)

In addition, we modelled the relationship between the number of both tagged and untagged Bank Swallows counted during the roost counts to compare the effect of wetland size along side other potentially significant variables in the following generalized mixed model with a Poisson distribution:
Number at roost \sim wetland size + mean age of young + proportion females + moon phase (% full moon) + standard pressure + dew point + precipitation + wind speed + (1|year)

Finally, we modelled the probability of Bank Swallows roosting (1) or remaining at the colony (0) in the following negative binomial mixed model to compare the effect of nest success along side of other potentially significant variables:
roosting (1) or colony (0) \sim nest success (survived or failed) + chick age + (chick age)² + (chick age)³ + sex + moon phase (% full moon) + standard pressure + dew point + precipitation + wind speed + (1| year) + (1| ID) + (1| colony).

We used a stepwise regression to remove-non-significant variables from all these models.

Results

Insect abundance and swallow breeding

There was a negative relationship between clutch initiation date and mean insect abundance during the first 12 days of nestling development (Pearson's $r = -0.572$; Figure 1). When examined by species, this negative correlation was largely driven by Cliff and Tree Swallows (Pearson's $r = -0.448$ and -0.605 , respectively) and there was no relationship between clutch initiation date and insect abundance for Barn Swallows (Pearson's $r = 0.074$).

The best-fit model from our logistic regression included mean insect abundance during the first 12 days of nestling development, species, site, year and brood size. In general, insect

abundance tended to be lower for nests that failed completely (0.38 ± 0.17 g), but there was little difference in mean insect abundance for nests that experienced partial (at least one nestling died; 0.44 ± 0.16 g) or no mortality (0.42 ± 0.15 g; Figure 2). The lack of a strong relationship between mortality rates and insect abundance may, at least in part, be due to the high survival of nestling swallows. Of the 231 nests monitored, only 11.7% and 10.4% had partial or complete nestling mortality, respectively. Interestingly, partial and complete nestling mortality rates varied by species. Barn Swallows experienced the lowest rates of partial and complete nestling mortality (7.9%), followed by Tree Swallows (18.0%) and then Cliff Swallows (42.6%; Table 1).

The best-fit model for within-clutch mean nestling mass included species and site ($p < 0.05$), and the best-fit models for within-clutch variation in nestling mass included species and brood size ($p < 0.05$). Mean nestling mass was lowest for Barn Swallows (16.4 ± 2.2 g), followed by Cliff (20.7 ± 4.1 g) and Tree Swallows (22.1 ± 1.8 g); and the mean coefficient of variation was greatest for Cliff Swallows (0.12 ± 0.12), followed by Barn (0.10 ± 0.06) and Tree Swallows (0.06 ± 0.03). There were also significant differences in nestling mass between sites. Smaller brood sizes were associated with higher variability in nestling mass (Figure 3).

Long-term trends in breeding

We found significant differences in the clutch initiation dates for all four species between 1962-1972 and 2005-2015 ($p < 0.05$). On average, Bank Swallows initiated clutches 3.3 days earlier in 1962-1972, whereas clutches for Barn, Cliff and Tree Swallows were initiated 9.5, 8.4 and 10.9 days earlier in 2005-2015, respectively (Table 2).

We also found that changes in reproductive success between 1962-1972 and 2005-2015 varied between species (Table 2). In general, reproductive success was lower for Bank Swallows and higher for Tree Swallows in 2005-2015 when compared to 1962-1972. There were few significant changes in reproductive success for Barn and Cliff Swallows. These results are detailed below by each measure of reproductive success.

There were significant differences in the clutch sizes of Bank, Cliff and Tree Swallows between 1962-1972 and 2005-2015 ($p < 0.05$), which corresponded with a mean decrease of 0.3 eggs/clutch for Bank and a mean increase of 0.5 eggs/clutch for Tree Swallows. There was no difference in clutch sizes for Barn or Cliff Swallows between these periods ($p > 0.05$).

The brood sizes of successful nests for Bank and Tree Swallows between 1962-1972 and 2005-2015 were significantly different ($p < 0.05$), which corresponded with a mean decrease of 0.3 nestlings/clutch for Bank Swallows and a mean increase of 0.5 nestlings/clutch for Tree Swallows. There was no difference in brood sizes for Barn and Cliff Swallows between these periods ($p > 0.05$).

There were significant differences in nestling survival of successful nests for Bank, and Tree Swallows between 1962-1972 and 2005-2015 ($p < 0.05$), which corresponded with a mean decrease in survival of 1.2 nestlings/clutch for Bank Swallows and a mean increase in survival of 0.6 nestlings/clutch for Tree Swallows. There was no difference in clutch sizes for Barn and Cliff Swallows between these periods ($p > 0.05$).

When we examined rates of hatching and fledging success between 1962-1972 and 2005-2015, we found significantly lower hatching success for all species in 2005-2015 ($p < 0.05$). The decrease in hatching success ranged from 7.0% (Tree) to 32.5% (Bank). There was also a significant 28.2% decrease in fledging success for Bank Swallows and a significant 14.2% increase in fledging success for Barn Swallows ($p < 0.05$). There was no change in fledging success for Cliff and Tree Swallows ($p > 0.05$).

Climatic conditions were associated with the timing of swallow breeding (Table 3). In particular, warmer spring temperatures were associated with earlier clutch initiation (Figure 4) and hatching dates, and years with low precipitation were associated with earlier clutch initiation dates (Figure 4). Year was also an important explanatory variable, suggesting that part of the shift to earlier breeding in recent years is not wholly due to spring climate on the breeding grounds (Table 3).

Climatic conditions were also associated with some changes in swallow reproductive success (Table 3). Warmer spring temperatures were associated with lower hatching and fledging success (i.e., whether or not the nest successfully hatched one young and raised one young to day 12) (Figure 5). Years with low precipitation were associated with low fledging success (Figure 6). There was a negative relationship between all five measures of reproductive success and clutch initiation date, with late breeding birds experiencing lower reproductive success (Table 3).

Bank Swallow roosting

Out of the 44 Bank Swallows tagged, 43 had useable data to monitor roosting habitat use. All 43 birds roosted away from the colony at least once. In total, we identified eight wetlands that were used in varying degrees by tagged or untagged roosting Bank Swallows and only three wetlands that remained unused during the breeding season. We found no significant relationship between the number of tagged birds detected at roosts and the area or distance of the roost ($p > 0.05$). In addition, there was no significant relationship between the number of birds counted during roost counts and the area of the wetlands ($p > 0.05$). These results signify that the area of the wetlands and the distance between colonies and roost sites alone cannot describe Bank Swallow roosting habitat. In tagged birds, the majority of roost site detections were at one

wetland (TINTA), although a considerable amount of roost switching was observed; on average, tagged Bank Swallows used 3.4 roosts during the season (range: 1-6 per individual). Both the preference for TINTA and the flexibility of roost site selection may explain the model results.

Finally, we found no strong relationship between nesting success and roosting behaviour ($p > 0.05$). This may be in part explained by the persistent use of both the colony and external roosts even after nests have failed. However, we did find a significant cubic relationship between the probability of roosting away and the mean age of the chicks ($p < 0.05$). The probability of both male and female Bank Swallows roosting away was lowest from the day before the young hatched until the young were 10 days old, and increases steadily before and after these dates (Figure 7). In addition, we found that the probability of roosting away decreases with moon phase (% full moon) and relative humidity ($p > 0.05$). The probability of roosting away also increases significantly with standard pressure and for males ($p > 0.05$).

Discussion

This was the second year of a multi-year project to determine the role of insect abundance on swallow population declines, however, these results provide some insight into the role of food availability on swallow breeding, long-term changes in the timing of swallow breeding and reproductive success. In addition, we also examined the unusual roosting behaviour of Bank Swallows.

Insect abundance and swallow breeding

Swallows that initiated clutches early in the breeding season had higher insect abundance during the nestling period. However, despite the potential benefits of breeding early, insect abundance had a weak relationship with nestling mortality and, overall, nestling survival is quite high. There was also no relationship between insect abundance and within-clutch nestling body mass (an important predictor of post-fledging survival; Naef-Daenzer et al. 2001). Together this suggests that for most nests, the impact of insect abundance on reproductive success, and ultimately population declines, for Barn, Cliff and Tree Swallows is likely small.

Long-term trends in breeding

There were significant changes in the timing of breeding and reproductive success of all four species of swallows.

Barn, Cliff and Tree Swallows are now breeding earlier in recent years and, for Barn and Tree Swallows, this is correlated with warmer spring temperatures and low spring precipitation. In the last 50 years, there were minor changes in the reproductive success of Barn and Cliff

Swallows, and Tree Swallows experienced a slight increase in reproductive success. For Barn and Tree Swallows, increases in spring temperature resulted in lower hatching and fledging success, which may be the result of a mis-timing between insect abundance and breeding in warmer years. This could result in adult swallows spending more time foraging during the incubation and nestling periods, and less time incubating eggs and feeding young. Increased spring precipitation was associated with higher fledging success for Barn and Tree Swallows. This increase in precipitation may provide more breeding habitat for aerial insects, which results in higher abundance during the nestling period. While a small decrease in reproductive success may contribute to population declines for these species, it is likely that there are other, more significant drivers of population declines, including low juvenile and adult survival during migration and overwintering.

Interestingly, Bank Swallows are breeding later in recent years and reproductive success declined by all five measures we analyzed. This may indicate that population declines in this species are being driven, at least in part, by changes in the timing of breeding and reproductive success. This could occur if there is a mis-match between food availability and the timing of breeding resulting in lower reproductive success when adults are raising young. However, it is also possible that poor wintering conditions may have carry-over effects on breeding.

Bank Swallow roosting

Although our results did not identify a significant relationship between roost use and habitat characteristics or Bank Swallow nest success and roosting behaviour, we did find a significant relationship with chick age, with the majority of Bank Swallows remaining at the colony when chicks are one day prior to hatching to 10 days old. This period of time coincides with the time young are ectothermic and require external heat to survive (Marsh 1979). Brooding during this time may be essential for nest success, making roosting away from the colony unfavourable at this time.

References

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Table 1. Summary of nestling mortality for Barn, Cliff and Tree swallows in 2014 and 2015 at sites where insect samples were collected.

Species	# Nests monitored	# Nests with no mortality (%)	# Nests with partial mortality (%)	# Nests with complete mortality (%)	Mean \pm SD brood size (total)	Mean \pm SD of young surviving to day 12 (total)
Barn	38	35 (9.2%)	2 (5.3%)	1 (2.6%)	4.3 \pm 1.1 (166)	4.1 \pm 1.3 (156)
Cliff	54	31 (57.4%)	8 (14.8%)	15 (27.8%)	3.4 \pm 0.8 (189)	2.4 \pm 1.7 (127)
Tree	139	114 (82.0%)	17 (12.2%)	8 (5.8%)	5.2 \pm 1.1 (735)	4.7 \pm 1.7 (654)

Table 2. Summary of comparisons in the timing of breeding and reproductive success of Bank, Barn, Cliff and Tree swallows between 1962-1972 and 2005-2015. Bolded values indicate significant difference between 1962-1972 and 2005-2015. Mean values are presented with the standard deviation and sample sizes are included in brackets.

Species	Years	Clutch initiation date	Clutch size	Brood size ¹	Nestling survival ¹	Hatching success	Fledgling success
Bank	1962-1972	39.0 ± 7.3 (25)	4.7 ± 0.7 (107)	4.4 ± 0.8 (117)	4.1 ± 1.0 (81)	95.6% (275)	78.8% (137)
	2005-2015	42.0 ± 2.0 (84)	4.4 ± 0.9 (177)	3.3 ± 1.0 (118)	2.9 ± 1.0 (80)	63.2% (201)	50.6% (164)
Barn	1962-1972	38.7 ± 6.6 (88)	4.6 ± 1.0 (350)	4.4 ± 0.8 (270)	4.2 ± 1.1 (86)	91.7% (630)	60.3% (156)
	2005-2015	29.2 ± 4.3 (153)	4.6 ± 1.0 (350)	4.4 ± 0.9 (250)	4.1 ± 1.1 (223)	81.1% (387)	74.4% (317)
Cliff	1962-1972	40.9 ± 3.2 (28)	3.7 ± 0.9 (114)	3.1 ± 1.0 (47)	3.1 ± 1.1 (9)	89.4% (180)	44.4% (45)
	2005-2015	32.5 ± 4.1 (118)	3.5 ± 0.8 (267)	3.1 ± 0.9 (125)	2.9 ± 1.1 (80)	66.9% (260)	44.5% (191)
Tree	1962-1972	30.4 ± 6.0 (68)	5.0 ± 1.2 (186)	4.6 ± 1.1 (160)	4.3 ± 1.4 (64)	93.4% (286)	77.9% (95)
	2005-2015	19.5 ± 4.6 (449)	5.5 ± 1.0 (827)	5.1 ± 1.2 (653)	4.9 ± 1.2 (411)	86.3% (811)	72.4% (576)

¹ Only data from successful nests are included in calculations of brood size and nestling survival.

Table 3. Best-fit models for the relationships between the timing of breeding and reproductive success, and climatic conditions for Barn and Tree Swallows.

	Estimate \pm SE	P value	# of records	AIC
Clutch initiation date ¹ ~				
Mean temperature	-0.033 \pm 0.003	<0.001	1472	8663.1
Mean precipitation	0.018 \pm 0.004	<0.001		
Species	-0.303 \pm 0.012	<0.001		
Year	-0.008 \pm 0.000	<0.001		
Latitude	0.062 \pm 0.008	<0.001		
Hatching date ¹ ~				
Mean temperature	-0.013 \pm 0.003	<0.001	1211	7419.3
Species	-0.155 \pm 0.012	<0.001		
Year	-0.003 \pm 0.000	<0.001		
Longitude	0.021 \pm 0.004	<0.001		
Clutch size ¹ ~				
Species	0.049 \pm 0.025	0.050	2533	9327.1
Clutch initiation date	-0.006 \pm 0.001	<0.001		
Brood size ¹ ~				
Clutch initiation date	-0.005 \pm 0.001	<0.001	1950	7196.6
Nestling survival to day 12 ¹ ~				
Species	0.070 \pm 0.038	0.064	1377	5114.3
Year	0.002 \pm 0.001	0.097		
Clutch initiation date	-0.005 \pm 0.001	<0.001		
Hatching success ² ~				
Mean temperature	-0.099 \pm 0.033	0.003	2401	1808.0
Year	-0.010 \pm 0.005	0.033		
Latitude	-0.513 \pm 0.122	<0.001		
Longitude	-0.145 \pm 0.065	0.025		
Clutch initiation date	-0.009 \pm 0.005	0.067		
Fledging success ² ~				
Mean temperature	-0.122 \pm 0.032	<0.001	1793	1834.4
Mean precipitation	0.111 \pm 0.057	0.049		
Latitude	-0.323 \pm 0.118	0.006		
Longitude	-0.162 \pm 0.070	0.020		
Clutch initiation date	-0.013 \pm 0.005	0.006		

¹ Generalized linear model with a poisson distribution.

² Generalized linear model with a binomial distribution for yes/no variables if young hatching and survived to day 12, respectively.

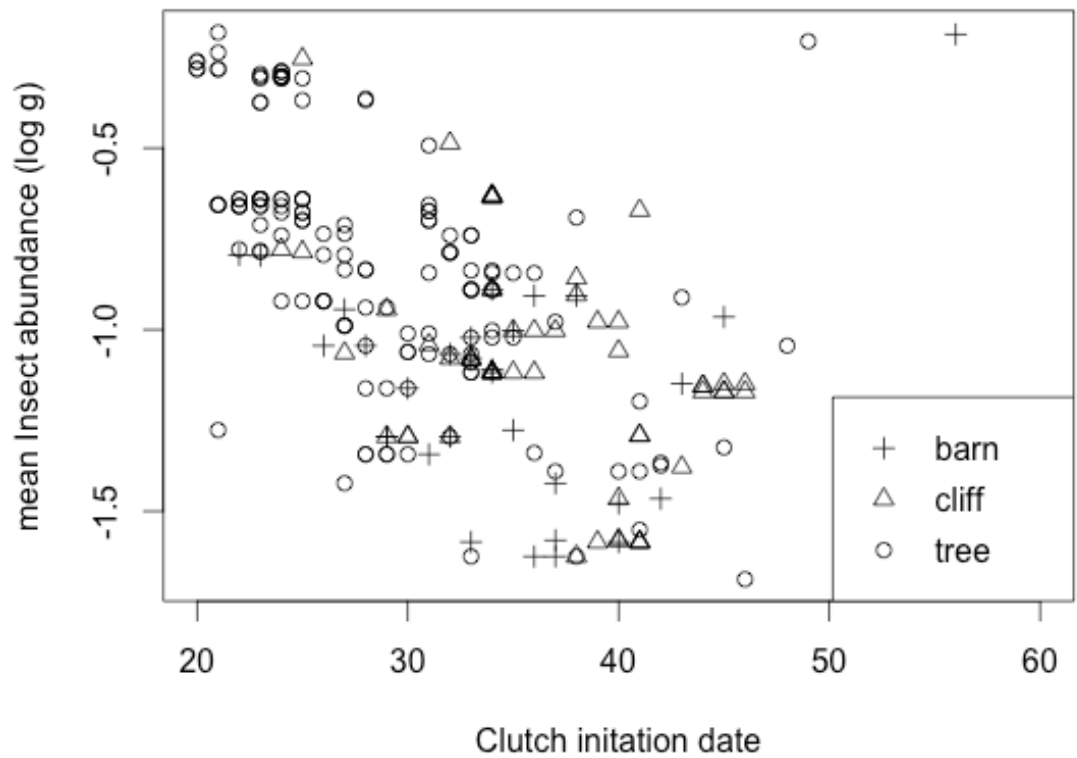


Figure 1. There is a negative relationship between clutch initiation date (day 1 = May 1) and mean insect abundance during the first 12 days of nestling development for Cliff and Tree swallows. There is no relationship between clutch initiation date and insect abundance for Barn swallows.

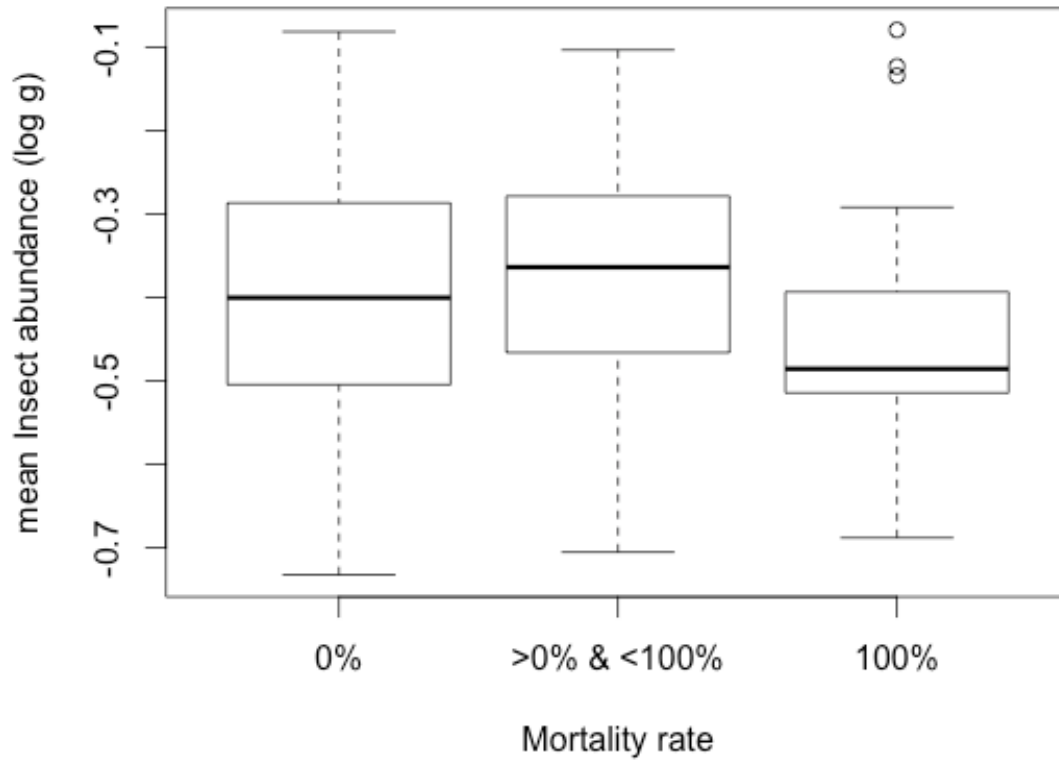


Figure 2. Mean insect abundance was slightly lower for swallow nests that experienced complete mortality, than nests with partial or no mortality.

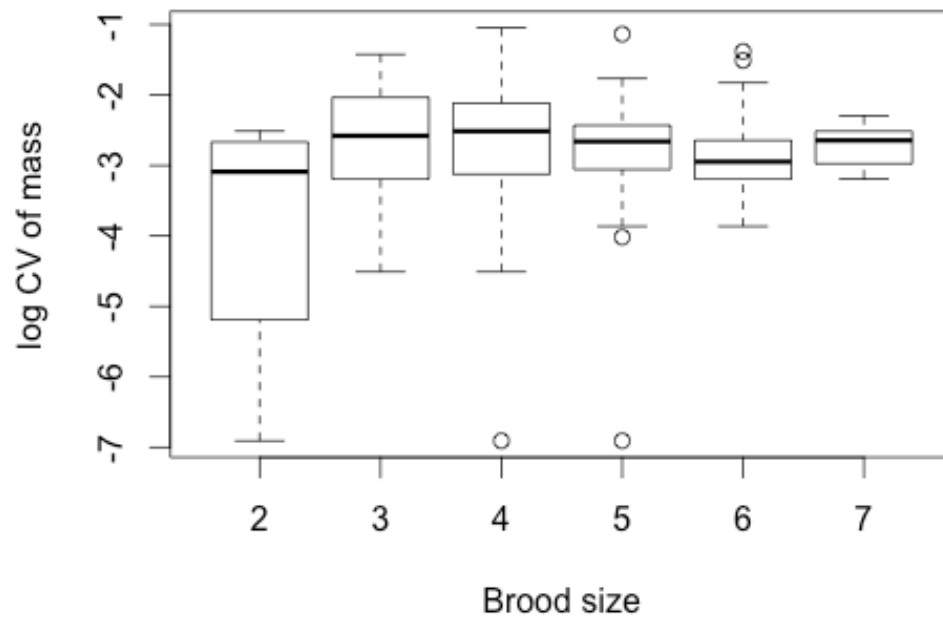


Figure 3. The coefficient of variation for within-clutch nestling mass was lower for smaller broods.

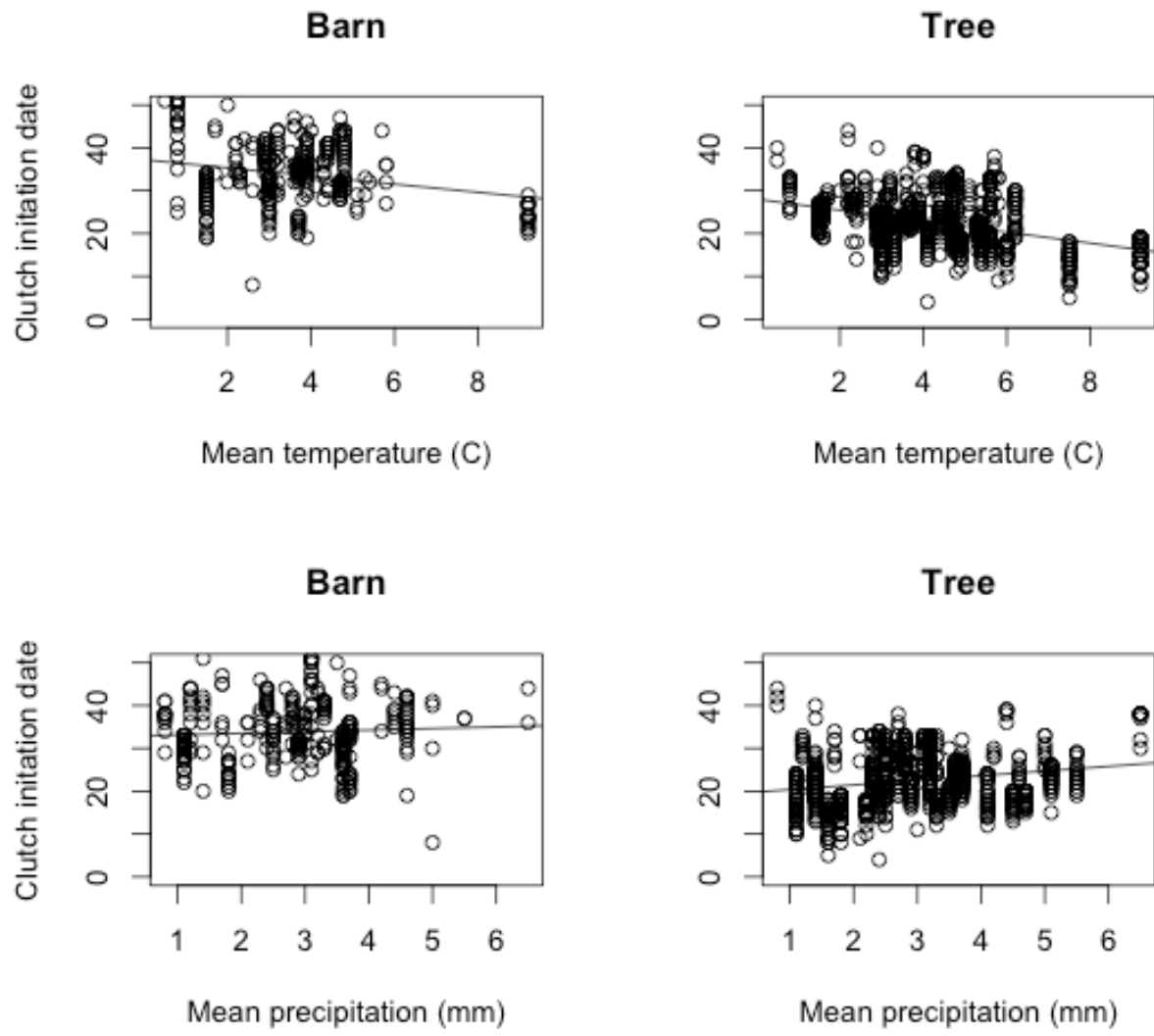


Figure 4. Earlier clutch initiation dates (May 1 = 1) were associated with warmer mean spring temperatures (C) and lower annual mean spring precipitation (mm) for Barn and Tree Swallows.

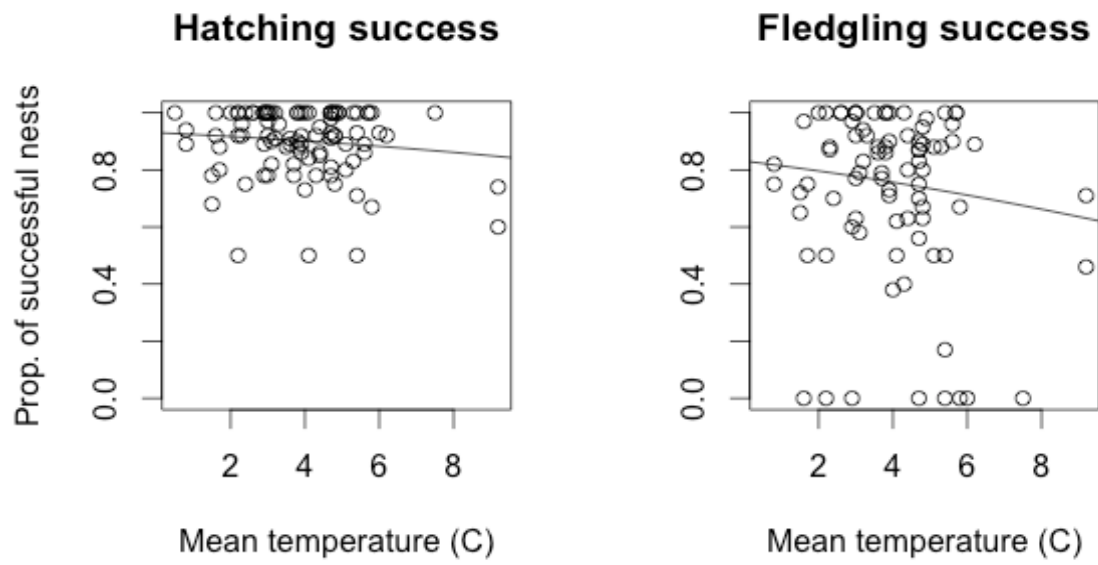


Figure 5. Warmer spring temperatures were associated with lower hatching and fledgling success for Barn and Tree Swallows.

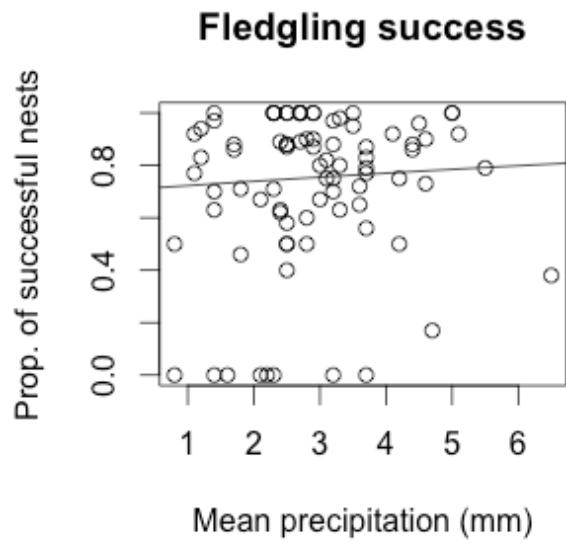


Figure 6. Fledgling success was higher in years with higher increased precipitation.

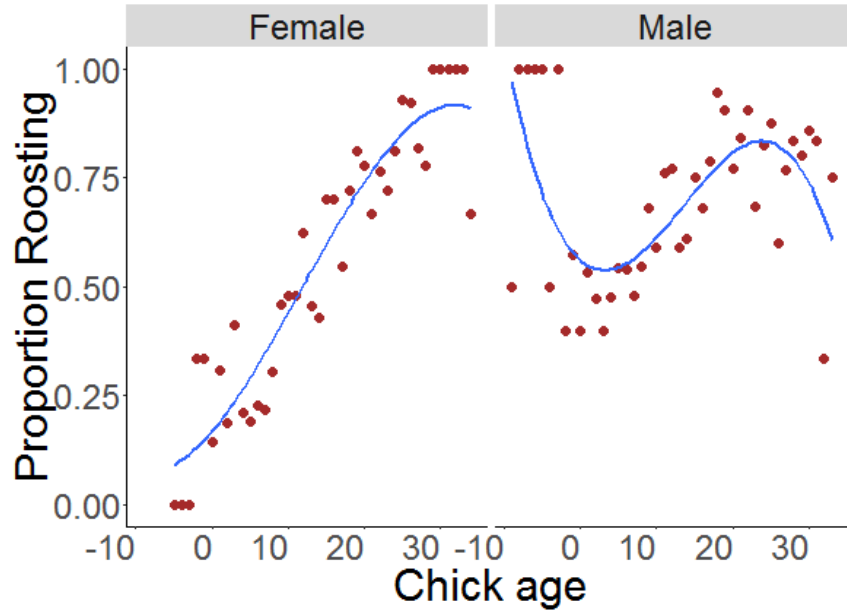


Figure 7. Proportion of male and female Bank Swallows roosting away from the colony with chick age.

Appendix I. Outreach and Communication

This project generated several opportunities for public outreach and stewardship in 2014. In addition, project results were presented at several working group meetings. All outreach, stewardship and communication activities are listed below. Support from the Nova Scotia Habitat Conservation Fund was indicated at all of these activities.

Conference Presentations

Imlay TL, Leonard ML. 2015. Changes in swallow breeding phenology and success over the last 50 years. Society of Canadian Ornithologists meeting, Wolfville NS.

Saldanha S, Leonard M, Imlay T, Taylor P. 2015. Bank Swallow foraging and roosting habitat use. Society of Canadian Ornithologists meeting, Wolfville NS.

Presentation to community group

Nova Scotia Bird Society (April 23, 2015).

Stewardship

Eight landowners and families engaged in swallow monitoring.