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Does prey availability affect the reproductive performance of Barn Swallows, *Hirundo rustica*, breeding in Ontario, Canada?

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ABSTRACT

Animal populations are often limited by food availability, particularly during the breeding season. In birds, food limitation can impact several components of the reproductive cycle, including the timing of reproduction and reproductive output. Barn Swallows (*Hirundo rustica* Linnaeus, 1758) have experienced a population decline over the past 40 years in North America that is thought to be related to changes in prey availability. We monitored Barn Swallow reproductive behaviour and prey availability throughout two breeding seasons at ten sites in Ontario, Canada to test the hypothesis that limited prey availability during the breeding season affected reproductive behaviour. We found no relationship between food availability and the number of eggs laid or the number of young fledged. Neither did we observe higher rates of second brooding or more pairs nesting at breeding sites with higher food availability. Barn Swallows did not time their reproductive effort to maximize prey availability during the nesting period, but any mismatch in phenology of prey and bird reproduction at a breeding site was not associated with lower reproductive success. The results of this study did not support our hypothesis and suggest that Barn Swallow reproductive behaviour was not negatively affected by limited prey availability on the breeding grounds.

Keywords: barn swallow, breeding, food supply, *Hirundo rustica*, prey availability, reproduction

INTRODUCTION

Many animal populations are limited by food availability and this effect can be especially strong during the breeding season when reproductive output may be impacted (Newton 1980; White 2008). High reproductive output, or fecundity, is especially important in maintaining populations of species with a limited number of reproductive seasons, including most songbirds (Sæther and Bakke 2000). Food supply is considered one of the most important factors affecting reproductive investment in birds (Martin 1987; Robb et al. 2008) and can limit various measures of reproductive output such as the number of nesting attempts, clutch size or the number of offspring fledged per attempt (Martin 1987; Nagy and Holmes 2005; Safran 2006).

Barn Swallows (*Hirundo rustica* Linnaeus, 1758) are a widespread species of aerial-foraging insectivorous bird that has declined by 77% since 1980 in Canada, where they are now listed as a Species at Risk (Environment Canada 2014). Several drivers of the decline have been suggested including predation, habitat loss, and declining insect prey (COSEWIC 2011). Similar population declines have been observed in North America across the aerial insectivore guild (Nebel et al. 2010). Given their shared food source (i.e. flying insects) and widespread declines in insect populations (Dirzo et al. 2014; Hallmann et al. 2017; Lister and Garcia 2018), limited prey availability is suspected to be a contributing factor across this guild. A decrease in the quality or quantity of insect prey during the breeding season could negatively impact Barn Swallow populations by altering breeding site selection and limiting clutch size and/or fledging success. Reproductive output may also be impacted by shifts in the timing of prey availability relative to the timing of reproduction.

Barn Swallows are colonial breeders and thus the prey available to any pair is influenced by the number of pairs at a nesting site (Turner 2006). Therefore, total prey availability can

affect breeding site selection. In Europe, Barn Swallow colony size was affected by a variety of factors, including food availability. The presence of livestock and traditional stables, lee from prevailing winds, and high food availability were all associated with larger colony sizes (Møller 1987; Ambrosini et al. 2002). Multiple studies from across the Barn Swallows' range have shown a positive correlation between the number of old nests and the number of pairs nesting at a breeding site (Safran 2004; Ringhofer and Hasegawa 2014). Old nests provide a resource to Barn Swallows by removing the need to build a new nest. In addition, they provide an indirect social cue of the presence and reproductive success of conspecifics in previous years (Ringhofer and Hasegawa 2014). Ultimately, Barn Swallows should be expected to select breeding sites that maximize reproductive success but must balance food availability with intraspecific competition.

Phenological shifts in food availability have led to asynchrony between the peak in food availability and the peak food demand for several bird species (e.g., Visser et al. 2006; Dunn et al. 2011; McKinnon et al. 2012; Charmantier and Gienapp 2014). Insect emergences are advancing due to warmer spring temperatures from climate change, while migratory birds are limited in their ability to shift the timing of reproduction (Dunn et al. 2011), which could lead to lower reproductive success (Both 2010). In Barn Swallows, temperature can predict clutch initiation date (Saino et al. 2004) and, in some parts of Europe, Barn Swallows appear to be laying earlier in response to warming spring temperatures (Crick and Sparks 1999; Møller 2007). However, if Barn Swallows are not shifting the timing of reproduction enough to match a shift in local insect populations, there may still be a mismatch between prey availability and demands with consequences for reproductive output.

Reproductive success in Barn Swallows has also been linked to prey availability (Turner 2006). In Europe, higher prey availability was associated with presence of livestock which, in

turn, was associated with higher reproductive success, larger clutch sizes and higher rates of second brooding (Møller 2001; Ambrosini et al. 2002; Gruebler et al. 2010). In urban areas, Barn Swallows had higher reproductive success at nests where food availability was higher (Teghløj 2017). In North America, there is no evidence suggesting a link between the presence of livestock at a nesting site and clutch size, reproductive success or the probability of double-brooding (S. Bossuyt, personal communication 2016). Furthermore, in Eastern Canada, insect abundance during the rearing period did not affect nestling survival (Imlay et al. 2017). However, the reproductive success of Barn Swallows in North America has been linked with weather variables, where cold, wet weather and very hot, dry weather both lead to lower prey availability and poor breeding success (Turner 2006).

We studied the reproductive performance of Barn Swallows breeding in Ontario, Canada, and addressed three hypotheses. First, we hypothesized that the number of pairs nesting at a breeding site and the number of those pairs that double brood are dependent on the prey availability at the breeding site. We predicted that sites with higher prey availability would have more nesting pairs and more of these pairs would have second broods. Second, we hypothesized that the timing of clutch initiation of the first brood is related to prey availability. We predicted that sites that have an earlier peak in prey availability would have nests that were laid earlier. Finally, we hypothesized that Barn Swallow reproductive output is limited by prey availability during the nesting period. We predicted that Barn Swallows would lay more eggs and fledge more young when there was more prey available.

METHODS

Study Site

We conducted our study at 10 Barn Swallow breeding sites within 20 km of the city of Peterborough in Ontario, Canada (Figure 1) over the 2015 and 2016 breeding seasons. Each breeding site consisted of a barn and associated buildings surrounded by a mixture of cropland, pasture, and/or hayfields. Most surrounding cropland was subject to standard management techniques which included occasional pesticide applications.

Nest Monitoring

At each breeding site, colony size was determined by counting the maximum number of active nests (i.e., those with pairs nest building, incubating or rearing young) during the first brood. Nests were checked every 2 to 3 days and any newly constructed nests were noted and subsequently checked. We recorded clutch initiation date, whether nests hatched, and the date that young fledged and counted the number of eggs, nestlings, and fledglings for each nest. If clutch initiation occurred on a day we did not check nests, the initiation date was back calculated based on the number of eggs in the nest, assuming that one egg was laid per day (Brown and Brown 1999; Møller et al. 2005). If eggs hatched on a day when we did not check the nests, hatch date could be determined by the age of nestlings as described in Turner (2006). If the young were not observed fledging, we considered the most recent nestling count made on day 16 after hatching or later as the number of fledglings (Barclay 1988). Nests were considered depredated if predators were observed at the nest, if the entire clutch of nestlings disappeared before the fledging stage or if deceased nestlings were found in the nest with apparent injuries from predation. We distinguished the first and second brood by assuming that nests that were

initiated before a full week when we observed no new nests at any sites were first broods and nests initiated after that week were second broods.

Insect Collection

We used land and air Malaise traps with bottom collectors (BioQuip® #2869 & #2892; see Figure S2 for photo) to monitor insect abundance and diversity at each breeding site. At each site, we set up a trap 1 m above the ground and 15-30 m from the structure used for nesting. Barn Swallows usually forage <10 m in height and often <1 m from the ground (Brown and Brown 1999) and spend most of their time foraging within a few hundred metres of the nest site (Møller 1987). Malaise traps paired with bottom collectors are effective at collecting flying insects from a range of taxa (Campos et al. 2000; van Achterberg 2009). While a single trap may not reflect the insect abundance of the entire foraging area for a nesting site, logistically we could only operate a single trap at each site. The traps were placed adjacent to areas where Barn Swallows were observed foraging throughout the breeding season. Collection bottles were placed on traps at dawn (sunrise +/- 30 minutes) and removed at dusk (sunset +/- 30 minutes). In 2015, we collected insects from 20 May - 29 August. The number of days the traps were open varied between sites (between 2-6 days/week). In 2016, we collected insects from 25 April – 29 August and all traps were open for 2 days/week at all sites. Specimens were stored in 95% ethanol at -20°C until processing. Temperature and precipitation can affect insect abundances (Rioux-Paquette et al. 2013); however, we found no correlation between daily temperature and precipitation and insect catch in this study, which ensures that variable trapping days between sites should not have biased our results (Supplementary Material 1).

Insect Identification

We sorted insect specimens collected in Malaise traps to morphospecies (Oliver and Beattie 1996). We measured the body length to the nearest 0.1 mm (excluding appendages such as antennae or cerci) of up to five specimens of each morphospecies. Average lengths were calculated for each morphospecies. Representative photos were taken of one specimen from each morphospecies. A representative from each morphospecies was identified using DNA barcoding. Specimens were processed at the Canadian Centre for DNA Barcoding following their standardized extraction, amplification and uni-directional sequencing protocols (see Ivanova et al. 2006; deWaard et al. 2008). The resultant sequences were identified using the BOLD Identification System (www.boldsystems.org, Ratnasingham and Hebert 2007). For any specimens that did not sequence successfully or did not match a reference sequence on BOLD, we used photos to identify the specimens to order and, where possible, to family using Marshall (2006).

Due to a variable number of insect trapping days between sites, the number of insect specimens caught per day of collection was used as an index of daily insect abundance. Insect biomass was estimated using length-mass equations from Sabo et al. (2002) for insect orders and families, where possible. Prey abundance was calculated by removing insect families that were not detected in Barn Swallow diet (McClenaghan et al. 2019) from the total insect abundance. Family level identifications were used because that was the highest level of taxonomic resolution where most insects from Malaise traps were identified. Our measure of prey abundance was further narrowed to preferred prey abundance based on prey size. Barn Swallows select larger prey items (Turner 1982; Orłowski and Karg 2013; McClenaghan et al. 2019). Thus, we considered prey longer than 3 mm in length as large prey (McClenaghan et al. 2019).

Data Analysis

All statistical analyses were conducted using program R v 3.2.0 (R Development Core Team 2015). For all models described below, plots of the residuals and Q-Q plots were examined to assess fit. Either r^2 or pseudo- r^2 values are presented with model results.

Colony Size. We used a Spearman rank correlation test to compare colony size for the 10 breeding sites between years. We used linear models to compare the number of old nests present at the beginning of the breeding season and prey availability with colony size in both 2015 and 2016. Prey availability was measured during the 12-week nesting period, which began when the first nests of the year hatched and ended when all nests had fledged (except for one especially late nest in 2016 that fledged 4 days outside of this period). Prey availability was quantified using four covariates: prey abundance, prey biomass, large prey abundance and large prey biomass. Additionally, we compared colony size in 2016 with the number of old nests, and prey availability during the arrival period, defined as a 4-week period beginning in late April when Barn Swallows arrived at nest sites in Ontario and ending in late May before the first nests hatched. For each model, we used the variance inflation factor (VIF) to measure multicollinearity and remove covariates with the highest score until all covariates had a $VIF < 3$ (Zuur et al. 2010).

Second Brooding. We used a generalized linear mixed model with a binomial distribution implemented using the '*lme4*' and '*lmerTest*' packages (Bates et al. 2015; Kuznetsova et al. 2016) to compare the proportion of pairs at each site that had a second brood with the peak clutch initiation date, the abundance and biomass of prey and the abundance and biomass of large prey during the early brood and during the late brood. Year and site were included as random effects to account for any group level differences in second brooding due to year and

breeding site. Collinearity was assessed using VIF and variables were removed until all VIF scores were < 3 .

Timing of Reproduction. To compare the timing of peak food demand and peak prey availability, we used data from 2016 only, when insect collection began early enough in the season to include the beginning of the laying period. Following Kwon (2016), we quantified the distribution of prey availability over the breeding season using prey biomass and we quantified the distribution of prey demand as the predicted temporal distribution of 13-day old broods, which is when the energy demands of the nest are the highest (Jones 1987). Prey biomass and the number of 13-day-old broods were plotted as percentiles of the season total value across all breeding sites, to standardize scales for direct comparison between the two distributions and to facilitate comparisons between breeding sites. A smoothing curve was applied to the prey availability distribution and the demand distribution at each breeding site against the day of the year using P-splines and a smoothing parameter of 0.6 in the ‘*mgcv*’ package in R (Wood 2006). The smoothed curve for demand was overlaid with the prey availability curve and the area of overlap between the two curves was calculated using the *integrate.xy* function in the ‘*sfsmisc*’ package (Maechler 2015). The coefficient of overlap between prey availability and demand at each breeding site was calculated, where a lower coefficient of overlap indicates more mismatch (Kwon 2016). To determine if phenological overlap had any effect on reproductive measures, we ran two linear models: one to compare the coefficient of overlap to the average number of fledglings per pair and one to compare the coefficient of overlap to the average number of successful nests per pair at each breeding site. To determine if swallows breed later at sites where prey availability peaks later, the date of peak prey availability was identified from the smoothed curves for each site and compared to the date of peak demand at each breeding site

using a linear model. We repeated this analysis using the predicted distribution of clutch initiation dates in place of the predicted prey demand dates to compare the timing of clutch initiation with the timing of prey availability.

Reproductive Output. We report the total number of nest attempts across all sites, hatch success (the percentage of nests that successfully hatched at least one chick), nest success (the percentage of nests that fledged at least one young), predation (the percentage of nests known to be depredated), the mean number of eggs, and the mean number of young fledged. Means are presented with standard errors. Using generalized linear models with a Poisson family distribution for count data using the ‘*lme4*’ package (Bates et al. 2015), we compared the number of eggs laid and the number of fledglings to predictor variables. In the model examining sources of variation in number of eggs laid, we included year, brood, clutch initiation date, prey abundance and prey biomass during the week prior to clutch initiation (2 days of insect collection) as predictors. This model excluded nests that were initiated prior to the start of our insect collection in 2015. In the model of the number of fledglings, we included all 2015 and 2016 nests and the following predictors: year, brood, prey abundance, prey biomass, prey abundance index, prey biomass index, large prey abundance, large prey biomass, large prey abundance index, and large prey biomass index. These variables were included for the three weeks after hatching or 6 days of insect collection, since the Barn Swallow nestling period usually lasts 20 to 21 days (Brown and Brown 1999). Index values were calculated by dividing the prey abundance or biomass on each collection day by the number of active nests at that site on that day. This index controls for variable colony sizes and provides a measure of the amount of prey available per nest at a site. Site was included as a random effect to account for any group

level differences in reproductive output due to breeding site. Collinearity was assessed using VIF and variables were removed until all VIF scores were < 3 .

RESULTS

Colony Size and Rates of Second Brooding

Breeding sites had between one and 26 nesting pairs each year with a mean of 12.6 ± 2.28 nest attempts per breeding season. Sites were very consistent in the numbers of nesting pairs between years (Spearman rank correlation test: $\rho = 0.99$, $p < 0.0001$). In both years, the number of old nests was a significant predictor of the number of pairs present (Figure 2, Table 1). No measures of prey availability throughout the breeding season were significant predictors of the number of pairs (Table 1). The number of old nests showed no relationship with the average number of successful nests per pair ($r^2 = 0.09$, $p = 0.2$) or the average number of fledglings produced per pair ($r^2 = 0.0005$, $p = 0.9$).

The rate of second brooding was significantly greater in 2015 (60.2 %) than in 2016 (37.9 %; two-sample proportion test: $\chi^2 = 7.162$, $df = 1$, $p = 0.007$). No measures of prey availability were significant predictors of the proportion of pairs that had a second brood nor was the average clutch initiation date a significant predictor of this variable (Table 2).

Timing of Reproduction

The peak in prey availability and the amount of overlap between the prey availability curve and the demand curve varied considerably between breeding sites, while the peak in food demand was much less variable between sites (Figure 3, 4). There was no significant relationship between the date of peak prey availability and the date of peak demand ($r^2 = 0.04$, $p = 0.6$). Nor was there a significant relationship between the coefficient of overlap and the average number of fledglings per pair ($r^2 = 0.01$, $p = 0.8$) or the average number of successful nests per pair at each

breeding site ($r^2 = 0.09$, $p = 0.5$). Similarly, we observed no relationship between peak clutch initiation date and peak prey availability ($r^2 = 0.04$, $p = 0.7$) or between the clutch initiation coefficient of overlap (Figure S3) and the average number of fledglings ($r^2 = 0.01$, $p = 0.8$) or the average number of successful nests per pair at each breeding site ($r^2 = 0.09$, $p = 0.5$).

Reproductive Output

There was a total of 242 nest attempts across all sites in 2015 and 2016 with an 80.1% success rate (Table 3). Hatching success and nest success were both higher in 2016 than in 2015 (Table 3). The percent of nests lost to predators varied considerably and there were no losses to predators in the second brood in 2016 (Table 3). There was no significant difference between years or between broods in the number of eggs laid or the number of young fledged (Table 4). No measures of prey availability were significant predictors of the number of eggs laid or the number of young fledged nor was year, brood, clutch initiation date or hatch date (Table 4).

DISCUSSION

Overall, our results did not support the hypotheses that limited prey availability was affecting Barn Swallow colony size, second brooding, timing of reproduction or reproductive output. Contrary to our prediction, colony size was not correlated with prey abundance. However, more Barn Swallows nested at breeding sites with more old nests. This relationship has been observed previously in Barn Swallows, which may be using old nests as a cue to reduce the time needed to assess nest sites (Safran 2004; Ringhofer and Hasegawa 2014). In this study, old nests did not appear to provide any cues about breeding site quality as there was no relationship between the number of old nests and the average nest success or the number of young produced at each site. Alternatively, old nests may be attractive to Barn Swallows because nest reuse can have reproductive benefits. Barn Swallows reusing nests raised more young than

those that built new nests (Safran 2006; Teglhøj 2018). However, reusing nests is not always advantageous since old nests are more likely to harbour parasites that are detrimental to chick health (Møller 1990). Very few nests in our study were newly constructed so we could not compare the reproductive output between old and new nests.

We observed a wide range in the proportion of pairs second brooding between sites, but this variation was not explained by variation in prey availability among sites. By contrast, studies on other species have shown a higher rate of second brooding and higher survival of second broods when food availability is high (Moore and Morris 2005; Nagy and Holmes 2005; Gruebler and Naef-Daenzer 2008). Several factors other than prey availability are known to affect the rate of second brooding in Barn Swallows and may explain the variation we observed. Barn Swallows are more likely to attempt a second brood if their first clutch was laid early (Verboven and Verhulst 1996) and the timing of the first brood is affected by other factors, including female age and weather conditions (Turner 2006). Older, more experienced females tend to lay earlier (Turner 2006) and tend to have more second broods (Bańbura and Zieliński 1998). Since we were studying an unmarked population, we were unable to account for female age but, we did not observe a higher rate of second brooding at sites with an earlier peak clutch initiation date. From 2015 to 2016, we saw a decrease in the rate of second brooding across all sites. In 2015, there was more than double than average precipitation during the month of June, while in 2016, there was less than half the average monthly precipitation from May through August (Table S4). This change in weather conditions was related to drastically reduced prey abundance in 2016 during the first brood but not the second brood (Supplementary Material 2). This decrease in prey abundance was not associated with fewer fledglings from nests in the first brood, but it may have affected individual decisions to produce a second brood. If parents had to

expend more energy providing food for the first brood, they may not have had enough energy to have a second brood (Nagy and Holmes 2005). As we had only two years of data for this study, we cannot currently make broad conclusions about how weather conditions affect prey abundance and the probability of producing a second brood. Additionally, other events in the breeding cycle, such as nest building, require energy and may affect investment in second brooding (Mainwaring and Hartley 2013; Teglhøj 2018).

Contrary to our second prediction, the timing of reproduction was not related to the timing of prey availability. We observed considerable variation in first clutch initiation dates between sites (range of peak clutch initiation dates: 11 May – 16 Jun) but no relationship between the date of peak prey availability and the date of peak clutch initiation or the date of peak food demand at each breeding site. Furthermore, the coefficient of overlap between the prey availability and demand curves was not related to reproductive success. This suggests that Barn Swallows in this population are not adjusting the timing of their reproductive behaviour in response to local prey availability during the clutch initiation or nesting period on the breeding grounds and that currently, there is no selective pressure within the observed breeding season on the timing of reproduction to maximize the prey available to offspring. Indeed, due to the variation in the date of peak prey availability across sites, prey availability appears to be too localized to be expected to have broad evolutionary impacts on our study population. If prey availability is not currently limiting reproductive success, as our results suggest, then there would not be strong selective pressure for clutch initiation to occur at a certain time. In addition, as generalist opportunistic foragers, Barn Swallows should not be affected by mismatch as much as specialist predators (Mallord et al. 2016). This idea was further supported in our study by a lack of relationship between the degree of overlap between prey availability and demand curves

and reproductive success at each breeding site. The data on the timing of reproduction presented here only represent one year of study and insect phenology can be very dependent on weather conditions, which can vary considerably between years (Both 2010), therefore further study is recommended.

Finally, we did not observe any relationship between prey availability and reproductive output in Barn Swallows. Our results are comparable to other studies of Barn Swallow reproduction across their range, which show high reproductive success with approximately 90% of eggs hatching and 80-96% of chicks fledging (Shields and Crook 1987; Safran 2004; 2006; Imlay et al. 2017). Despite wide variation in prey availability over time and between sites, this was not related to variation in the number of eggs laid or the number of young fledged. The lack of relationship between prey availability during the breeding season and reproductive success suggests that food on the breeding grounds is not currently limiting the number of offspring that Barn Swallows can produce. Elsewhere in the North American range of Barn Swallows, insect abundance had no effect on nestling mass or survival, which further supports our results (Imlay et al. 2017). There are several factors that were unaccounted for in our models that may play a larger role in the variation in reproductive output than prey availability. First, the age and condition of the female upon arrival on the breeding grounds may affect the reproductive success of the nest (Turner 2006). Older females tend to lay larger clutches and lay earlier in the season (Bańbura and Zieliński 1998; Safran 2006). We included clutch initiation date in our models, however, this could not account for all the individual variation between females. Second, we observed several instances of nest predation but did not compare predation rates between sites. The nest predation rate we observed across sites was similar to rates observed in Barn Swallows elsewhere in North America (Donahue et al. 2018) but higher than predation rates reported from

Europe (Møller 1987; Teglhøj 2018). We observed a seasonal decline in rates of nest predation indicated by lower predation on second broods than first broods, similar to other studies in North America (Donahue et al. 2018). The main nest predators of Barn Swallows in our study area were raccoons, *Procyon lotor* (Linnaeus, 1758), and squirrels, *Tamiasciurus hudsonicus* (Erxleben, 1777) and *Sciurus carolinensis* (Gmelin, 1788), although ravens (*Corvus corax* Linnaeus, 1758) entered one barn, knocking down nests and eating nestlings (personal observation; Brown and Brown 1999). Third, ambient temperature can also affect clutch size (Saino et al. 2004; Ambrosini et al.; 2006; Turner 2006). Differences in ambient temperature at breeding sites in Europe were mostly driven by the presence/absence of livestock at the breeding sites (Saino et al. 2004; Ward and Bryant 2006). While we did not measure ambient temperature in barns, previous work at these sites showed no effect of barn temperature on clutch size or clutch initiation date (S. Bossuyt, personal communication 2016).

While our results suggest that prey availability is not currently affecting reproductive performance, it is possible that prey availability is having an effect that we were unable to detect. Low prey availability may have decreased chick quality leading to low post-fledgling survival, which has been documented in Europe (Teglhøj 2018). We did not monitor chick quality during the nestling period. However, studies from Eastern Canada show no effect of prey abundance on nestling mass, a common measure of quality (Imlay et al. 2017). Alternatively, there must be a minimum threshold of food requirements and, as long as prey availability is above that threshold, nests can be raised successfully and variation in clutch/brood size would be explained by other factors, such as those discussed above. It is possible that prey availability was always high but high-quality prey may not have been available. Barn Swallows consume a wide range of prey items and their diet is flexible, so they appear to take advantage of whatever prey is available

even if high quality prey is not available (McClenaghan et al. 2019). To control for this, we quantified the total prey availability and the availability of large prey to represent high quality prey, and we used both biomass and abundance as measures of availability. This suggests that Barn Swallows are not currently limited by low availability of high-quality prey as measured by energy content. However, prey may vary in quality based on other measures which we did not test, such fatty-acid or micronutrient content (Twining et al. 2016). Our study was also limited to two years of data and food limitation may have impacted the Barn Swallow population prior to our study or food limitation may be having stronger effects in certain years depending on weather conditions and prey availability. Despite the limited time frame of our study, Barn Swallows experienced very different weather conditions and prey availability between years, suggesting that our results should apply more broadly.

Our ability to detect an effect of prey availability on reproductive performance may have been limited by our insect sampling method. The Malaise traps we used cannot represent the patchiness of prey resources which may display local abundances in microhabitats, such as along hedgerows (Lewis 1969). Our traps caught most of the prey diversity consumed by Barn Swallows (McClenaghan et al. 2019), however, small-scale changes in prey availability across the landscape are not reflected in our trap catch. It is possible that these local abundances could offset low prey abundance in our trap catch.

Limited food availability during the breeding season has been proposed as a driver of the population decline in Barn Swallows in North America. Our results do not support the hypotheses that limited prey availability is affecting colony size, reproductive success, second brooding, or the timing of reproduction in Barn Swallows. We observed high reproductive success and no relationship between prey availability and reproductive performance. Food

limitation during the breeding season may still affect the population by causing negative carry-over effects on adults and/or juveniles during migration and wintering (Holmes 2007; Seward et al. 2013). Food limitation may also occur during other stages of the annual cycle, a possibility which should be addressed in future studies. While our study is short-term, the results presented here and the high reproductive success that we observed suggest that prey availability on the breeding grounds is not currently affecting the Barn Swallow population we studied during the breeding season.

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Figure Captions

Figure 1 Location of Barn Swallow (*Hirundo rustica* Linnaeus, 1758) breeding sites shown by black dots with numbers indicating the number of pairs at each site in each year of the study (2015/2016). The inset maps show the location of the study area within Canada and within Ontario. Map data obtained from the Ontario Ministry of Natural Resources and Forestry - Provincial Mapping Unit (<https://www.javacoeapp.lrc.gov.on.ca/geonetwork/srv/en/main.home>).

Figure 2 Relationship between the number of old Barn Swallow (*Hirundo rustica* Linnaeus, 1758) nests at 10 breeding sites near Peterborough, Ontario, Canada with the number of pairs nesting at each site in (A) 2015 and (B) 2016. 95% confidence intervals are represented in grey. This relationship was significant in both years at $\alpha = 0.05$.

Figure 3 Prey availability (A) and prey demand (B) curves for Barn Swallows (*Hirundo rustica* Linnaeus, 1758) at seven breeding sites near Peterborough, Ontario, Canada plotted as proportional occurrence of the season total by day of the year (2016). Each breeding site is represented by a separate curve. Three additional breeding sites were monitored but not included here due to the very low number of nests (≤ 3).

Figure 4 Prey availability and demand curves for Barn Swallows (*Hirundo rustica* Linnaeus 1758) plotted together for each breeding site by day of the year. The gray line represents the demand curve and the black line represents the prey availability curve. Curves are plotted as proportional occurrence of the season totals. Overlap is shown in grey. Data was collected in 2016 at breeding sites near Peterborough, Ontario, Canada.

Table 1. Summary of three linear models examining the number of Barn Swallow (*Hirundo rustica* Linnaeus, 1758) pairs nesting at breeding sites in 2015 and 2016. All predictors retained in the model after assessing collinearity are listed below and significant predictors in each model are shown in bold ($\alpha = 0.05$).

Model	n	df	r ²	Model Variables	Estimate	SE	t-value	p-value
Nesting Period 2015	10	6	0.45	Prey Abundance	-0.001	0.003	-0.36	0.73
				Large Prey Biomass	-0.002	0.003	-0.58	0.58
				Number of Old Nests	0.205	0.064	3.2	0.02
Nesting Period 2016	10	6	0.77	Prey Abundance	0.003	0.003	1.05	0.33
				Large Prey Biomass	-0.011	0.004	-2.27	0.06
				Number of Old Nests	0.269	0.058	4.62	0.003
Arrival Period 2016	10	5	0.78	Prey Abundance	-0.014	0.009	-1.49	0.2
				Large Prey Abundance	0.033	0.024	1.34	0.24
				Large Prey Biomass	-0.015	0.023	-0.67	0.54
				Number of Old Nests	0.251	0.042	5.9	0.002

Table 2. Summary of the generalized linear mixed effects model comparing the proportion of Barn Swallow (*Hirundo rustica* Linnaeus, 1758) pairs at each breeding site that had a second brood with measures of prey availability and peak clutch initiation date. Year and site were included as random effects. All predictors retained in the model after assessing collinearity are listed below.

Model	n	df	pseudo-r ²	Model Variables	Estimate	SE	z-value	p-value
Second Brooding	20	7	0.05	Peak Clutch Initiation	-0.177	0.186	-0.95	0.34
				Brood 1 Prey Abundance	0.419	0.258	1.62	0.11
				Brood 1 Large Prey Biomass	-0.069	0.304	-0.23	0.82
				Brood 2 Large Prey Biomass	0.047	0.235	-0.19	0.84

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Table 3. Summary of the reproductive output and success of Barn Swallows (*Hirundo rustica* Linnaeus, 1758) at ten breeding sites near Peterborough, Ontario, Canada in 2015 and 2016. Mean number of eggs and number of young fledged are presented with standard errors of the mean. In both 2015 and 2016, nests initiated prior to June 22 were considered brood 1 and nests initiated after were considered brood 2.

	# Nests	% Hatch Success	% Nest Success	% Depredated	# Eggs	# Fledged
2015	126	88.1	76.9	19	4.5 ± 0.09	3.3 ± 0.16
Brood 1	80	85	72.5	22.5	4.7 ± 0.13	3.4 ± 0.22
Brood 2	46	93.4	84.7	13	4.4 ± 0.11	3.2 ± 0.23
2016	116	91.3	83.6	12.1	4.5 ± 0.11	3.6 ± 0.17
Brood 1	86	89.5	80.2	16.3	4.6 ± 0.12	3.6 ± 0.21
Brood 2	30	96.7	93.3	0	3.9 ± 0.19	3.4 ± 0.25
Total	242	89.7	80.1	15.7	4.51 ± 0.07	3.4 ± 0.12

Table 4. Summary of generalized linear mixed models of Barn swallow (*Hirundo rustica* Linnaeus, 1758) reproductive output using the number of eggs and the number of fledglings as measures of reproductive output. Single predictors included eight measures of prey availability, clutch initiation date and hatch date. All measures of prey availability for the fledgling model were from the 3-week period after hatching. Site was included in all models as a random effect. All predictors retained in the model after assessing collinearity are listed below.

Model	n	df	pseudo -r ²	Model Variables	Estimate	SE	z-value	p-value
# Fledglings	171	7	0.03	Hatch Date	-0.08	0.05	-1.70	0.08
				Year	0.03	0.08	0.42	0.67
				Prey Abundance	-0.01	0.06	-0.13	0.89
				Prey Abundance Index	-0.01	0.05	-0.16	0.87
				Large Prey Biomass	0.02	0.05	0.39	0.69
# Eggs	151	5	0.02	Clutch Initiation Date	-0.08	0.04	-1.73	0.08
				Initiation Prey Abundance	0.01	0.04	0.15	0.88
				Year	-0.03	0.09	-0.32	0.74

Figure 1 Location of Barn Swallow (*Hirundo rustica* Linnaeus, 1758) breeding sites shown by black dots with numbers indicating the number of pairs at each site in each year of the study (2015/2016). The inset maps show the location of the study area within Canada and within Ontario. Map data obtained from the Ontario Ministry of Natural Resources and Forestry - Provincial Mapping Unit (<https://www.javacoeapp.lrc.gov.on.ca/geonetwork/srv/en/main.home>).

138x72mm (300 x 300 DPI)

Figure 2 Relationship between the number of old Barn Swallow (*Hirundo rustica* Linnaeus, 1758) nests at 10 breeding sites near Peterborough, Ontario, Canada with the number of pairs nesting at each site in (A) 2015 and (B) 2016. 95% confidence intervals are represented in grey. This relationship was significant in both years at $\alpha = 0.05$.

316x180mm (300 x 300 DPI)

Figure 3 Prey availability (A) and prey demand (B) curves for Barn Swallows (*Hirundo rustica* Linnaeus, 1758) at seven breeding sites near Peterborough, Ontario, Canada plotted as proportional occurrence of the season total by day of the year (2016). Each breeding site is represented by a separate curve. Three additional breeding sites were monitored but not included here due to the very low number of nests (≤ 3).

73x97mm (300 x 300 DPI)

Figure 4 Prey availability and demand curves for Barn Swallows (*Hirundo rustica* Linnaeus 1758) plotted together for each breeding site by day of the year. The gray line represents the demand curve and the black line represents the prey availability curve. Curves are plotted as proportional occurrence of the season totals. Overlap is shown in gray. Data was collected in 2016 at breeding sites near Peterborough, Ontario, Canada.

152x203mm (300 x 300 DPI)