# MULTIPLE BROODING IN BARN SWALLOWS (*HIRUNDO RUSTICA*): EXTRINSIC DETERMINANTS AND IMPLICATIONS ON POPULATION GROWTH

by

Hilary Anne Ruston Mann

Submitted in partial fulfilment of the requirements
for the degree of Master of Science

at

Dalhousie University
Halifax, Nova Scotia
January 2021

# DEDICATION

This thesis is dedicated to my sister, Emily Mann.

My most ardent supporter, enthusiastic outdoor adventure partner and my constant inspiration to do good. Though she is unable to see this thesis completed, she is the reason it exists.

# Table of Contents

## List of Tables

# List of Figures

# Abstract

In many species of birds, the number of broods produced in a breeding season is an extremely important component of reproductive success. However, for many multi-brooded species, we have a poor understanding of both the specific factors that affect the incidence of the behaviour and the impact that changes in the incidence have on population growth rates. Without this information, conservation strategies aimed at protecting multi-brooded species at risk may miss targets for conservation interventions. Therefore, I assessed the implications of multiple brooding on the conservation of a species at risk, the Barn Swallow (*Hirundo rustica*), in New Brunswick and Nova Scotia, Canada. To do this, I first identified extrinsic factors that affect the behaviour to inform potential intervention. Then, I assessed the influence of multiple brooding on the population growth rate to inform the extent to which changes in multiple brooding would impact the status of the population.

In Chapter 2, I determined the effect of spring weather, landcover surrounding Barn Swallow breeding sites and the presence of livestock and metal roofs above swallow nests on the incidence of multiple brooding. I found that warmer, drier and less windy sites, and sites with less human based landcover (i.e. roads and buildings) were associated with a higher probability of multiple brooding, and therefore a higher incidence of the behaviour. In contrast, I found no effect of other landcover, including wetlands and open fields and pasture, or the presence of livestock and metal roofs, on multiple brooding. Therefore, with changes in weather and the intensity of human development at breeding sites, the incidence of multiple brooding should be expected to change in the future.

In Chapter 3, I examined the influence of multiple brooding on the population growth rate in Maritime Barn Swallows. I first combined estimates of reproductive success, including the proportion of multi-brooded pairs, with estimates of hatch year and adult survival in a population model. Then, I applied a Life Stage Simulation analysis and perturbation analyses to this model, to determine the relative influence of each demographic rate on the population growth rate. I found that although an increased proportion of multi-brooded pairs would positively affect the population growth rate, the expected influence of increases in survival, especially in hatch year swallows, would be significantly stronger. Still, an increase in the rate of multiple brooding could help buffer population declines due to reductions in survival, or other components of reproductive success.

My results suggest that conservation interventions targeted at increasing the incidence of multiple brooding would improve population growth rates in Maritime Barn Swallows. Prioritizing the conservation of breeding sites with little infrastructure in the surrounding landscape, and sites in regions with warmer and drier, and less windy springs, will ensure that high quality breeding sites are not lost, and may help improve the stability of the population in the future.

# List of Abbreviations Used

| Abbreviation | Description |
|---|---|
| AHY | after hatch year; adult |
| β | beta coefficient |
| °C | degrees celsius |
| CI | credible/confidence interval |
| FB | failed breeder |
| HY | hatch year |
| km | kilometer |
| km/h | kilometres per hour |
| λ | population growth rate |
| LOO | leave-one-out criterion |
| LSA | life stage simulation analysis |
| MB | multiple brood |
| mm | millimetres |
| NB | New Brunswick |
| NS | Nova Scotia |
| Φ | apparent survival |
| PSIS-LOO | pareto smoothed importance-sampling leave-one-out cross-validation |
| σ | sigma |
| SB | single brood |
| SD | standard deviation |
| SE | standard error |

# Acknowledgements

This thesis would not have been possible without the scientific advice, and the personal support of many people. First and foremost, thank you to my supervisor, Marty Leonard, for the words of wisdom, constructive criticism and patience over the last three years. I am immensely grateful for your guidance. I am also grateful for the positive introduction to Bayesian statistics that I received from Aaron MacNeil, and all the statistical advice he provided over the course of the thesis. Joe Nocera also provided valuable insight throughout the process, and I am grateful for the comments from Greg Mitchell.

My introduction to the world of swallows came from Tara Imlay, whose expertise and support was always just a phone call away. This work is a direct result of her tireless efforts to discover why Maritime swallows have declined so dramatically, and her monitoring records from 2014-2016 were crucial to this project. Further, I am very grateful for Becky Jardine and Katie McGuire for being the best field assistants I could have possibly asked for. Their enthusiasm, dedication and friendship made long days, endless hours in the car and unexpected situations memorable and enjoyable.

Thank you to Sydney and Anik- I can’t imagine a more supportive, little group of labmates. Countless other peers were responsible for making such a supportive, welcoming and positive community in the biology department, for which I am grateful.

The landowners who allowed me onto their farms are true champions to the swallows. Thank you for opening your homes, providing an endless source of dogs, cows and alpacas to visit, and offering a safe space for the swallows to thrive. Also, thank you to Peter Thomas at the Canadian Wildlife Service for providing equipment and always being keen to talk about the state of the swallows.

Lastly, thank you to all my friends and family who have gotten me through the last three years. To Gill and Emma for the morning coffee runs. To Erin (and Mach and Toffee), Denise, Alanna and Margaret for keeping me grounded at home. To Matt. And thank you to my parents, who have been my rock and steadfast supporters over trying times.

# Chapter 1: General Introduction and Methods

## 1.1.Introduction

Animals face a range of constraints throughout their life cycle. In seasonal climates, variation in resources and environmental conditions requires either migration to more favourable locations, or cessation of energy expensive reproductive activities; both actions restrict the window for reproduction (Alerstam et al. 2003). To optimize fitness, animals use different life history strategies to balance the allocation of resources between reproductive success in this limited window and survival across their annual cycle (Stearns 1992). Species that have a 'fast' life history strategy, characterized by early maturity and short lifespans, generally prioritize resources towards reproduction (Oli 2004, Healy et al. 2019). These species aim to maximize their current reproductive effort, and use reproductive strategies that increase the number of young they produce in a given breeding season (Drent and Daan 1980, Healy et al. 2019). One such strategy is known as multiple brooding, where an individual initiates a second brood following the success of a prior brood, within the same breeding season (as defined in Podolsky et al. 2007, Husby et al. 2009, Grüebler and Naef-Daenzer 2010, Carro et al. 2014).

### Benefits and Costs of Multiple Brooding

Multiple brooding is a widespread strategy across a variety of taxa. In birds, it is found in at least 64 families (Bennett and Owens 2002), where it is known to increase reproductive success by shortening the interbrood period and increasing the frequency of reproduction (Ogden and Stutchbury 1996, Weggler 2006, Naef-Daenzer et al. 2011). Indeed, multiple brooding can double or triple the number of young produced in a single breeding season (Cooper et al. 2005), and for many species, is a major component of annual (Ogden and Stutchbury 1996, Weggler 2006, Carro et al. 2014, Béziers and Roulin 2016, Cornell and Williams 2016, Woodworth et al. 2017), and lifetime reproductive success (Husby et al. 2009, Johns et al. 2018, Zabala et al. 2020). For instance, multi-brooded Great Tits (*Parus major*) recruited more young to a population than single brooded individuals (Husby et al. 2009), and multi-brooded Cassin's Auklets (*Ptychoramphus aleuticus*) produced seven times the number of chicks as single brooded individuals over their lifetime (Johns et al. 2018). Therefore, it can be an effective strategy to increase fitness.

Multiple brooding is, however, a costly behaviour. Producing more than one brood requires significant investment of energy into egg laying, incubating and raising young (Tinbergen and Dietz 1994) and may involve reduced parental care for fledglings from first broods (Verhulst et al. 1997, Grüebler and Naef-Daenzer 2010, Jamieson 2011). Also, subsequent broods are produced later in the season, which corresponds with deteriorating conditions on breeding grounds (Harriman et al. 2017) and a shorter pre-migratory period for juveniles (Raja-aho et al. 2017, Evans et al. 2020). These costs are often reflected in reductions in survival and recruitment for individuals from first (Naef-Daenzer et al. 2011) or subsequent broods (Tarof et al. 2011, Saino et al. 2012, Raja-aho et al. 2017 but see Morrison 1998, Weggler 2006, Evans et al. 2020). Despite the costs, multiple brooding is a widespread behaviour and appears to be effective at increasing reproductive success.

## Determinants of Multiple Brooding

Despite the potential of producing multiple broods in a season, not all individuals in multi-brooded species do so. Inter-annual variation in the incidence of the behaviour is often high. For example, the proportion of multi-brooded Black Redstarts (*Phoenicurus ochruro*) ranged from 16-58% (Weggler 2006) and 0-87% in Black-throated Blue Warblers (*Setophaga caerulescens*, Nagy and Holmes 2005a) across years. Further, spatial variation in the incidence of multiple brooding is also often high. For example, the proportion of multi-brooded Barn Swallows (*Hirundo rustica*) varied from 30% in Ontario, to 90% in Manitoba and 49% in New York (Brown and Brown 2020)

Variation in the incidence of multiple brooding is often explained by a number of factors. Early breeding ensures there is time to raise more than one brood before the cessation of the breeding season and as such, pairs that breed earlier are more likely to have multiple broods across species (Ogden and Stutchbury 1996, Safran 2006, Bulluck et al. 2013, Jacobs et al. 2013, Townsend et al. 2013, Béziers and Roulin 2016). In addition, if conditions are such that the energetic costs of foraging, thermoregulation and provisioning young are reduced, there should be more energy to allocate towards costly reproductive behaviours, and more pairs should be multi-brooded (Stearns 1992). As such, greater food availability is related to a greater incidence of multiple brooding in food supplementation experiments (Simons and Martin 1990, Nagy and Holmes 2005b, O'Brien and Dawson 2013) and select correlational studies (Nagy and Holmes 2005a but see O'Brien and Dawson 2013, McClenaghan et al. 2019). Lastly, some individuals are inherently of higher quality, and are more likely to have multiple broods; they are often more experienced, older, compete for higher quality sites and inherently breed earlier (Holmes et al. 1992, Weggler 2006, Bulluck et al. 2013).

Ecological factors that impact the timing of breeding, food availability, or the quality of breeders will act as extrinsic determinants of multiple brooding. Two such extrinsic determinants are weather and habitat characteristics, which are known to affect the incidence of multiple brooding (Møller 2001, Nagy and Holmes 2005a, Weggler 2006, Bulluck et al. 2013, Jacobs et al. 2013, Townsend et al. 2013, Béziers and Roulin 2016, Drake and Martin 2018). Warmer springs often drive the earlier initiation of breeding activity (Weggler 2006, Townsend et al. 2013, Drake and Martin 2018 but see Husby et al. 2009) and weather, including temperature, precipitation and rain, can also have a strong impact on food availability, particularly of flying insects (Bryant and Turner 1982, Sillett and Holmes 2005, Møller 2013, Winkler et al. 2013, Teglhøj 2017). Further, the characteristics of the breeding habitat, such as the vegetation structure, territory quality or the characteristics of the surrounding landscape, can affect multiple brooding by altering food availability and attracting either high or low quality individuals (Møller 2001, Nagy and Holmes 2005a). Understanding the specific weather and habitat characteristics that act as determinants of multiple brooding in different species will help us understand why the incidence of multiple brooding varies.

## Potential Implications of Multiple Brooding

Multiple brooding is clearly dependent on a variety of extrinsic factors. This suggests that the incidence of the behaviour will change in the future, especially given predictions of significant, worldwide climactic and land use changes in the future (Collins et al. 2013, Zabel et al. 2019). Indeed, increasingly warm spring temperatures associated with climate change have extended the breeding season by 0.4-0.6 days per year for several multi-brooded species (Møller et al. 2010, Halupka and Halupka 2017), which is the likely mechanism behind increases in the incidence of the behaviour in Reed Warblers (*Acrocephalus scirpaceus;* Halupka et al. 2008) and Barn Swallows (Engen et al. 2001) in Europe.

Changes in the incidence of multiple brooding has implications for population trends. As an important component of reproductive success, increases in the incidence of multiple brooding can positively impact population growth rates (Podolsky et al. 2007). Therefore, increases in the incidence of multiple brooding may help buffer potential declines that would otherwise occur due to reductions in, for example, clutch size or survival (Engen et al. 2001). Understanding how multiple brooding influences population growth rates is particularly important for short-lived species with high reproductive success, because growth rates in these species are more likely to be influenced by changes to reproductive parameters than survival (Saether and Bakke 2000, Clark and Martin 2007).

### Barn Swallows

Barn Swallows are one species where multiple brooding may have an important influence on population growth. They are small, migratory aerial insectivores that lay clutches of up to 7 eggs, and can raise 1-4 broods in a single breeding season (Brown and Brown 2020). Their nests are found almost exclusively in anthropogenic structures, such as barns, sheds and culverts (Brown and Brown 2020). Though they can live up to nine years, annual survival is estimated to be approximately 0.33-0.6 (García-Pérez et al. 2014, Brown and Brown 2020) and therefore opportunities to reproduce are limited.

Understanding the influence of multiple brooding on population growth rates is important for Barn Swallows because such knowledge could help inform conservation strategies for the species. While global population declines are insufficient to dictate listing by the International Union for Conservation of Nature at an international scale (BirdLife International 2020), they are Threatened in Canada, due an overall decline of 78% in the country's population from 1970-2017 (Smith et al. 2017). These declines are likely due to a combination of factors that impact their survival and reproduction, including the degradation of habitat across their range, declines in insect availability and quality, contaminants and climate change (COSEWIC 2011, Imlay and Leonard 2019, Spiller and Dettmers 2019, Nebel et al. 2020). Understanding the determinants of multiple brooding in the species is important because several of the potential causes of these population declines, such as climate change and changes to their breeding habitats, likely affect the incidence of multiple brooding.

There are few studies that have assessed the extrinsic determinants of multiple brooding for Barn Swallows. In Ontario, insect abundance had no effect on the incidence of multiple brooding (McClenaghan et al. 2019), while in Switzerland and Denmark**,** the presence of livestock was related to an increase in the number of multi-brooded pairs on farms (Møller 2001, Grüebler et al. 2010). However, a number of other extrinsic factors likely play a role in dictating multiple brooding behaviour. These are factors that impact abundance of insect prey, timing of reproduction and the thermodynamic properties (therefore energetic demands) of nesting sites, including weather (Bryant and Turner 1982, Winkler et al. 2013), the types of landcover in the vicinity of breeding sites (Evans et al. 2007, Henderson et al. 2007, Orłowski and Karg 2013, Teglhøj 2017, Bellavance et al. 2018, McHugh et al. 2018, Kusack et al. 2019) and building architecture (Anthony and Ely 1976, Møller 2001, Ambrosini et al. 2002). Such factors also impact other components of reproductive success (Anthony and Ely 1976, Møller 2013, Teglhøj 2017). Therefore, they likely influence multiple brooding behaviour. Understanding the determinants of multiple brooding may play a role in helping to manage breeding sites to increase the incidence of the behaviour and potentially reduce popualtion declines.

In addition to this information, managing Barn Swallow populations will also require an understanding of how changes in the incidence of the behaviour will affect population growth rates. Limited studies on the demographics of the subspecies of Barn Swallow that breeds in Europe (*Hirundo rustica rustica*) suggested that survival has a greater influence on population growth rates than reproductive success (Robinson et al. 2014, Schaub et al. 2015). Nonetheless, in the 1970's and 1980's, declines in reproductive success were correlated with population declines in Denmark (Møller 1989), suggesting that reproductive parameters may affect population growth. It is not clear what demographic factors influence population growth in the subspecies that breeds in North America (*H. r. erythrogaster*) and, in particular, whether multiple brooding could contribute meaningfully to population growth or persistence. If management decisions could be made to increase the incidence of multiple brooding, knowing that it could have a positive impact on population growth rate, it could be a useful target for conservation interventions.

### Purpose of Study

The overarching goal of my thesis was to determine the implications of multiple brooding on the conservation of a Threatened population of Barn Swallows in the Canadian Maritimes. Here, the Barn Swallow population declined by >90% between 1970 and 2017 (Smith et al. 2019). This is consistent with the observation that aerial insectivores in general are at a greater risk off decline in North America in the most Eastern and Northern portions of their range, potentially due to lingering effects of acid rain and stronger effects of habitat loss or climate change in these areas (Nebel et al. 2010).

In Chapter 2, I assessed the extrinsic determinants of multiple brooding, including weather and breeding site characteristics such as land cover, the presence of livestock and building characteristics. In doing so, I filled in knowledge gaps on the factors that may alter the incidence of multiple brooding, and inform potential conservation interventions. In Chapter 3, I used population modelling to determine the relative influence of multiple brooding on the population growth rate. This informed the extent to which changes in multiple brooding would impact the status of the population. In Chapter 4, I consider the implications of this thesis as a whole on the conservation of Barn Swallows.

## 1.2. General Methods

### Study Sites

My study was conducted from 2012-2019, at 18 Barn Swallow breeding sites (Table 1.1) in Nova Scotia and New Brunswick, Canada (Figure 1.1). The sites were coincident with areas of greatest Barn Swallow abundance in the region (Stewart et al. 2015). On average, the sites contained 8.9 pairs (range 1-23 pairs) of swallows.

I divided the sites into two types: 1) monitoring sites (n =6) that were visited every 2-3 days throughout the breeding season, and were used to track individual reproductive success, the incidence of multiple brooding and survival of Barn Swallows and 2) survey sites (n =12) that were visited on 2-4 occasions during the breeding season, and were used to estimate the incidence of multiple brooding at a broader spatial scale (Table 1.1).

The sites were a mix of working cattle farms and rural properties and had varying degrees of development, agriculture and wetlands in the surrounding area (see Chapter 2). Though most nests were found within barns and sheds, swallows also nested in salt storage domes at one site (DT).

### Determining Incidence of Multiple Brooding

To determine the incidence of multiple brooding, I used five years of observations of breeding activity across 60 buildings, at 18 sites in New Brunswick and Nova Scotia. Since swallows may nest in multiple buildings at a single site, I determined the total number of pairs, and the number of multi-brooded pairs, in each building, or part of a building (i.e. floor), at each site. To observe breeding activity in 2014-2016 and 2018-2019, I visited up to six Barn Swallow breeding sites (‘monitoring sites’; Table 1.1) every 2-3 days, from May through August. In 2018-2019, I also visited up to eleven Barn Swallow breeding sites (‘survey sites’; Table 1.1) two to four times, from June through August (Figure 1.2). During these visits, I recorded the number of eggs or chicks in each nest, and noted a nest as active if it contained either.

To determine the total number of pairs that bred within a building, I assumed that the number of nests initiated prior to July 5 (the earliest clutch initiation date for second broods of multi-brooded pairs at my monitoring sites across all years; unpublished data) represented the total number of breeding pairs. I estimated the number of nests by counting the number of active nests during two visits (one visit for 2018 survey sites) to each breeding site, prior to July 5 (Figure 1.2). To remain consistent in my methods between monitoring and survey sites, I only used observations from two visits at monitoring sites, coincident with the timing of visits at survey sites, for my estimate of total pairs.

To determine the number of multi-brooded pairs, I counted the number of active nests during two visits (one visit for 2018 survey sites) to each breeding site, after July 5.

These counts would include second clutches of multi-brooded pairs and replacement clutches of pairs that had a previously failed nest. To distinguish between second broods and replacement clutches, I assumed that all nests initiated prior to July 5 that failed (i.e. egg did not hatch between visits, or no chicks in nest after eggs observed in previous visit) would be followed by a replacement clutch that would be active after July 5. Therefore, I assumed the minimum number of multi-brooded pairs was equal to the number of pairs observed after July 5, minus the number of failed nests observed prior to July 5.

In 2018, I was only able to determine the incidence of multiple brooding at five of nine surveyed sites and five monitoring sites, where I had confidence in my estimates of the number of pairs (total and multi-brooded; Table 1.1).

## 1.3 Tables

**Table 1.1**- Summary of research activities at Barn Swallow breeding sites in New Brunswick (NB) and Nova Scotia (NS) from 2012-2019. A 'Y' indicates that data were collected at a site in a given year. Monitored sites were used to determine all reproductive and survival rates, and were supplemented by data from survey sites, to determine the incidence of multiple brooding.

| site | province | type of site | active during year | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 |
| WE | NB | monitor | Y[1] | Y[1] | Y | Y | Y | Y[1] | Y | Y |
| DW | NB | monitor | Y[1] | Y[1] | Y | Y | Y | Y[1] | Y | Y |
| ET | NB | monitor | - | - | - | Y | Y | Y[1] | Y | Y |
| JB | NB | monitor | - | - | - | - | - | - | Y | Y |
| BK | NB | monitor | - | - | - | - | - | - | Y | Y |
| GA | NB | monitor | - | - | - | - | - | - | - | Y |
| PV | NB | survey | - | - | - | - | - | - | Y | Y |
| MX | NB | survey | - | - | - | - | - | - | Y[2] | Y |
| KR | NB | survey | - | - | - | - | - | - | Y[2] | Y |
| DT | NB | survey | - | - | - | - | - | - | Y[2] | Y |
| LN | NB | survey | - | - | - | - | - | - | Y[2] | Y |
| CM | NS | survey | - | - | - | - | - | - | Y | Y |
| OM | NS | survey | - | - | - | - | - | - | Y | Y |
| MT | NS | survey | - | - | - | - | - | - | Y | Y |
| WB | NS | survey | - | - | - | - | - | - | - | Y |
| HF | NS | survey | - | - | - | - | - | - | - | Y |
| HH | NS | survey | - | - | - | - | - | - | Y | - |

[1] Data from 2012, 2013 and 2017 were only used for mark-recapture analyses (Ch. 3)

[2] Data were collected but due to uncertainty, were excluded from analyses

## 1.4 Figures

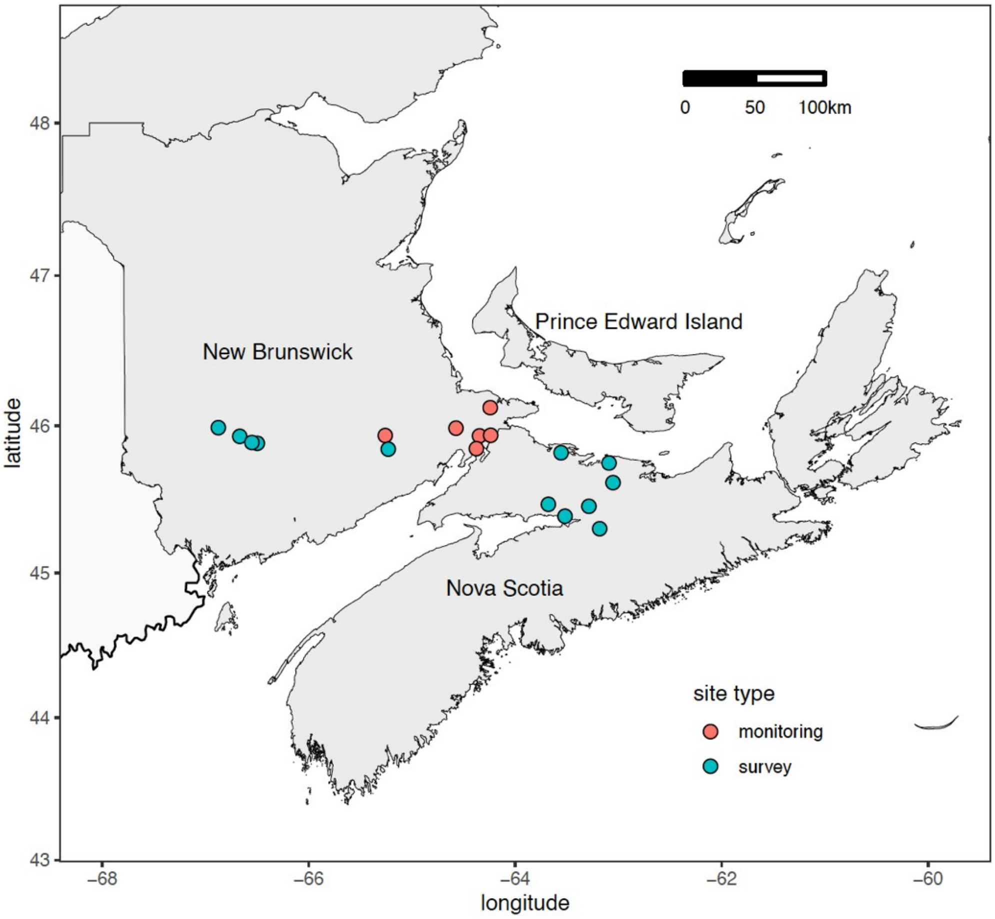


**Figure 1.1-** Distribution of monitoring and survey sites in New Brunswick and Nova Scotia, Canada.

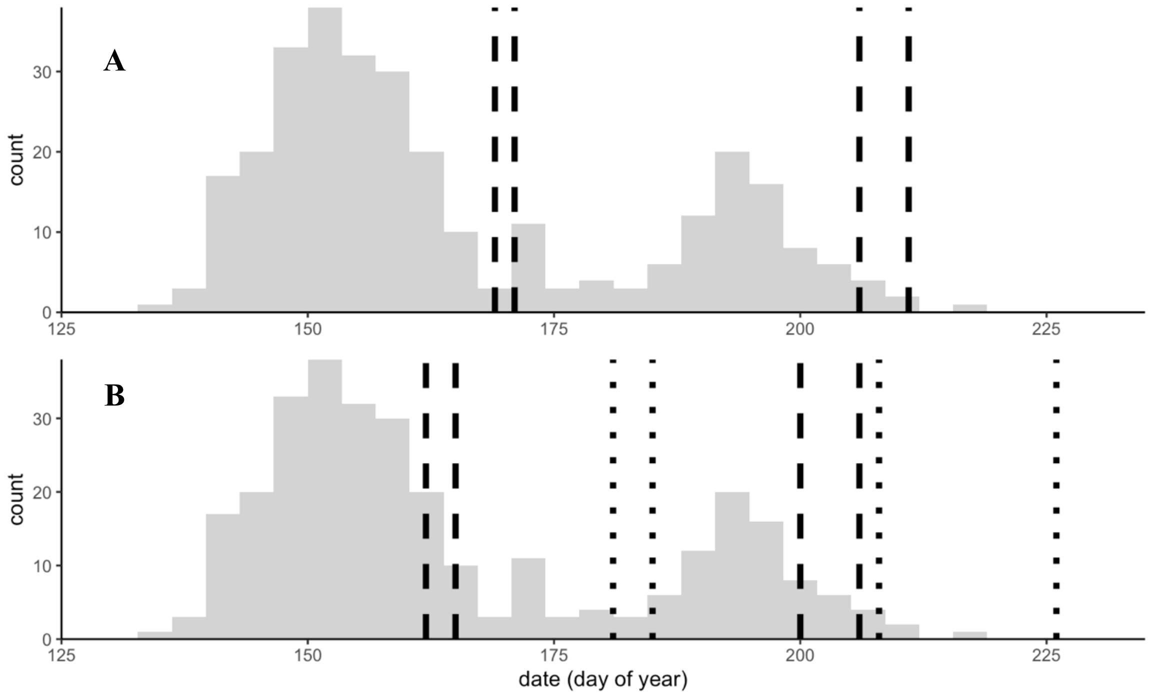


**Figure 1.2-** Timing of nest checks at 2018 survey sites (A) and all other sites (B) used to determine the incidence of multi-brooded pairs, in relation to the timing of breeding activity. Breeding activity is represented by the frequency of nests with specific clutch initiation dates observed at monitoring sites in 2014-2015 and 2018-2019 (shaded bars; n=303). Each pair of dotted or dashed lines represents the span of dates when each visit occurred across sites. The days of the year correspond with May 25 (125), May 30 (150), June 24 (175), July 19 (200) and August 13 (225).

# Chapter 2. Extrinsic Determinants of Multiple Brooding in Barn Swallows (*Hirundo Rustica*)

## 2.1 Abstract

Ecological changes act as extrinsic factors that affect the reproductive and survival rates of organisms, which ultimately affect population growth rates. Understanding which extrinsic factors impact multiple brooding, an important component of reproductive success in many birds, may help us evaluate potential threats and make sound conservation recommendations. However, for Barn Swallows (*Hirundo rustica*), a Threatened species in Canada, we do not know how a number of factors relating to weather and breeding site characteristics affect the behaviour. Therefore, I assessed the extrinsic determinants of multiple brooding in Barn Swallows in Nova Scotia and New Brunswick. I determined the incidence of multiple brooding across five years, at 18 breeding sites. Then, I used a hierarchical Bayesian generalized linear model to determine the effect of spring weather, landcover and the presence of livestock and metal roofs above nests on the probability of multiple brooding. Warm, dry and less windy sites, with less human infrastructure in close proximity to the nest sites, were associated with a higher probability of multiple brooding. In contrast, the presence of wetlands or row crops (i.e. corn, soy, vegetables) and the proportion of wooded or open (i.e. hayfields, grassy areas) landcover had no effect. Similarly, neither the presence of livestock nor metal roofs affected the probability of multiple brooding. My results suggest that prioritizing the conservation of breeding sites in warm, dry areas, with little human-associated landcover, will prevent the loss of high quality breeding sites characterized by higher rates of multiple brooding. This may help prevent future population declines.

## 2.2 Introduction

By the end of this century, climate change is predicted to increase global mean temperature, precipitation and extreme weather events (Collins et al. 2013). Furthermore, urbanization, agricultural intensification and deforestation are expected to rapidly expand and dramatically alter all habitats (Zabel et al. 2019). These ecological changes, or extrinsic factors, are significant threats to the survival of species around the world (Jenouvrier 2013; Allek et al. 2018; Wagner 2020), and could lead to population declines by reducing reproductive success and survival, which ultimately affect population growth. If conservation and management plans are to be successful, they must be based on knowledge of how these extrinsic factors affect the behaviours that determine reproductive success and survival.

One behaviour that can be important to reproductive success for many species of birds is multiple brooding, where individuals initiate a new nest after having a successful, prior brood within the same breeding season. Changes in the incidence of the behaviour may be significant because multiple brooding can significantly increase the number of young produced in a year (Ogden and Stutchbury 1996, Nagy and Holmes 2005a, Weggler 2006, Woodworth et al. 2017), and increasing the incidence can increase population growth rates (Podolsky et al. 2007). While it is a common behaviour (Bennett and Owens 2002), not all individuals of multi-brooded species will have multiple broods.

Typically, the incidence of multiple brooding is highly dependent on a number of factors. First, there must be sufficient time to raise multiple broods and therefore, it is most common when conditions are favourable to early initiation of breeding activity (Safran 2006, Weggler 2006, Bulluck et al. 2013, Jacobs et al. 2013, Townsend et al. 2013, Béziers and Roulin 2016, Drake and Martin 2018). Further, individuals must be capable of raising multiple broods, and therefore, it is most common when high quality individuals, which are typically older and inherently breed earlier, are present (Holmes et al. 1992, Nagy and Holmes 2005a, Weggler 2006, Bulluck et al. 2013). Lastly, there must be sufficient resources and energy to allocate towards reproduction, and therefore, multiple brooding is more common when food availability is high (Nagy and Holmes 2005b, O'Brien and Dawson 2013). As such, factors that alter the timing of breeding, quality of the breeding population or food availability, such as spring weather (Weggler 2006, Bulluck et al. 2013, Jacobs et al. 2013, Townsend et al. 2013) and habitat quality (Møller 2001, Nagy and Holmes 2005a, Teglhøj 2017), are important extrinsic determinants of multiple brooding. It is important to determine exactly what characteristics of weather and habitat quality constitute the extrinsic determinants of the behaviour, especially for multi-brooded species at risk, where the behaviour could impact their population growth.

One such species at risk is the Barn Swallow (*Hirundo rustica*), a short lived and frequently multiple brooded aerial insectivore. In Canada, this species declined by 78% between 1970-2017 (Smith et al. 2017), and is listed as Threatened on the Species at Risk Act. Although multiple brooding is a common feature of Barn Swallow populations (Brown and Brown 2020), only three studies have directly assessed the extrinsic determinants of the behaviour. In Europe, the presence of livestock at breeding sites increased the incidence multiple brooding (Møller 2001, Grüebler et al. 2010), while in Ontario, changes in insect availability did not affect the behaviour (McClenaghan et al. 2019). Other characteristics of their breeding sites, such as weather, landcover and architectural features like roofing material, likely play a role in dictating multiple brooding behaviour and should receive attention. Such factors are known to impact other components of reproductive success (Anthony and Ely 1976, Grüebler et al. 2010, Møller 2013, Sicurella et al. 2014, Teglhøj 2017, Kusack et al. 2019), or insect abundance and the thermodynamic properties of breeding sites (Evans et al. 2007, Ambrosini and Saino 2010, Winkler et al. 2013, Teglhøj 2017), and therefore likely impact multiple brooding. They may also cause nest failure (Anthony and Ely 1976, Tate 1986), such that by the time young are successfully fledged from a nest, it is unlikely that there would be time to initiate a second brood. Identifying which of these factors are determinants of multiple brooding will help inform conservation practices by identifying the site characteristics that correspond with high quality habitat, based on a higher incidence of multiple brooding.

Therefore, my objective was to identify the extrinsic determinants of multiple brooding in Barn Swallows breeding in New Brunswick and Nova Scotia, Canada. Specifically, I investigated if weather, the landcover composition in the vicinity of each site and the presence of livestock and metal roofs above nests, affected the probability of multiple brooding.

I expected that poor weather, characterized by high winds, high precipitation and low temperatures, would decrease the probability of multiple brooding, since it is associated with reduced insect activity (Bryant and Turner 1982, Sillett and Holmes 2005, Møller 2013, Winkler et al. 2013, Teglhøj 2017), and in insectivores, generally decreases nestling survival and condition (Møller 2013, Winkler et al. 2013, Cox et al.

2019). I also expected that sites with wetlands present, and a higher proportion of open areas (including hayfields and pastures) and wooded spaces in close proximity to the nest sites would have an increased probability of multiple brooding, since such landcover is associated with higher insect abundance and is often selected as foraging sites (Evans et al. 2003, Grüebler et al. 2008, Liu et al. 2018). In contrast, I expected that the presence of row crops (i.e. corn, soy, vegetables) and an increase in human related landcover (i.e. roads, buildings) would decrease the probability of multiple brooding because increased urbanization and increased agricultural intensification (associated with more crops) decreases insect abundance and general reproductive success in Barn Swallows (Evans et al. 2007, Osawa 2015, Teglhøj 2017 but see Kusack et al. 2019). I also expected that the presence of livestock at breeding sites would increase the probability of multiple brooding, because they are associated with higher rates of multiple brooding in Europe (Møller 2001, Grüebler et al. 2010), and are associated with increased insect abundance and warmer conditions within barns (Møller 2001, Ambrosini and Saino 2010, Musitelli et al. 2016). Lastly, I expected that within individual buildings, the presence of a metal roof without a lower insulative layer (i.e. wood) directly above a nest, would decrease the influence of multiple brooding, since metal roofs can cause thermal stress (Imlay et al. 2019b) and are linked with higher nestling mortality (Anthony and Ely 1976, Tate 1986).

## 2.3 Methods

### Incidence of multiple brooding

To determine the incidence of multiple brooding, I used five years of observations of breeding activity across 60 buildings, at 18 sites in New Brunswick and Nova Scotia. Details of how I determined the total number of breeding pairs, and multi-brooded pairs, within a building, at each site, are found in Chapter 1 (General Methods).

### Weather

To characterize spring weather at my breeding sites, I downloaded weather data (see below) including total precipitation, mean daily maximum wind gusts and the total number of cold days (maximum daily temperature < 18.5°C) for each site in May and June. This includes the period when most pairs arrive at breeding sites and initiate their first nests. I considered a cold day to be a day where the temperature failed to reach 18.5°C because this temperature is an important threshold for flying insect activity (Winkler et al. 2013), and previous research on Tree Swallows (*Tachycineta bicolor*) suggests these cold days are important for nestling growth and survival (Winkler et al. 2013, Cox et al. 2019)

I downloaded archived Environment Canada (2019) weather data from the weather station (n=5) closest to each breeding site, for each year. If the closest station did not have complete data for the months of May and June, I used data from the next closest station that had data for precipitation, wind and temperature (mean distance 21.4 km, range 4.7- 47.1).

### Landcover

I classified the proportion of six different landcover categories (adapted from Lenske 2018; Table 2.1) within a 400m radius of each site (Appendix A). Barn Swallows typically forage within a 400-600m radius of their nest (Bryant and Turner 1982, Ambrosini et al. 2002), and variation in the type of landcover within this radius is likely to impact insect abundance, foraging behaviour and reproductive success (see Sicurella et al. 2014).

To classify landcover, I used QGIS 3.10 (QGIS 2020) to digitize a 400m radius around 18 sites, based on Google Earth satellite imagery (imagery from 2017-2019). Although I only classified landcover using satellite imagery from one year between 2017-2019 for each site, there were no significant changes in landcover during the years of my study (Mann, personal observation). I excluded the proportion of open water in my analyses because it represented a very low proportion of landcover across all sites (0.02 ±0.06 SD; Figure 2.1).

### Livestock

I recorded the presence or absence of horses, cattle, sheep, llamas or goats within a 400m radius of each site (Table 2.2). Although the number of livestock present at a site sometimes changed over the breeding season, there were no sites where livestock changed from present to absent in a year. I considered the presence/absence of livestock because where livestock are present, manure is also present and is an important source of insect prey (McMahon et al. 2010).

### Roofing

I recorded the type of surface directly above each nest in each building or building section (i.e. floors; Table 2.2). Specifically, I noted if there was a metal roof or another surface (i.e. metal with wood directly underneath, wood of a floor). This is because having a metal roof, exposed to the elements, above a Barn Swallow nest, can cause nestling mortality and nest failure (Anthony and Ely 1976); having a failed nest would reduce the chances of having multiple broods in a time limited breeding season.

### Statistical Analyses

To determine the relationship between the factors of interest and the probability of multiple brooding (which ultimately dictates the incidence of the behaviour), I fitted a hierarchical Bayesian linear model with a binomial distribution and logit link. Using a hierarchical model is appropriate because it takes into account variation that is due to clustering at different levels, (i.e. site, year) and improves estimates by learning from other clusters (McElreath 2020). It also improves estimates with small and unbalanced sample sizes because it accounts for variation between clusters without allowing the sites with the most buildings, or years with the most sites, to dominate estimates (McElreath 2020). In my models, I included year, site and building (nested within site) as levels (random factors).

For inclusion in my hierarchical model, all factors needed to vary at a single level. Weather variables were the only factors to vary both across sites and year. Therefore, for inclusion at the site level, I averaged the number of cold days, total precipitation and mean wind gust across all years, at each site (Table 2.2). For inclusion at the year level, I averaged the number of cold days, total precipitation and mean wind gust across all sites, in each year (Table 2.3). To reduce the number of weather related variables, I then conducted a principal components analysis on each set of variables (site or year level), and included the first two components from each, which accounted for >90% of the variation in the data (Tables 2.4 and 2.5).

To determine the effect of each factor on the probability of multiple brooding (MB), I first constructed a full hierarchical model (Equation 1), including all weather, landcover, livestock and roof variables. At the year level (*y*), I included the principal components from the analysis of the annual variation in weather. At the site level (*s*), I included the principal components from the analysis of spatial variation in weather, the presence of livestock and landcover. While I included the extent of human, wooded and open landcover as proportions in the model, I included only the presence or absence of wetland or row crop land cover, because they were found in low proportions, at relatively few sites (Figure 2.1). Lastly, at the building level (*b*), I included the presence of a metal roof above nests. All presence-absence variables were included as dichotomous variables (present=1, absent=0), and I centered and standardized all other variables to better compare the effects of each on the probability of multiple brooding.

Equation 1:

$$MB \sim Binomial(n, p_{ybs})$$

$$\begin{aligned} logit(p_{ybs}) = {} & \alpha_0 + \alpha_{0,bs} + \alpha_{0,y} + \beta_1 ROOF_b + \beta_2 WEATHst1_{bs} + \beta_3 WEATHst2_{bs} \\ & + \beta_4 WETLAND_{bs} + \beta_5 HUMAN_{bs} + \beta_6 WOODED_{bs} + \beta_7 OPEN_{bs} \\ & + \beta_8 LIVE_{bs} + \beta_9 WEATHyr1_y + \beta_{10} WEATHyr2_y \end{aligned}$$

$$\alpha_{0,bs} \sim Normal(\alpha_{0,s}, \sigma_{0,bs})$$

$$\alpha_{0,s} \sim Normal(0, \sigma_{0,s})$$

$$\alpha_{0,y} \sim Normal(0, \sigma_{0,y})$$

$$\alpha_0 \sim Normal\ (0,1.5)$$

$$\beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \beta_6, \beta_7, \beta_8, \beta_9, \beta_{10} \sim Normal(0,1.5)$$

$$\sigma_{0,bs}, \sigma_{0,s}, \sigma_{0,y} \sim Exponential(1)$$

$$where\ b = 1 \dots 60, s = 1 \dots 18, y = 1 \dots 5$$

In addition to the full model, I also constructed an intercept only model, and three other models that included only the building, site or year level variables in addition to random intercepts (equations in Appendix B). I compared the fit of these models using the difference in the models' Pareto smoothed importance sampling leave-one out cross-validation (PSIS-LOO; Vehtari et al. 2017) values and model weights based on the LOO value. For each model, there were observations with a pareto k>0.7, which suggests these points could have an undue influence on the model and can be problematic for PSIS-LOO (Vehtari et al. 2017). Therefore, I used moment matching, which is an alternative sampling method that can better include the problematic observations, to get better measures of model fit (Paananen et al. 2020). For each model, I also assessed if the inclusion of covariates explained the variability observed between building, sites and years by comparing the variation among building, site and year levels ($\sigma_{\text{building}}$, $\sigma_{\text{building:site}}$, $\sigma_{\text{year}}$) to the variation observed in the intercept only model; a perfect model would reduce the variation in each level to zero.

I fit models using the ‘brms’ package (Bürkner 2017) in R 4.0.2 (R Core Team 2020). This package fits models using Hamiltonian Monte Carlo process, through Stan (Carpenter et al. 2017). I used regularizing priors to set constraints on the possible range of parameters and reduce the risk of overfitting (McElreath 2020): all sigma priors were set to *Exponential*(1) and beta and intercept priors were set to *Normal*(0,1.5). For each model, I ran four chains, of 4000 iterations, including 1000 warmup iterations, which resulted in 12,000 samples. For each model, I ensured model convergence through examination of the Gelman-Rubin statistic (less than 1.01) and trace plots. To assess model fit, I used posterior predictive checks to compare fitted and observed values (Figures can be found in Appendix B).

To interpret the effect of each variable, I report the estimate and 90% credible interval (CI). A variable was determined to have strong support for an effect on multiple brooding if the 90% CI did not overlap zero, and the further the distribution was from zero, the stronger the effect.

## 2.4 Results

I determined the incidence of multiple brooding in 60 buildings across 18 sites, though not all sites were visited in each of the five years of study (see Chapter 1). The mean number of multiple brooded pairs within each building was 0.7 pairs (range: 0-7). Overall, in 114 building-year combinations, 81 of 311 pairs (26%) were multiple brooded (Figure 2.2). Based on the intercept only model, and thus controlling for imbalances between buildings, sites and years, the mean probability of multiple brooding was 0.22 (0.14-0.31 90% CI).

The best fit model included only site level parameters (weather, landcover and presence of livestock; Table 2.6). The other models were not competitive because the ΔLOO >2 , though they did have relatively large errors (Table 2.6). The inclusion of the site level parameters considerably decreased the building, and building nested in site level variability (Table 2.7).

Based on the site level model, weather affected the probability of multiple brooding (Figure 2.3). There was a positive effect of the first principal component (WEATHst1), corresponding to sites with fewer cold days and less precipitation and the second component (WEATHst2), corresponding to sites with weaker wind gusts, on the probability of multiple brooding (Figure 2.3). However, there was little support for an effect of weather at the year level, as it was excluded from the top model. Furthermore, in the full model, the coefficient estimates for the first component (WEATHyr1), corresponding to years with more cold days and weaker wind gusts, and the second component (WEATHyr2), corresponding to years with high precipitation, considerably overlapped zero (Figure 2.4). Therefore, warmer and drier sites, and less windy sites were associated with an increased probability of multiple brooding, while annual differences in weather did not have an effect.

Landcover also affected the probability of multiple brooding. In the site level model, there was a negative effect of human landcover (roads and buildings), on the probability of multiple brooding (Figure 2.3). Given the posterior estimate (-0.59), an increase of approximately 4 hectares of human related landcover within a 400m radius of a breeding site would mean that a Barn Swallow was 55% as likely to be multi-brooded. In contrast, there was no support for an effect of the presence wetlands or row crops, or changing proportions of wooded or open landcover on the probability of multiple brooding (Figure 2.3).

Lastly, there was also little support for an effect of the presence of livestock and metal roofs directly above nests on the probability of multiple brooding. While the presence of livestock was included in the best model, the coefficient spanned zero (Figure

2.3). In contrast, the presence of a metal roof was not included in the best model, and in the full model, the coefficient also spanned zero (Figure 2.4).

## 2.5. Discussion

The goal of my study was to determine the extrinsic factors associated with multiple brooding in Barn Swallows. Overall, I found that weather and land cover characteristics at breeding sites influenced the probability, and therefore incidence, of multiple brooding. Specifically, I found that warmer, drier and less windy sites were associated with an increased probability of multiple brooding, while sites with more human based landcover such as roads and buildings were associated with a decreased probability of the behaviour. These factors likely influence the timing of breeding, and the availability of food, which are critical in determining multiple brooding behaviour across many species of birds (Nagy and Holmes 2005b, Safran 2006, Weggler 2006, Bulluck et al. 2013, Jacobs et al. 2013, O'Brien and Dawson 2013, Townsend et al. 2013, Béziers and Roulin 2016, Drake and Martin 2018). In contrast, I found that annual variation in weather, in addition to the presence and extent of other landcover types and the presence of livestock and metal roofed buildings, did not affect multiple brooding.

### Weather

Consistent with my predictions, I found that variation in spring weather across sites affected the probability of multiple brooding. Specifically, the probability increased at sites with fewer cold days, less precipitation and less wind in May and June. This is consistent with studies of other species. For example, Western Bluebirds (*Sialia 21exicana*) had an increased incidence of multiple brooding when the breeding season was warmer and drier (Jacobs et al. 2013), and warm springs also increased the incidence of multiple brooding in Prothonotary Warblers (*Protonotaria citrea*; Bulluck et al. 2013). The effect of wind on the probability of multiple brooding has not been previously examined.

There are two likely mechanisms by which weather could impact multiple brooding. Flying insects, the primary Barn Swallow prey, are more active with warmer, less rainy and less windy days (Bryant 1975, Grüebler et al. 2008, White 2008, Winkler et al. 2013). Therefore, warmer, drier and less windy sites would have fewer days marked by poor foraging conditions, and would potentially have more multi- brooded pairs since more resources are allocated towards reproductive behaviours when conditions are good (Schifferli et al. 2014). While numerous studies of other songbirds found that greater food availability increases the incidence of multiple brooding (Black-throated Blue Warblers, *Setophaga caerulescens*, Nagy and Holmes 2005b; Cactus Wrens, *Campylorhynchus brunneicapillus*, Simons and Martin 1990; Mountain Bluebirds, *Sialia currucoides*, O'Brien and Dawson 2013), the only study to date to look at the relationship between insect abundance and multiple brooding in Barn Swallows found no effect (McClenaghan et al. 2019). However, there could still be an effect of insect abundance at stages of the breeding period (i.e. during arrival, pair formation and nest building) that were not assessed by McClenghan et al. (2019), or during years when insect abundance was lower than the two years examined in the study. Future work examining the interaction between weather and insect abundance, and the subsequent effect on multiple brooding would help investigate this mechanism.

Another mechanism by which weather impacts multiple brooding is by altering the timing of reproduction. Warmer spring weather is nearly universally linked with earlier breeding in Barn Swallows (Møller 2008) and other species of birds (Jacobs et al. 2013, Townsend et al. 2013, Drake and Martin 2018). In turn, early breeding extends the breeding season and increases the incidence of multiple brooding in many species (Ogden and Stutchbury 1996, Weggler 2006, Bulluck et al. 2013). Spring weather can also dictate when food is available (i.e. needs to be threshold temperature for insect activity, Lahlah et al. 2006, Winkler et al. 2013), and as such, the timing of reproduction could be related to when food becomes more abundant. Therefore, variation in spring weather could have affected the probability of multiple brooding by affecting food availability and the timing of breeding.

It is important to highlight that the effect of weather on multiple brooding was only based on variation in weather between sites, and I did not find an effect of weather between years. This may be because there was less variation, particularly in temperature, between years than between sites (Tables 2.2 and 2.3).

### Land Use

Consistent with my prediction, I found that the probability of multiple brooding decreased with increases in the proportion of human related infrastructure, such as roads and buildings, within 400m of the breeding sites. In fact, a 4 hectare increase in the amount of human landcover would mean a Barn Swallow was 55% as likely to be multi-brooded. While no studies have directly addressed the influence of such infrastructure, or other types of landcover, on multiple brooding, general habitat quality (often measured by food abundance) does influence multiple brooding in Barn Swallows (Møller 2001) and other species (Nagy and Holmes 2005a,b).

There are a number of possible mechanisms by which an increase in the amount of human infrastructure would decrease the probability of multiple brooding. First, an increase in the amount of human infrastructure likely decreases insect abundance (Teglhøj 2017), leading to less energy to allocate to reproduction and therefore reducing the probability of multiple brooding (Stearns 1992). Indeed, in Denmark, there were fewer flying insects in urban centers than the edge of urban areas, which ultimately caused decreased nestling mass, and lower fledgling production in Barn Swallows in those areas (Teglhøj 2017). Furthermore, an increase in human landcover could also increase the energy needed to access foraging sites in a more fragmented landscape (Kociolek et al. 2011) and in turn, reduce the energy available to be allocated towards multiple brooding. Another way in which human infrastructure may influence the incidence of multiple brooding is by affecting the intrinsic quality of the swallows that breed at a particular site. Although no research has been done to examine the relationship between the intrinsic quality of swallows at a breeding site and the extent of human infrastructure in the surrounding landscape, sites with more infrastructure are less desirable and lower quality, since Barn Swallows breed at lower densities when there is increased urbanization (Osawa 2015). Therefore, lower quality swallows that would be less prone to have multiple broods, particularly those that are younger and intrinsically breed later (Safran 2004, Saino et al. 2012), may be more abundant at lower quality sites, with more human infrastructure in the surrounding area, and may decrease the incidence of multiple brooding. Together, decreases in insect abundance, increased foraging costs and the presence of lower quality individuals may cause a reduction in multiple brooding at sites where roads and buildings are more prevalent.

Contrary to my predictions, I found no effect of other landcover types on the probability of multiple brooding. The presence of wetlands and row crops, in addition to the extent of wooded and open landcover did not affect multiple brooding, despite their expected effects on habitat quality. Wetlands and open areas, like pastures and hayfields, are generally associated with high insect abundance and are common foraging habitat for insectivorous birds (Møller 2001, Ambrosini et al. 2002, Evans et al. 2007, Grüebler et al. 2008, Davies et al. 2016, Musitelli et al. 2016). Wooded areas are also beneficial, because they can concentrate insects in windy weather, and can therefore be important sources of insects in poor weather conditions (Evans et al. 2007, Henderson et al. 2007, McHugh et al. 2018). Therefore, they would be higher quality sites and would be expected to increase the energy available for multiple brooding. In contrast, row crops are typically associated with lower insect abundance due to the use of pesticides and lack of plant diversity (Evans et al. 2007, Grüebler et al. 2008), and therefore they would be expected to decrease the probability of multiple brooding.

The most likely explanation for why I only found an effect of human landcover is that insect availability was sufficiently high, regardless of the extent of wetlands, row crops, wooded and open areas. This may be true, because I only expected a negative effect of row crops, which were relatively low in abundance, even at the sites where they were present, on insect abundance. However, without data on insect abundance, this is just a hypothesis.

One limitation of the interpretation of the effect of landcover on multiple brooding is a small sample size. Due to logistical reasons, it was not possible to have as large a sample size as desired. Row crops and wetlands were only found in the vicinity of breeding sites at ten and seven sites, respectively. Therefore, the results should be interpreted cautiously.

### Livestock

Contrary to my prediction, the probability of multiple brooding was not related to the presence of livestock near breeding sites. This contradicts prior research in Europe that found that livestock are associated with a higher incidence of multiple brooding (Møller 2001, Grüebler et al. 2010). A positive effect of livestock would be expected because livestock are nearly always associated with greater insect abundance (Møller 2001, Ambrosini et al. 2002, Evans et al. 2007, Grüebler et al. 2008, Orłowski and Karg 2013, Musitelli et al. 2016). Further, the presence of livestock increases the temperature of buildings where swallows nest (Ambrosini and Saino 2010), and is associated with the presence of higher quality breeders (Ambrosini et al. 2006 but see Grüebler et al. 2010). Therefore, livestock are expected to either increase the energy available to allocate towards reproduction, extend the breeding season or increase the quality of the breeding pairs at a site.

One possible explanation for why I did not find an effect of livestock was the scale at which I considered their presence. Grüebler et al. (2010) found an effect of livestock on multiple brooding, but specifically when the livestock were housed in the same space as nests. I considered the presence of livestock at a site level and not within buildings. Therefore, the benefit of livestock on multiple brooding may come primarily from having a warmer microclimate in buildings where swallows and livestock coexist (Saino et al. 2002), rather than the any impacts the livestock may have on insect abundance in the surrounding area. Furthermore, Grüebler et al. (2010) and Møller (2001) focused on cattle and pig, and intensive dairy farms, respectively, while all but two of my sites where livestock were present were hobby farms, with generally few animals (i.e. two horses or five cows). Therefore, the number and type of livestock may play a role in leveraging their effect on multiple brooding.

Another possible explanation for why my results differed from Møller (2001) and Grüebler et al. (2010) is because of differences in the extent of livestock farming in the Barn Swallow's breeding range in North America compared to Europe, where nearly all of the reference studies are done. For example, in 2016 the density of livestock per hectare of total land area in the United Kingdom, compared to New Brunswick, was 44 times larger for cattle (0.4/ha in UK, 0.009/ha in NB) and 1,400 times larger for sheep (1.4/ha in UK. 0.001/ha in NB; Department for Environment Food and Rural Affairs 2016, Province of New Brunswick 2017). Such differences in the density of livestock may alter the selective pressures placed on the Barn Swallows and alter their response to livestock.

### Roof

Finally, contrary to my prediction, the probability of multiple brooding was not related to the presence of a metal roof directly above Barn Swallow nests. While no studies have assessed the impact of roofing material on multiple brooding, metal roofs can alter the microclimate and increase temperatures at nests in close proximity to the surface (Tate 1986; Mann, unpublished data). Such high temperatures were shown to induce Cliff Swallow (*Petrochelidon pyrrhonota*) chick mortality (Imlay et al. 2019b), and likely induce mortality in Barn Swallows as well (Anthony and Ely 1976, Tate 1986). If nests fail, pairs would be unable to have multiple broods. However, one explanation for why I did not find an effect is that other factors, such as shading, ventilation, and the distance between a nest and the roof, play an important role in moderating the thermal effects of metal roofs. Further research into how architectural features affect breeding Barn Swallows would be beneficial to determine any conservation implications.

### Limitations of study

My study successfully identified the effect of a number of extrinsic factors that explained a substantial portion of the inter-site variation in the probability of multiple brooding. However, there was unexplained variation in the model, especially between years, which suggests that there are other factors I did not consider. One factor that I did not examine, that may affect multiple brooding is winter weather. Winter precipitation on breeding grounds can vary significantly year to year, and can impact insect abundance (Finn and Poff 2008, Templer et al. 2012). Furthermore, Imlay et al. (2018) found that Barn Swallows in the Maritimes bred earlier after winters with less precipitation. Given the importance of food availability and timing to multiple brooding, the inclusion of winter weather in my model could improve its ability to predict annual changes in the incidence of multiple brooding. Other factors that I did not examine that likely affect multiple brooding are carry over effects from other aspects of the life cycle. Indeed, Imlay et al. (2019a) found that Barn Swallows in the Maritimes bred earlier depending on where they spent their non-breeding season, as determined by stable isotopes. Depending on conditions during their migration or non-breeding season, Barn Swallows may vary in their probability of double brooding across years. The inclusion of other information in the model, such as winter weather and carry over effects, could create a model that is better able to explain differences in the incidence of multiple brooding from year to year.

## 2.6 Conclusions

This study emphasizes the importance of extrinsic factors in the determination of multiple brooding in the Barn Swallow. Based on my results, multiple brooding is more likely to occur at warm, dry and less windy sites, with fewer roads and buildings in close proximity to the breeding sites. Without information on insect abundance and clutch initiation dates, for example, it is not possible to determine the mechanisms by which these factors impacted multiple brooding. Nonetheless, sites with these features should be preferentially maintained as high quality breeding habitat.

This study also provides more evidence that the incidence of multiple brooding is likely to change in the future. Roads, parking lots and new houses are likely to become more prevalent around Barn Swallow breeding sites, especially in suburban areas, due to urban sprawl. To reduce the risk of deteriorating swallow breeding site quality, informed conservation strategies need to recognize the importance of Barn Swallow colonies that are not surrounded by such landcover. If they do not, we are at risk of reducing the incidence of multiple brooding through our actions. Further, climate change will likely increase global mean temperature from 1986-2005 by up to 3°C by the end of the century, and will result in fewer cold temperature extremes (Collins et al. 2013). Such climatic change will likely shift the regions in the Maritimes that typically had more cold days in the spring to more closely match the weather in the warmer regions, which may increase the incidence of multiple brooding. However, we also expect increased precipitation in the future (Collins et al. 2013), which would not increase multiple brooding, based on my findings. There will likely be complex relationships between multiple brooding and climate change in the future, that would be worthwhile to monitor.

## 2.7 Tables

**Table 2.1**- Categories of landcover classified within a 400m radius of breeding sites.

| category | description |
|---|---|
| open | pastures, grass, hayfields, mowed lawns |
| row crops | row crops (i.e. corn, soybeans, vegetables), orchards |
| open water | ponds, rivers and lakes |
| wetland | bogs, fens, open marsh, peatland, swamp |
| wooded | tree cover 25-100% |
| human | roads (paved and gravel), driveways, parking lots, buildings |

**Table 2.2**- Summary of the variation in building and site level extrinsic factors, including the mean and standard deviation (SD) of weather variables across all sites. Weather based parameters are averaged across years, and multiple sites used weather data from the same weather station.

| site | livestock present | buildings with metal roofs above nests (total number buildings) | total precipitation (mm) | mean maximum wind gust (km/h) | number of cold days |
|---|---|---|---|---|---|
| PV | Y | 1 (3) | 249 | 42.9 | 29.6 |
| DW | N | 0 (5) | | | |
| GA | Y | 1 (4) | 207 | 45.4 | 37.0 |
| WE | Y | 5 (15) | | | |
| JB | Y | 0 (1) | 222 | 43.7 | 33.4 |
| BK | N | 0 (1) | | | |
| ET | Y | 1 (6) | | | |
| KR | N | 1 (2) | 193 | 41.1 | 24.2 |
| LN | Y | 2 (2) | | | |
| MX | Y | 3 (3) | | | |
| DT | N | 0 (1) | | | |
| CM | Y | 1 (2) | 219 | 40.9 | 31.8 |
| OM | Y | 0 (1) | | | |
| MT | Y | 0 (1) | | | |
| HH | Y | 0 (2) | | | |
| HF | Y | 1 (3) | | | |
| LI | Y | 3 (4) | | | |
| WB | N | 1 (3) | | | |
| mean (SD) | | | 218 (21) | 42.8 (1.9) | 31.2 (4.7) |

**Table 2.3**- Annual variation in weather, including the mean and standard deviation (SD) across years. Precipitation, wind and temperature data were averaged across sites for each year.

| year | total precipitation (mm) | mean maximum wind gust (km/h) | number of cold days |
|---|---|---|---|
| 2014 | 212 | 40.5 | 31.2 |
| 2015 | 234 | 44.8 | 30.0 |
| 2016 | 157 | 42.9 | 29.4 |
| 2018 | 252 | 45.1 | 29.2 |
| 2019 | 234 | 40.7 | 36.2 |
| mean (SD) | 218 (37) | 42.8 (2.2) | 31.2 (2.9) |

**Table 2.4**- Loadings and summary of the principal components analysis on spatial variation in weather. Bold values highlight the landcover categories with the highest loadings for each component. Component one (WEATHst1) was consistent with warmer, drier sites, while component two (WEATHst2) was consistent with less windy sites.

| variable | component | |
|---|---|---|
| | WEATHst1 | WEATHst2 |
| number of cold days | **-0.69** | -0.11 |
| total precipitation | **-0.67** | -0.25 |
| mean wind gust | -0.26 | **-0.96** |
| eigenvalue | 2.03 | 0.93 |
| standard deviation | 1.43 | 0.97 |
| cumulative variance explained | 0.68 | 0.99 |

**Table 2.5**- Loadings and summary of the principal components analysis on annual variation in weather. Bold values highlight the landcover categories with the highest loadings for each component. Component one (WEATHyr1) was consistent with colder, less windy years, while component two (WEATHyr2) was consistent with wetter years.

| variable | component | |
|---|---|---|
| | WEATHyr1 | WEATHyr2 |
| number of cold days | **0.70** | 0.29 |
| total precipitation | -0.02 | **0.92** |
| mean wind gust | **-0.71** | 0.29 |
| eigenvalue | 1.70 | 1.15 |
| standard deviation | 1.30 | 1.07 |
| cumulative variance explained | 0.57 | 0.95 |

**Table 2.6-** Comparison of models predicting the probability of multiple brooding (MB), based on Leave One Out Criterion (LOO). ΔLOO is the difference in LOO between the best model (smallest LOO) and a given model; a smaller ΔLOO indicates smaller improvement in model performance, in addition to a larger model weight. Values are shown with the standard error.

| model name | model | LOO[1] | ΔLOO | weight |
|---|---|---|---|---|
| site level | MB~ (1\|building:site)+(1\|year) + WEATHst1+ WEATHst2+ wetland +human + wooded + open +livestock | -116.9 (12.0) | 0 | 0.91 |
| building level | MB~ (1\|building:site)+(1\|year) + roof | -120.1 (11.7) | -3.2 (4.9) | 0.04 |
| full | MB~ (1\|building:site)+(1\|year) + roof + WEATHst1+ WEATHst2+ wetland + human + wooded + open +livestock + WEATHyr1 + WEATHyr2 | -120.4 (12.7) | -3.5 (1.4) | 0.03 |
| intercept | MB~ (1\|building:site)+(1\|year) | -120.6 (11.7) | -3.7 (5.1) | 0.02 |
| year level | MB~ (1\|building:site)+(1\|year) + WEATHyr1 + WEATHyr2 | -122.9 (12.1) | -6.1 (5) | 0 |

[1] Based on expected log pointwise predictive density (elpd_loo)

**Table 2.7-** Comparison of models predicting the probability of multiple brooding, based on the variation ($\sigma$) among buildings (*b*), buildings nested in sites (*bs*), and years (*y*). A better model would explain more variation within levels (i.e. building, year), and would have a smaller $\sigma$. Values are shown with the standard error.

| model | $\sigma_b$ | $\sigma_{bs}$ | $\sigma_y$ |
|---|---|---|---|
| site level | 0.39 (0.31) | 0.39 (0.31) | 0.36 (0.30) |
| building level | 0.54 (0.37) | 0.58 (0.38) | 0.36 (0.29) |
| full | 0.40 (0.32) | 0.41 (0.32) | 0.60 (0.48) |
| intercept | 0.59 (0.38) | 0.55 (0.37) | 0.39 (0.31) |
| year level | 0.58 (0.38) | 0.54 (0.37) | 0.59 (0.59) |

## 2.8. Figures

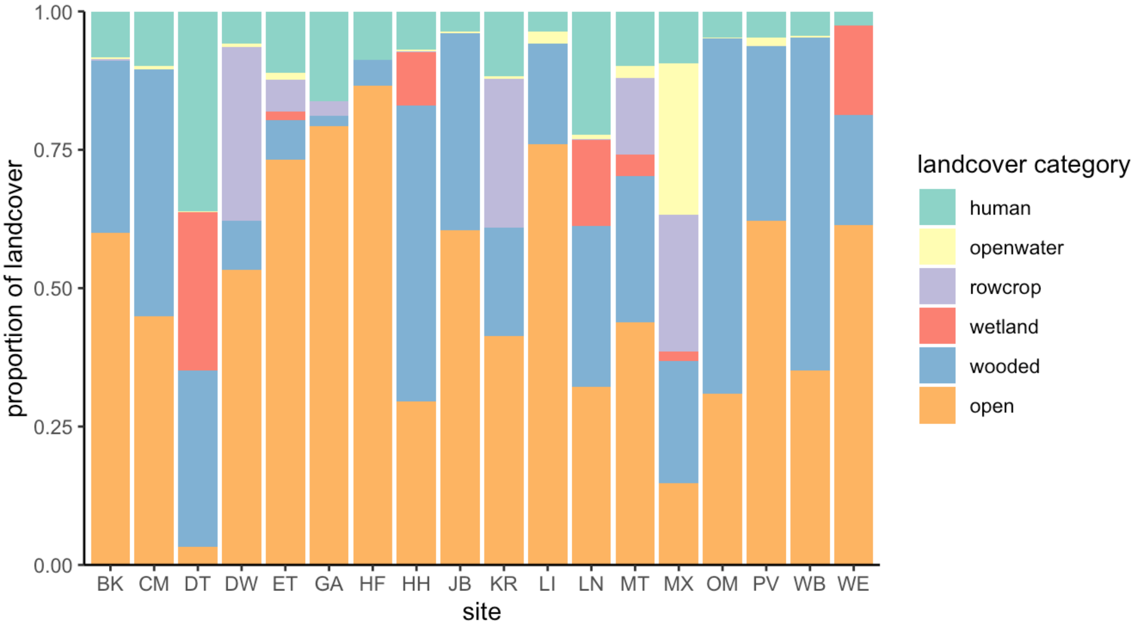


**Figure 2.1**- Proportion of landcover found across all breeding sites.

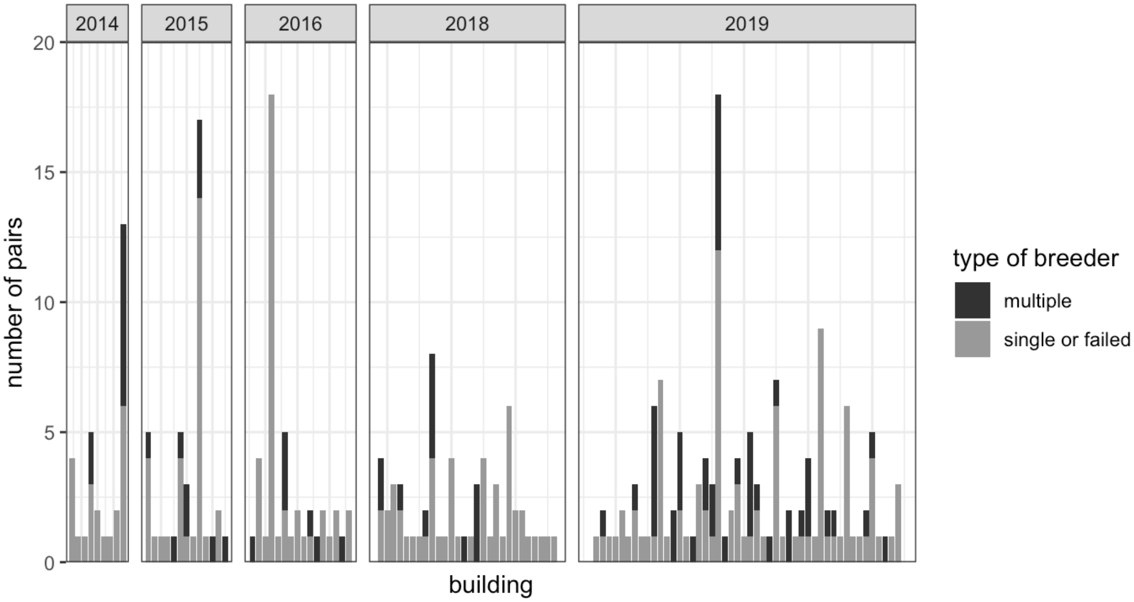


**Figure 2.2**- Incidence of multiple and single or failed Barn Swallow pairs across 60 distinct buildings, over five years.

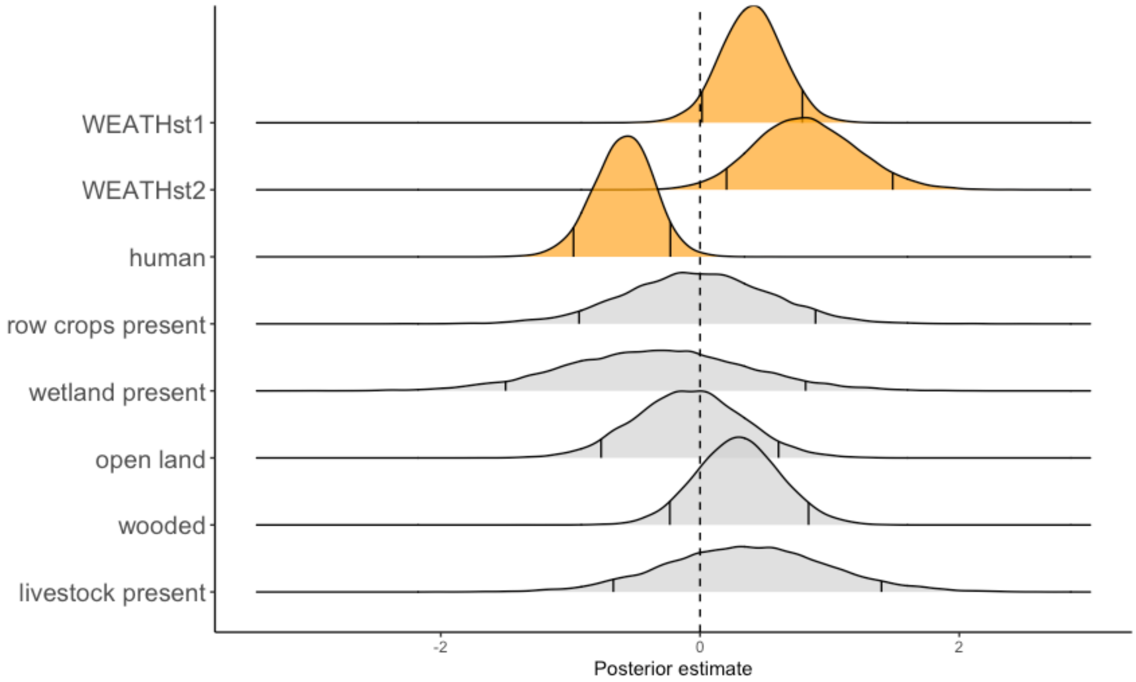


**Figure 2.3-** Posterior distributions of the effect of factors on the probability of multiple brooding, from the best model including only site level factors. The vertical lines within each distribution represent the lower and upper bounds of the 90% credible interval. The factors where the credible interval did not overlap 0, and therefore had the strongest support for an effect, are coloured in orange.

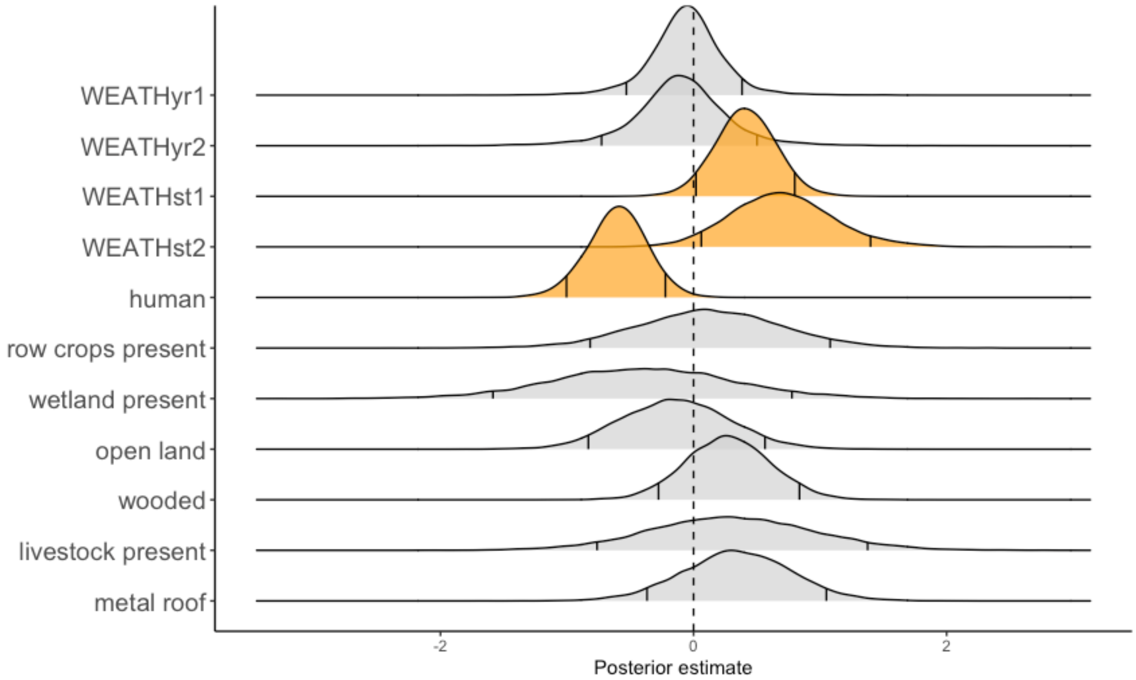


**Figure 2.4-** Posterior distributions of the effect of factors on the probability of multiple brooding, from the full model including building, site and year level factors. The vertical lines within each distribution represent the lower and upper bounds of the 90% credible interval. The factors where the credible interval did not overlap 0, and therefore had the strongest support for an effect, are coloured in orange.

# Chapter 3: Influence of Multiple Brooding on Population Growth Rates

## 3.1 Abstract

Understanding which demographic rates strongly influence population growth can inform effective conservation strategies. While studies often assess the relative influence of reproductive and survival rates on population growth, there is typically limited attention given to the specific influence of behaviours that can alter these reproductive and survival rates. For instance, few studies have quantified the potential effect of changes to the proportion of multi-brooded pairs in a population on population growth rates, despite the fact that the behaviour can have a large impact on reproductive success. Therefore, I determined the influence of multiple brooding on the growth rate of a population of Barn Swallows (*Hirundo rustica*), a small, short lived aerial insectivore. Using reproductive monitoring and mark-recapture data from breeding sites in New Brunswick and Nova Scotia, Canada, I estimated six demographic rates: fledgling production of single and multi-brooded birds, the proportion of failed and multi-brooded breeders, and adult and hatch year survival. I then constructed a two stage matrix population model and used life stage simulation and perturbation analyses to determine the sensitivity of the population growth rate to changes in each rate. I found that multiple brooding positively influenced population growth, with a 7% increase in the proportion of multi-brooded pairs associated with a 0.023 (± 0.009 SD) increase in the population growth rate. However, both adult and hatch year survival were stronger drivers of the population growth rate, with, for example, a 7% increase in hatch year survival associated with a 0.15 (± 0.014 SD) increase in the population growth rate. My results suggest that conservation interventions targeting hatch year and adult survival rates would be the most effective method of improving growth in this population. Although less effective, efforts to increase the rate of multiple brooding could, nonetheless, help stabilize or improve population growth rates, and potentially buffer negative effects of ecological change on other demographic parameters.

## 3.2 Introduction

The need for effective conservation strategies is greater now than ever before. An estimated 30% of terrestrial vertebrate species are experiencing population declines (Ceballos et al. 2017), largely due to human induced threats such as pollution, overexploitation, habitat loss and climate change (Stuart et al. 2004, Arthington et al. 2016, Stanton et al. 2018, Falaschi et al. 2019, Sánchez-Bayo and Wyckhuys 2019, Spiller and Dettmers 2019). These threats have caused the rapid acceleration of extinction rates across all taxa (Pimm et al. 2014, Ceballos et al. 2015), and their impacts are expected to worsen in the future (Tilman et al. 2017) .

Many conservation strategies effectively reduce extinction risk (Monroe et al. 2008, Hoffmann et al. 2010). Strategies are effective when they improve demographic rates like reproductive success and survival, which may be impacted by human induced threats and ultimately dictate population growth rates. However, to direct resources and attention towards the strategies that would have the greatest impact, it is essential to know which parameters ultimately drive population change, by having the strongest influence on population growth rates (Caswell 2000). Such efforts have informed conservation strategies across taxa (Crouse et al. 1987, Chapron et al. 2003, Gerber et al. 2004, Buehler et al. 2008).

Differences in behaviours and life history strategies between species impact the relative influence of demographic rates on population growth. Among many songbird species, changes in adult and hatch year survival rates are the major drivers of population growth (Buehler et al. 2008, Walker et al. 2016, Cox et al. 2018, McHugh et al. 2018, Taylor et al. 2018). However, changes in reproductive rates may be more influential for those for species of birds further to the ‘fast’ end of life-history continuum (Sæther et al. 1996), characterized by earlier maturation, higher reproductive success and lower survival rates (Saether and Bakke 2000, Clark and Martin 2007). While these patterns are often observed between species, populations within a species that show higher rates of reproductive success may also be more influenced by changes to reproductive rates than survival (Buehler et al. 2008). As such, behaviours that increase reproductive success could be drivers of changes to population growth.

Multiple brooding is one behaviour that increases reproductive success (Ogden and Stutchbury 1996, Weggler 2006) and is found in many songbird species. Multiple brooding occurs when an individual initiates a new clutch following a successful breeding attempt (Carro et al. 2014). By shortening the inter-brood period and therefore producing additional broods in a limited time frame, multiple brooding can double or triple the number of fledglings produced annually and is an important component of reproductive success in many species (Ogden and Stutchbury 1996, Weggler 2006, Townsend et al. 2013, Cornell and Williams 2016). Therefore, changes in the rate of multiple brooding may drive changes in population growth rates in species where reproductive rates influence population growth.

It is particularly important to understand the effect of multiple brooding on population growth because ecological changes are expected to alter the rate of the behaviour in the future. Warmer springs are expected to extend the breeding season and subsequently increase the frequency of multiple brooding (Halupka and Halupka 2017). Indeed, increases in the frequency of double brooding have already been observed in Reed Warblers (*Acrocephalus scirpaceus*; Halupka et al. 2008) and European Barn Swallows (*Hirundo rustica rustica*; Engen et al. 2001), likely due to climate change (but see Husby et al. 2009). If multiple brooding substantially influences population growth rates, such increases in the incidence may help stabilize or increase population size in multi-brooded species that would otherwise decline.

Despite the potential implications of multiple brooding on population growth rates, the impact of the behaviour on reproductive success and population growth often receives little attention. Indeed, it is often not incorporated into calculations of reproductive success or is combined with renesting rates (Thompson et al. 2001, Robinson et al. 2014 but see Podolsky et al. 2007, Schaub et al. 2015). Yet, given the potential contribution of multiple brooding to reproductive rates and the expected changes to the behaviour in the future, conservation strategies aimed at multi-brooded species would benefit from research into the effect of multiple brooding on population growth rates.

Therefore, my overarching goal for this study was to assess the influence of multiple brooding on population growth rates of Barn Swallows (subspecies *H.r.*

*erythrogaster*) in the Canadian Maritimes. Barn Swallows breeding in this region show some of the steepest population declines in North America (Nebel et al. 2010, Smith et al. 2019). The likely causes for these declines in this small, aerial insectivore include factors such as climate change, contaminants, reductions in insect availability and habitat loss (COSEWIC 2011, Imlay and Leonard 2019, Spiller and Dettmers 2019). While this species is known to have two broods per year in the region (Imlay et al. 2019a), there are no estimates of the incidence of double brooding nor have the demographic drivers of population growth been identified. Therefore, determining the relative influence of multiple brooding, and other demographic rates, will help inform conservation actions for this species in the region.

Studies on the drivers of population growth in European Barn Swallows suggest that multiple brooding, and reproduction in general, may not play an important role in determining population growth rates (Schaub et al. 2015). In Switzerland, for example, population growth was highly influenced by adult survival and immigration, and reproductive parameters, including multiple brooding, had little influence on population growth rates (Schaub et al. 2015). This is typical of populations with natal dispersal that are located in relatively small geographic areas, where immigrants are often an important source of new recruits into a population, and are highly influential to population growth (Matthysen et al. 2001, Pasinelli et al. 2011). However, if the geographic scale were broadened and a greater proportion of recruits were hatched in the population, changes in reproductive rates, rather than changes to immigration rates, would have a stronger influence on the number of recruits (Matthysen et al. 2001, Robinson et al. 2003). Then, the influence of multiple brooding, and reproductive success in general, on population growth rates should increase (Matthysen et al. 2001, Schaub et al. 2006, 2015, Robinson et al. 2014). Without estimates for many demographic rates, such as survival or the proportion of multi-brooded pairs, for the Maritimes, it is difficult to know how the different demographic rates influence population growth rates in that region. However, because I am considering a broader spatial scale than Schaub et al. (2015), I do expect that multiple brooding may have a stronger influence over population growth.

My specific objective was to determine how changes to the proportion of multi-brooded pairs influences population growth rates, both relative to other reproductive and survival rates, and in terms of the magnitude of the response. To reach this objective, I first determined the population’s demographic rates, including fledgling production of single and multi-brooded birds, the proportion of failed and multi-brooded breeders, and adult and hatch year survival, using reproductive monitoring from 2014-2016 and 2018-2019, and mark-recapture data from 2012-2019. Then, I created a stage based matrix population model and conducted a life stage simulation analysis (LSA) and perturbation analyses to determine the relative importance of the proportion of multi-brooded breeders, compared to the other rates, and the expected change in population growth rates given changes to each reproductive and survival rate.

## 3.3. Methods

### Determination of demographic rates

To estimate demographic rates, I used data collected from breeding sites in New Brunswick and Nova Scotia between 2012 and 2019.

*Estimates of reproductive success*

To estimate the number of fledglings from multi-brooded (initiate nest following a successful nest) and single brooded individuals (one successful nest), and the proportion of failed breeders (no fledglings from any nest), I monitored breeding activity at up to six sites from 2014-2017 and 2018-2019. I visited these sites every 2-3 days from mid-May until the end of August, during which, I recorded the number of eggs or nestlings in each nest (n=306 nests). I used the number of nestlings at day 12 (hatch day= day 1) as a proxy for the number of fledglings from a nest, because survival after this point is typically extremely high (>95%; Ambrosini et al. 2012). I removed dead nestlings that I encountered after day 12 from the final count (n = 17 nests), and considered a nest successful if at least one chick fledged. Then, I determined if each nest belonged to a single, multi-brooded or failed female. I assigned nests based on the female parent because they are more reliably caught than males, so I have more data on individual breeding behaviour of females than males. Furthermore, extra pair paternity is common in North American Barn Swallows (22-42% of nestlings sired by extra-pair copulation; Robinson et al. 2014, Schaub et al. 2015) and therefore, the social father may not be the offspring's genetic parent.

To assign each nest to a parent, I applied a small amount of non-toxic paint (All-Weather Paintstik, LA-CO Ltd.) of different colours to the rim of all active (containing eggs or nestlings) nests at a site. Then, I captured adult swallows using mist nets and assigned them to a nest by matching the colour of paint that had been transferred to their feet or feathers to the nest corresponding with that colour. I identified females by the presence of a brood patch. Occasionally, nests were inaccessible and could not be painted. Therefore, to identify which adult attended those nests, when I caught birds with no paint, I applied paint to the underside of their tail and used binoculars to observe the nest at which they were incubating or provisioning.

In 67 of 306 nests, I could not assign the nest to a female. For 17 of these nests, there were no other nests in the same building that were active before or after the nest in question; therefore, I assumed these nests were the sole nesting attempts of the parent. For the other nests, I made a series of assumptions to identify which nest belonged to which female, and ultimately determine if they belonged to a single, multiple or failed brooder. First, if there were multiple nesting attempts in the same nest, I assumed it was the same female (n=14 nests), because nest fidelity is high for females (Shields 1984). Second, if a male bird was assigned to two sequential nests, including a nest with an unknown female parent, I assumed it was the same female for both nests as well because female-male pairs are more likely to remain together than they are to split (n=4 nests; mate switching between nests in 5 of 28 known pairs, unpublished data; also see Shields 1984). Third, if a nest was in a building and there was one nest that preceded or followed the period when the nest with the unknown female was active (including incubation and nestling stages), I assumed that both nests had the same female parent (n=12 nests). Fourth, if a nest was in a building and there were multiple nests that preceded or followed the period when the nest was active, but one of those multiple nests was in closer proximity to the original nest I assumed that the closest nest had the same female (n=11 nests), since significant movement between consecutive nesting attempts is limited (modal distance moved between nesting attempts at one site was 1.4m (n=27, mean=3.4m

± 2.5m SD); unpublished data). I excluded 24 nests where I could not determine the type of breeder they belonged to because of uncertainty in the identity of the female parent.

Based on these data, I calculated the mean number of fledglings produced in a given year for single brooded (n=103) or multi-brooded (n=53) females, across all sites. I also calculated the proportion of failed breeders as the number of failed breeders, divided by the total number of females, pooled across sites (not including the 24 excluded nests). However, I excluded 2014 in my estimate of failed breeders, because the high number of excluded nests in this year (n=12) biased the number of failed breeders, and resulted in an unrealistically low proportion (0.03) due to only one observed failed breeder.

To determine the proportion of multi-brooded pairs, I used data from monitoring sites from 2014-2016 and 2018-2019, as well as survey sites from 2019. Details on how I determined the total number, and number of multi-brooded pairs, within a building at each site, can be found in Chapter 1 (General Methods). To determine the proportion of multi-brooded pairs, I pooled the number of multi-brooded pairs from across all buildings and sites, and divided it by the total number of pairs observed in a given year.

*Estimates of Survival*

To determine adult survival, I used mark-recapture data from three sites where birds were captured and banded with a USGS metal band between 2012-2019. I only considered female survival, because subsequent analyses are female based. I excluded females that were caught after 31 July of each year and not assigned to a nest at a breeding site. These individuals were assumed to be individuals from other sites completing pre-migratory movements, and were unlikely to have bred at the site and therefore unlikely to return the following year. Therefore, their inclusion would artificially decrease apparent survival. In total, adult survival estimates were based on recapture data for 143 individuals.

To calculate adult survival in each year, I used a Cormack Jolly Seber model (CJS; Lebreton et al. 1992). CJS models determine apparent survival probability ($\phi$), which is the probability of an individual living and returning to the study area, and recapture probability ($p$), which is the probability of detecting an individual if it returned (White and Burnham 1999). Since breeding site fidelity is typically >99% for Barn

Swallows (Safran 2004, Turner 2004), I expected $\phi$ to be an accurate estimate of actual survival. To determine annual estimates of survival, I constructed a model where apparent survival ($\phi$) was variable over time and recapture probability (p) was constant. I assumed p was constant because there was high capture effort across years, and it was necessary to estimate survival in the final year (White and Burnham 1999). To determine if this model was a good fit of the survival data, I examined the deviance residual plot. I also tested for overdispersion by calculating the variation inflation factor (c-hat; White and Burnham 1999).

I was unable to use data from my field sites to estimate hatch year survival ($\phi_{HY}$) because hatch year Barn Swallows disperse and very rarely return to their natal breeding site in subsequent years (Safran 2004, Brown and Brown 2020). Therefore, I used an estimate of 0.21 from a recent study of Barn Swallows in Ontario (Evans et al. 2020), which is consistent with estimates of hatch year survival of Barn Swallows in Europe (Grüebler et al. 2014). The annual variation in hatch year survival was unknown, so I assumed it was equivalent to the annual variation in adult survival.

### Population Model

To mathematically represent population growth, I created a female based, two stage Lefkovich matrix model (Equation 2). Matrix population models, especially when combined with perturbation analyses, have long been used to determine vulnerability to threats (Wilson and Martin 2012), predict population growth and extinction risk (Calvert et al. 2006, Grüebler et al. 2014, Cox et al. 2018, Gallardo et al. 2019) and identify processes or groups that should be targeted to help population recovery (Calvert et al. 2006, Beissinger et al. 2008, Gallardo et al. 2019).

My model was based on hatch year (HY) and adult (AHY) stages. Since it is conceptually based on a post-breeding census, a hatch year bird would have hatched prior to the census, while an adult was at least one year old, and would have bred prior to the census. The analysis was female based because it is common to consider a single sex to simplify population modelling (Caswell 2001).

There were four main demographic rates in the model: the number of fledglings contributed in the census year by a hatch year ($F_{HY}$) or adult ($F_{AHY}$) bird, and the survival of hatch year ($S_{HY}$) and adult ($S_{AHY}$) birds until the following census year. To contribute young in a given census year, a bird would need to survive through to the next breeding season. Therefore, $F_{HY}$ and $F_{AHY}$ were a product of survival through that stage and per capita rates of reproductive success (total number of fledglings; $R$). In turn, reproductive success was a combination of lower level parameters, including the number of fledglings from single ($b_{SB}$) and multi-brooded ($b_{MB}$) females, the proportion of multi-brooded pairs ($p_{MB}$), and the proportion of single brooded pairs (1-$p_{MB}$- $p_F$, where $p_F$ is proportion of failed breeders).

$$\begin{bmatrix} F_{HY} & F_{AHY} \\ S_{HY} & S_{AHY} \end{bmatrix} = \begin{bmatrix} S_{HY} * R & S_{AHY} * R \\ S_{HY} & S_{AHY} \end{bmatrix} \qquad \text{[Equation 2]}$$

$$\text{Where } R = \left(\left(p_{MB} * \frac{b_{MB}}{2}\right) + (1 - p_{MB} - p_F)\frac{b_{SB}}{2}\right)$$

I made the assumption that reproductive success and survival of all adult birds is equal, irrespective of age. This assumption likely overestimates the reproductive success of hatch years because experienced breeders tend to have higher brood sizes and incidence of multiple brooding (Saino et al. 2012). However, it is not possible to age adult Barn Swallows through plumage or morphometric differences, and monitoring is too limited in the Maritimes to have complete records of age. Therefore, this is a necessary assumption (like with survival in Clark and Martin 2007). Furthermore, I made the assumption that all individuals in the population breed because there is no evidence of non-breeding females (Brown and Brown 2020). Lastly, I assumed that immigration and emigration were equal. There is no information on dispersal in North American Barn Swallows, so we do not know the degree to which they could move and it is also a common assumption among population models (i.e. Cox et al. 2018, Hepp et al. 2020).

To determine the population growth rate, I conducted a Life Stage Simulation Analysis (LSA; Wisdom et al. 2000). A LSA uses a simulation approach to create thousands of iterations of matrix models, by creating random combinations of demographic rates, sampled from representative distributions. A LSA is an improvement over traditional matrix modelling approaches that assume invariable demographic rates, because it creates thousands of iterations of the matrix model that are populated with biologically relevant yet variable estimates of demographic rates, and therefore better reflects stochasticity in population dynamics (Wisdom et al. 2000, Mills and Lindberg 2002). Therefore, I randomly sampled 10,000 values from the distributions of each demographic rate, which were modelled by a Normal distribution defined by the distribution parameters (mean and standard deviation across years) for each demographic rate (Table 1.1). Since the most extreme values in each distribution may represent highly unlikely values, I took the 9500 values that were within the 2.5 and 97.5 percentile quantiles (as in Meehan et al. 2018). Then, I populated 9500 matrices with these random combinations of values and calculated the asymptotic population growth rate (λ) for each matrix. Determined as the dominant eigenvalue of each matrix, the asymptoptic growth rate represents growth rate of the population defined by the particular set of demographic rates, when it would reach a stable age distribution (Caswell 2001).

### *Determining influence of demographic rates*

To determine the influence of each component of reproductive success and survival on population growth rate (λ), I used perturbation analyses to assess the sensitivity of λ to small changes in each demographic rate. The first perturbation analysis I used was elasticity, to assess the relative change in λ expected for proportional changes (i.e. 1% increase) in each demographic rate. An elasticity further from zero, either positive or negative, indicates a stronger influence on population growth rates (Caswell 2001). While elasticity is a mechanistic measure of which rates can theoretically have the largest influence on population change, it does not consider whether proportional changes in each demographic rate are equally as likely in nature, and therefore whether their potential influence is constrained by differences in the natural variability of demographic rates. Therefore, the second perturbation analysis I used was measuring the change in λ resulting from a standard deviation (SD) increase in each rate. This better reflects the natural variability in the system than increases of equal magnitude, which is typically done in standard sensitivity analyses (Caswell 2001, Manlik et al. 2018). The larger the change in λ, the larger the influence of the rate on population growth in nature. I display these results as the expected population growth rate given a one SD increase in each parameter.

All summary statistics are presented as mean (±SD).

### 3.4 Results

The average multi-brooded female produced 75% (±17%) more fledglings than single brooded females in a given year (Table 3.1). Considering the average proportion of failed, single and multi-brooded birds across years, (Table 3.1) multi-brooded pairs would theoretically produce 41% of the fledglings in the population, while representing 24% (± 7% ) of all pairs.

*Population Growth and Perturbation Analyses*

The mean population growth rate for all 9,500 population matrices was 0.93 (±0.15), indicating a decline of 7% per year.

An increase in the incidence of multiple brooding increased the population growth, as indicated by a positive elasticity (Table 3.2). Further, a 7% increase in the proportion of multi-brooded pairs (equal to the standard deviation across years), increased the mean population growth rate by 0.023 (± 0.009), to 0.95 (± 0.16; Figure 3.1). To reach a stable population growth rate (λ=1), the proportion of multi-brooded pairs would need to increase to 0.45, assuming the mean values of all other parameters.

Although multiple brooding had a positive influence, the population growth rate was influenced more by survival than by any component of reproduction, including the proportion of multi-brooded pairs. Both adult and hatch year survival had higher elasticities than any reproductive parameter (Table 3.2), and therefore would have a stronger influence on the population growth rate than a proportional increase in any other rate. Further, a 7% increase in adult and hatch year survival (equal to the standard deviation across years) would increase the mean population growth rate by 0.07 (± 0.0) to 1.00 (± 0.15), and by 0.15 (± 0.014) to 1.08 (± 0.16), respectively (Figure 3.1).This is greater than the expected increase driven by changes to any component of reproductive success when constrained by the variability observed in the study system (Figure 3.1).

Other measures of reproductive success were also more influential over population growth rates than changes to the proportion of multi-brooded pairs. The number of fledglings from adult and hatch year birds had higher elasticities than the proportion of multi-brooded pairs and therefore greater influence on population growth rate (Table 3.2). However, the greatest change in the population growth rate from a change in a reproductive parameter came from the proportion of failed breeders (-0.031 ± 0.010), followed by multi-brooded pairs (Figure 3.1). Therefore, the population growth rate would be changed more by the rate of nest failure than the other components of reproductive success when constrained by the variability observed in the study system.

## 3.5 Discussion

I found that increasing the proportion of multi-brooded pairs would increase the population growth rate, but that improvements in survival would have the greatest influence on population growth rates. In fact, a 7% increase in the proportion of multi-brooded pairs would increase the population growth rate from 0.93 to 0.95, while an equivalent increase in hatch year survival would increase population growth to 1.08 (Figure 3.1). My results suggest that increasing the proportion of multi-brooded pairs in the population could contribute to the recovery of Barn Swallow populations, though the contribution would be small compared to improvements to survival.

I found that although survival had the strongest influence on population growth rates, multiple brooding did positively contribute to population growth based on both perturbation analyses. This result is a consistent with previous work from Switzerland that showed that increases in proportion of multi-brooded Barn Swallows increased population growth rate (Schaub et al. 2015). Similarly, elasticity analyses on a population of Ovenbirds (*Seiurus aurocapilla*) showed the positive influence of multiple brooding on population growth rates (Podolsky et al. 2007). These results are expected because multiple brooding increases the number of fledglings that an individual can produce. In my study, I found that multi-brooded swallows produced 75% more fledglings than single brooders. Similarly, in many other species, multiple brooding increased the number of young produced/individual by 50-100% (i.e. Hooded Warbler, Setophaga citrina, Ogden and Stutchbury 1996; Black Redstart, *Phoenicurus ochruros,* Weggler 2006; European Starlings, *Sturnus vulgaris*; Cornell and Williams 2016). Thus, an increase in the proportion of multiple brooders necessarily increases annual reproductive success and contributes positively to population growth.

To reach stable population growth, 45% of Barn Swallow pairs would need to multiple brood in this population. Although this would be nearly double the current rate of multiple brooding, it is biologically possible. In Denmark, for example, up to 60% of pairs initiate second broods (Møller 1994). Similarly, almost 50% of Barn Swallows in New York (Snapp 1976) and nearly all pairs in Ontario (Peck and James 1987) were historically multi-brooded. There is strong evidence to suggest that warming temperatures due to climate change will result in increases in multiple brooding among birds, including Barn Swallows, in the future due to extended breeding season length (Halupka et al. 2008, Møller et al. 2010, Halupka and Halupka 2017). Indeed, this was the hypothesized reason for a 20-25% increase in the proportion of multi-brooded Reed Warblers in Denmark between the 1970-1980s and 1994-2006 (Halupka et al. 2008). If climate change, in addition to conservation strategies aimed to encourage more multiple brooding (see Chapter 2), helps increase the proportion of multi-brooded Barn Swallows in the population, the population growth rate could be stabilized.

Although there was a clear benefit of more multi-brooded pairs on population growth rates, I found that adult and hatch year survival were more influential. Specifically, elasticities indicated that a proportional change in adult survival would have the strongest influence on population growth rates, while a 7% increase in hatch year survival would result in the greatest improvement in the population growth rate. This is in part consistent with Schaub et al. (2015), which found that Barn Swallows in Switzerland were most strongly influenced by adult survival, using elasticity analyses. However, they found that the influence of hatch year survival was nearly as low as the influence of components of reproductive success because immigration, rather than local reproductive efforts, was an important source of new recruits into the population (Schaub et al. 2015). In my model, I was considering the population at a broader spatial scale, and assumed that any input from immigration would be negligible. However, if there is significant immigration into the Maritime population, I would expect a similar decrease in the importance of hatch year survival, in addition to the influence of multiple brooding and reproduction in general, as immigrants would be a new source of recruits to the population (Schaub et al. 2006, 2015). More research on the dispersal of Barn Swallows in North America would be necessary to assess the full implications of this assumption. Regardless, in both studies, the influence of multiple brooding was small.

One explanation for why I did not find a greater influence of multiple brooding on population growth rates is that despite multiple brooding, reproductive success was too low to compensate for a low hatch year survival rate (0.21). The average swallow would need to successfully breed in two breeding seasons to replace themselves; however, based on my survival rates, there would only be about a 10% chance of a fledgling surviving to that point. Even if the rates of multiple brooding or reproductive success in general were doubled, it would take two years for replacement. This is in contrast to the Black-capped Vireo (*Vireo atricapilla*), another multi-brooded species, where despite lower reproductive success (2.4, fledglings/pair), a significantly higher hatch year survival rate (0.48; Walker et al. 2016) means that reproductive success would only need to increase ~76% for replacement in one breeding season (0.48; Walker et al. 2016). As such, the relative influence of reproduction is higher (Walker et al. 2016). Therefore, multi-brooding, and reproduction in general, would be more influential in Barn Swallows if hatch year survival was higher.

Interestingly, although improvements to survival would clearly have the greatest benefit to population growth, even the modest changes to population growth rates expected from an increase in the proportion of multi-brooded pairs would have important implications for Barn Swallow populations. For example, a 2% annual decline in a population would result in nearly a 20% reduction in the population size over a 10 year period. As such, a 2% increase could substantially improve the population trajectory, even if it is insufficient to reach stable growth. For Threatened Barn Swallows in Canada, even modest improvements in the population growth rate could contribute to the stabilization or recovery of the species.

## Limitations of Study

There are several limitations to this study to consider. First, I had a relatively small sample size to determine demographic rates. With reproduction data from five years and relatively few breeding sites (i.e. two in 2014, up to 16 in 2019), my demographic rate estimates may not be an accurate representation of the population. Using the life stage simulation analysis, rather than a model with a single mean for each demographic rate, helps to integrate uncertainty from sampling into my estimates (Wisdom et al. 2000, Mills and Lindberg 2002), though it does not allow the separation of sampling and process variation. A more sophisticated integrated population model would be able to account for sampling error, and as such, provide a more nuanced understanding of population growth (Schaub et al. 2007).

The second limitation was the use of a hatch year survival estimate from Ontario, rather than a regionally specific estimate. Though the Ontario estimate of 0.21 from Evans et al. (2020) was higher than an estimate for Barn Swallow populations from Switzerland (0.16; Grüebler et al. 2014), it was within the range of other aerial insectivores (0.27; Purple Martin, *Progne subis,* Tarof et al. 2011) and other passerines (i.e. 0.11 Prothonotary Warbler, *Protonotaria citrea,* McKim-Louder et al. 2013; 0.26 Golden-cheeked Warbler, *Setophaga chrysoparia,* Duarte et al. 2016). Importantly, the measure of variation in the estimate may not be reflective of the true variation in the study system, so the expected change in population growth given a standard deviation increase in the parameter should be interpreted carefully.

The final limitation to consider was the lack of age specific reproductive success data. Barn Swallows and other birds generally have reduced reproductive success in their first year, including lower rates of multiple brooding (Holmes et al. 1992, Møller and De Lope 1999), and also undergo senescence (Holmes et al. 1992, Møller and De Lope 1999). The inclusion of age specific reproductive success would have likely decreased the influence of multiple brooding and other components of reproductive success because individuals would be less likely to recruit young to the population. However, more detailed data would be necessary to evaluate the full impact of this assumption.

Despite these limitations, my population growth estimates are similar to estimates from regional breeding bird surveys, used to track the size of avian populations.

Estimates from the breeding bird surveys from 2007-2017 estimate annual change in population size as -0.06% (-4.52, 5.02 95% CI) for New Brunswick and -2.03% (-5.59, 2.01 95% CI) for Nova Scotia and Prince Edward Island, though with low certainty (Smith et al. 2019). I estimated that the population was declining at an annual rate of -7%, but there was considerable uncertainty around the estimate (75% of matrix iterations produced population growth rates between 0.82 to 1.04), such that the breeding bird survey estimates would be well within the expected error. Therefore, this model is likely a fair representation of the population.

### 3.6 Conclusions

This study provides insight into the mechanistic dependence of population growth rates in a Threatened Barn Swallow population on the incidence of multiple brooding, and other components of reproductive success and survival. This is the first study to use a population model of Barn Swallows in North America, to investigate the drivers of population growth. I found that although multiple brooding increased reproductive success and benefited the population growth rate, hatch year and adult survival had the strongest influence over population growth. Given my findings, conservation efforts aimed at increasing survival, especially hatch year survival, would be the most effective in increasing population growth. Most hatch year mortality, including for Barn Swallows, occurs in the post-fledging phase, between leaving the nest and the start of migration, when fledglings are still reliant on parental care, have limited mobility and are more vulnerable to predators (Vitz and Rodewald 2011, Cox et al. 2014, Grüebler et al. 2014, Evans et al. 2020). While many factors affecting survival such as intrinsic quality (Tarof et al. 2011) and weather events (Newton 2007), are largely out of our control, management of high quality habitat with lower predator pressure and ample food supplies, especially on breeding grounds, may be an effective step to take. Future work should identify what constitutes high quality habitat in the post-fledging period, and what interventions will have the greatest impact on survival rates.

While the influence of reproductive success was not as strong as the influence of survival, improving reproductive success would still be beneficial to the population. The smaller improvements in population growth expected with an increase in the proportion of multi-brooded pairs could compensate for unexpected reductions in survival or other components of reproductive success. In fact, Engen et al. (2001) found that an increase in the proportion of multi-brooded pairs in a population in Denmark compensated for a reduction in clutch size, which ultimately kept reproductive success stable. Efforts to increase the incidence of multiple brooding, such as prioritizing the conservation of high quality breeding sites with less human infrastructure and warmer weather (see Chapter 2), would be beneficial. There would be additional benefits, since the factors associated with increased multiple brooding are typically associated with improved fledgling condition (Møller 2001, Teglhøj 2017), which in turn increases post-fledgling survival (Evans et al. 2020). Other efforts such as reducing predation risk by domestic cats and other species, would also benefit multiple demographic parameters and ultimately improve the population growth rate. It is clear that continued efforts to manage breeding habitats will be beneficial to the recovery or maintenance of Barn Swallow populations.

## 3.7 Tables

**Table 3.1-** Demographic rate estimates (mean ± SD (sample size)) of female Barn Swallows in New Brunswick and Nova Scotia, both within and across years.

| rate[a] | | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 | mean |
|---|---|---|---|---|---|---|---|---|---|
| number of fledglings from MB | $b_{MB}$ | - | 8.6 ± 1.4<br>(11) | 6.8 ± 2.4<br>(12) | 7.4 ± 2.5<br>(10) | - | 6.9 ±2.3<br>(14) | 8.0 ± 2.0<br>(6) | 7.5 ± 0.08 |
| number of fledglings from SB | $b_{\mathrm{SB}}$ | - | 4.7 ± 0.8<br>(10) | 4.6 ± 1.1<br>(16) | 4.2 ± 1.3<br>(23) | - | 4.0 ± 1.1<br>(25) | 4.1 ± 1.3<br>(29) | 4.3 ± 0.03 |
| proportion of MB | $p_{MB}$ | - | 0.30 (9) | 0.25 (10) | 0.15 (7) | - | 0.20 (12) | 0.31 (43) | 0.24 ± 0.07 |
| proportion of FB | $p_F$ | - | 0.09 (2) | - | 0.21 (9) | - | 0.11 (5) | 0.24 (11) | 0.16 ± 0.07 |
| AHY survival[c] | $\varphi_{\mathrm{AHY}}$ | 0.45 ± 0.12 | 0.57 ± 0.11 | 0.41 ± 0.10 | 0.48 ± 0.08 | 0.37 ± 0.08 | 0.50 ± 0.10 | 0.45 ± 0.08 | 0.47 ± 0.07 |
| HY survival | $\varphi_{\mathrm{HY}}$ | - | - | - | - | - | - | - | 0.21[b] ± 0.07 |

[a] MB=multi-brooded, FB= failed breeder, SB=single brooded, AHY= adult, HY= hatch year

[b] Estimate from Evans et al. (2020)

[c] variation within a year for adult survival is the standard error, not the standard deviation

**Table 3.2**- Elasticity of demographic rates (±SD). An elasticity further from zero represents a larger influence on population growth rates.

| demographic rate[a] | notation | elasticity |
|---|---|---|
| number of fledglings from MB | $b_{MB}$ | 0.20 (± 0.06) |
| number of fledglings from SB | $b_{\mathrm{SB}}$ | 0.29 (± 0.07) |
| proportion of MB | $p_{MB}$ | 0.08 (± 0.03) |
| proportion of FB | $p_F$ | -0.08 (± 0.03) |
| HY survival | $\varphi_{\mathrm{AHY}}$ | 0.48 (± 0.09) |
| AHY survival | $\varphi_{\mathrm{HY}}$ | 0.52 (± 0.09) |

[a] MB=multi-brooded, FB= failed breeder, SB=single brooded, AHY= adult, HY= hatch year

### 3.8 Figures

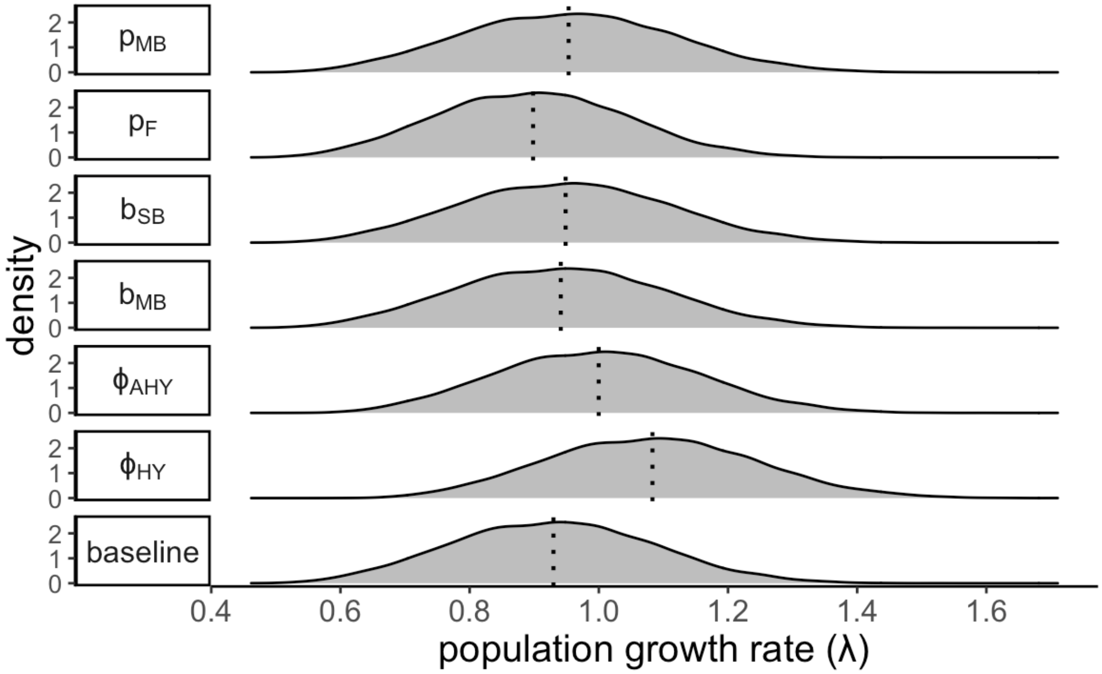


**Figure 3.1-** Expected distribution of population growth rates (λ), given a one standard deviation increase in each demographic rate. The demographic rates include the number of fledglings from single brooded ($b_{SB}$) and multi-brooded females ($b_{MB}$), the proportion of multi-brooded ($p_{MB}$) and failed breeders ($p_F$), and adult ($\varphi_{AHY}$) and hatch year survival ($\varphi_{HY}$). The mean population growth rate for each rate is indicated by the vertical dotted lines and the baseline distribution, which is the expected population growth rate with no change in any demographic rate, is displayed on the bottom.

# Chapter 4: General Discussion

## Summary of findings

The overarching goal of my thesis was to determine the implications of multiple brooding on the conservation of Barn Swallows in New Brunswick and Nova Scotia, Canada, where declines have been among the greatest in Canada (Nebel et al. 2010, Smith et al. 2019). To do this, I first examined the extrinsic factors affecting the probability, and therefore incidence, of multiple brooding, to identify potential conservation interventions that might increase the incidence of the behaviour (Chapter 2). Second, I examined how changes in the proportion of multi-brooded pairs impacted population growth rates, to inform the extent to which changes in multiple brooding would impact the status of the population (Chapter 3).

In Chapter 2, I found that spring weather and the landcover in close proximity to Barn Swallow breeding sites impacted the probability of multiple brooding. Specifically, sites with warmer and drier, and less windy spring weather, and that were surrounded by less human infrastructure like roads and buildings, were associated with a higher probability of multiple brooding. Such conditions likely led to a longer breeding season, increased insect availability and an increase in the energy available to be allocated towards producing multiple broods.

In Chapter 3, I found that increased rates of multiple brooding had a positive effect on population growth rates, though changes to the behaviour alone were unlikely to bring the population growth rate to a stable level. Instead, increasing survival, especially in hatch year swallows, had a much stronger effect on the population growth rate.

Together, these results show that although population growth rates of Maritime Barn Swallows are not most strongly influenced by multiple brooding, there are still implications of the behaviour on the conservation of the species. The incidence of the behaviour will likely change in the future, due to its relationship with weather and landcover, and such changes would impact the population growth rate, even if minimally. Conservation interventions that increase the incidence of the behaviour and conserve high quality habitat for multi-brooded pairs may help prevent or slow Barn Swallow population declines in the future.

## Implications of study

My study is one of only a few to consider the implications of multiple brooding, despite the potential for this behaviour to impact populations. Prior research into how the environment impacts multiple brooding in the Barn Swallow was limited to few factors (livestock, Møller 2001, Grüebler et al. 2010; insects, McClenaghan et al. 2019). Therefore, my study significantly adds to our understanding of what characteristics of breeding sites affect multiple brooding, and therefore, how anthropogenic activities, such as development of new infrastructure, may impact the success of breeding Barn Swallows. Further, this is the only study that I am aware of that uses population modelling to study the demographic drivers of population growth in North America Barn Swallows. My use of a population model adds to our mechanistic understanding of population growth rates, and can be used to make realistic inferences about how much the population can change if we target improvements in specific demographic rates, such as the proportion of multi-brooded pairs.

I recommend that to prevent or slow future declines in Barn Swallow populations, the conservation of high quality sites, as characterized as sites with little human infrastructure in areas that are warmer and drier, and have less wind, should be a high priority. Loss of these sites would likely have disproportionately negative impacts on population change in the region if compared to sites where multiple brooding is less likely to occur, and thus require more extensive conservation efforts directed at other parameters to mitigate their loss. Further, because human infrastructure and cold weather can affect other measures of swallow reproductive success, such as nestling condition (Teglhøj 2017) and survival (Winkler et al. 2013, Cox et al. 2019), the conservation of these sites will likely have benefits beyond increasing rates of multiple brooding.

## Limitations of study

One limitation of this study is that I had a relatively small sample size. I used data collected over eight years (five for reproductive data) from two to 16 study sites within a year, which is a small sample size when examining the population demographics (Doak et al. 2005, Fiske et al. 2008). Across demographic studies of many species, limited data is a consistent issue (Doak et al. 2005), and will continue to be an issue, especially in the Maritimes where swallow density is relatively low over a large spatial area. This makes it logistically challenging to have a large sample size. Using the data that do exist for the region, with cautious interpretation, is better than having no regionally relevant data to inform conservation decisions.

Another limitation of this study results from imperfect assessment of multiple brooding. In the absence of complete monitoring data, where reproductive success of every individual can be tracked over an entire breeding season, the determination of multiple brooding will always rely on assumptions. While I used an approach based on the timing of nests to distinguish between first/single and double broods, as is common among studies that consider multiple brooding (i.e. Podolsky et al. 2007, Imlay et al. 2018, McClenaghan et al. 2019), it may differ from the actual rate of multiple brooding within my study system. There are two potential sources of error that would result in an underestimate in the proportion of multi-brooded pairs. First, I may have overestimated the total number of pairs at a site if an individual had a failed nest early in the breeding season and quickly renested, because they would have been counted twice when estimating the total pairs. Second, I may have underestimated the number of multi-brooded pairs if not all pairs that failed prior to July 5 renested, because I would have incorrectly identified second broods as renests. Since I used the same method to estimate the incidence of multiple brooding across all sites, the imperfect estimates likely did not impact results of the extrinsic factors influencing multiple brooding. Further, although an error in the estimate of the proportion of multi-brooding pairs could affect my estimate of reproductive success in my population model, even a 100% increase in the proportion would not change the overall conclusion that multiple brooding does not affect population growth rates as significantly survival. Therefore, my conclusions are likely robust to error in estimates of multiple brooding.

### Directions for future research

To work further towards the conservation of Barn Swallows, there are still considerable knowledge gaps to fill. As outlined in Chapter 3, we need more studies of dispersal in hatch year birds. Given the substantial impact that this life stage has on population growth, it is of utmost importance to determine where swallows disperse, where mortality occurs and the effect of factors such as natal site characteristics and location on dispersal patterns, and survival. As tracking technologies get smaller and less expensive, there will be more opportunities to use these methods to monitor the movements of large numbers of hatch year swallows and determine dispersal movements.

While this study examined the conservation implications of multiple brooding, I did not examine the feasibility of altering the incidence of the behaviour through intervention. Studies like mine, which use observational data to determine the effect of factors like landscape, can help guide decisions, but the most useful information will come from controlled studies that directly assess the impact of potential interventions. For example, there could be longitudinal studies comparing changes in breeding activity and success at existing swallow breeding sites in areas where there is increasing human development (i.e. edge of urban areas), compared to those that see little change in the surrounding landscape.

Lastly, in the future, there is significant potential for community science to play an important role in supplementing long term monitoring data. More engagement from landowners would greatly improve the data available, and help combat data deficiencies that are common in demographic studies. In the context of multiple brooding, we must improve the protocols of programs like Project NestWatch, so they are more capable of detecting multiple broods. These protocols need to both encourage the monitoring of breeding activity beyond first broods, and ensure that there is a method to report whether this effort was taken. Such information would help track changes in the incidence of multiple brooding in the future.

# References

Alerstam, T., A. Hedenström, and S. Åkesson (2003). Long-distance migration: Evolution and determinants. Oikos 103:247–260.

Ambrosini, R., A. M. Bolzern, L. Canova, S. Arieni, A. P. Møller, and N. Saino (2002). The distribution and colony size of barn swallows in relation to agricultural land use. Journal of Applied Ecology 39(3):524–534.

Ambrosini, R., R. P. Ferrari, R. Martinelli, M. Romano, and N. Saino (2006). Seasonal, meteorological, and microhabitat effects on breeding success and offspring phenotype in the barn swallow, *Hirundo rustica*. Ecoscience 13(3):298–307.

Ambrosini, R., D. Rubolini, P. Trovò, G. Liberini, M. Bandini, A. Romano, B. Sicurella, C. Scandolara, M. Romano, and N. Saino (2012). Maintenance of livestock farming may buffer population decline of the Barn Swallow *Hirundo rustica*. Bird Conservation International 22(4):411–428.

Ambrosini, R., and N. Saino (2010). Environmental effects at two nested spatial scales on habitat choice and breeding performance of barn swallow. Evolutionary Ecology 24(2):491–508.

Anthony, L. W., and C. A. Ely (1976). Breeding biology of Barn Swallows in west-central Kansas. Kansas Ornithological Society Bulletin 27(4):37–44.

Arthington, A. H., N. K. Dulvy, W. Gladstone, and I. J. Winfield (2016). Fish conservation in freshwater and marine realms: status, threats and management. Aquatic Conservation: Marine and Freshwater Ecosystems 26(5):838–857.

Beissinger, S. R., J. M. Wunderle, J. M. Meyers, B. E. Saether, and S. Engen (2008). Anatomy of a bottleneck: Diagnosing factors limiting population growth in the puerto rican parrot. Ecological Monographs 78(2):185–203.

Bellavance, V., M. Bélisle, J. Savage, F. Pelletier, and D. Garant (2018). Influence of agricultural intensification on prey availability and nestling diet in Tree Swallows (*Tachycineta bicolor*). Canadian Journal of Zoology 96(9):1053–1065.

Bennett, P. M., and I. P. F. Owens (2002). Evolutionary Ecology of Birds: Life Histories, Mating Systems, and Extinction. First Edition. Oxford University Press, Oxford.

Béziers, P., and A. Roulin (2016). Double brooding and offspring desertion in the barn owl *Tyto alba*. Journal of Avian Biology 47(2):235–244.

BirdLife International (2020). Species factsheet: *Hirundo rustica*. [Online.] Available at http://datazone.birdlife.org/species/factsheet/barn-swallow-hirundo-rustica

Brown, M. B., and C. R. Brown (2020). Barn Swallow (*Hirundo rustica*), version 1.0. *Birds of the World*. [Online.] Available at https://birdsoftheworld-org.ezproxy.library.dal.ca/bow/species/barswa/cur/introduction.

Bryant, D. M. (1975). Breeding Biology Of House Martins *Delichon Urbic*a In Relation To Aerial Insect Abundance. Ibis 117(2):180–216.

Bryant, D. M., and A. K. Turner (1982). Central place foraging by swallows (Hirundinidae): The question of load size. Animal Behaviour 30(3):845–856.

Buehler, D. A., J. J. Giocomo, J. Jones, P. B. Hamel, C. M. Rogers, T. A. Beachy, D. W. Varble, C. P. Nicholson, K. L. Roth, J. Barg, R. J. Robertson, et al. (2008). Cerulean Warbler Reproduction, Survival, and Models of Population Decline. Journal of Wildlife Management 72(3):646–653.

Bulluck, L., S. Huber, C. Viverette, and C. Blem (2013). Age-specific responses to spring temperature in a migratory songbird: Older females attempt more broods in warmer springs. Ecology and Evolution 3(10):3298–3306.

Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. Journal of Statistical Software 80(1):1–28.

Calvert, A. M., D. L. Amirault, F. Shaffer, R. Elliot, A. Hanson, J. McKnight, and P. D. Taylor (2006). Population Assessment of an Endangered Shorebird: the Piping Plover (*Charadrius melodus melodus*) in Eastern Canada. Avian Conservation and Ecology 1(3):4.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. A. Brubaker, J. Guo, P. Li, and A. Riddell (2017). Stan: A probabilistic programming language. Journal of Statistical Software 76:1.

Carro, M. E., M. E. Mermoz, and G. J. Fernández (2014). Factors affecting the probability of double brooding by Southern House Wrens. Journal of Field Ornithology 85(3):227–236.

Caswell, H. (2000). Prospective and retrospective perturbation analyses: Their roles in conservation biology. Ecology 81(3):619–627.

Caswell, H. (2001). Matrix Population Models: Construction, Analysis, and Interpretation. 2nd Edition. Sinauer Associates Inc., Sunderland, UK.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. Science Advances 1(5):e1400253.

Chapron, G., P. Y. Quenette, S. Legendre, and J. Clobert (2003). Which future for the French Pyrenean brown bear (*Ursus arctos*) population? An approach using stage-structured deterministic and stochastic models. Comptes Rendus - Biologies 326:174–182.

Clark, M. E., and T. E. Martin (2007). Modeling tradeoffs in avian life history traits and consequences for population growth. Ecological Modelling 209(2-4):110–120.

Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W. J. Gutowski, T. Johns, G. Krinner, M. Shongwe, et al. (2013). Long-term climate change: Projections, commitments and irreversibility. In Climate Change 2013 the Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Doschung, A. Nauels, Y. Xia, V. Bex and P. M. Midgley, Editors). Cambridge University Press, Cambridge, pp. 1029–1136.

Cooper, C. B., W. M. Hochachka, G. Butcher, and A. A. Dhondt (2005). Seasonal and latitudinal trends in clutch size: Thermal constraints during laying and incubation. Ecology 86(8):2018–2031.

Cornell, A., and T. D. Williams (2016). Individual quality and double-brooding in a highly synchronous songbird population. The Auk 133(2):251–260.

[COSEWIC] Committee on the Status of Endangered Wildlife in Canada (2011). Assessment and Status Report on the Barn Swallow *Hirundo rustica* in Canada. Ottawa, CAN. ix + 37pp.

Cox, A. R., R. J. Robertson, B. C. Fedy, W. B. Rendell, and F. Bonier (2018). Demographic drivers of local population decline in Tree Swallows (*Tachycineta bicolor*) in Ontario, Canada. The Condor 120(4):842–851.

Cox, A. R., R. J. Robertson, Á. Z. Lendvai, K. Everitt, and F. Bonier (2019). Rainy springs linked to poor nestling growth in a declining avian aerial insectivore (*Tachycineta bicolor*). Proceedings of the Royal Society B: Biological Sciences 286(1898):20190018.

Crouse, D. T., L. B. Crowder, and H. Caswell (1987). A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68(5):1412–1423.

Davies, S. R., C. D. Sayer, H. Greaves, G. M. Siriwardena, and J. C. Axmacher (2016). A new role for pond management in farmland bird conservation. Agriculture, Ecosystems and Environment 233:179–191.

Department for Environment Food and Rural Affairs (2016). Farming Statistics. Final crop areas, yields, livestock populations and agricultural workforce at June 2016-United Kingdom. London, England. 23pp.

Doak, D. F., K. Gross, and W. F. Morris (2005). Understanding and predicting the effects of sparse data on demographic analyses. Ecology 86(5):1154–1163.

Drake, A., and K. Martin (2018). Local temperatures predict breeding phenology but do not result in breeding synchrony among a community of resident cavity-nesting birds. Scientific Reports 8(1):1–10.

Drent, R. H., and S. Daan (1980). The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

Duarte, A., F. W. Weckerly, M. Schaub, and J. S. Hatfield (2016). Estimating golden-cheeked warbler immigration: Implications for the spatial scale of conservation. Animal Conservation 19(1):65–74.

Eikenaar, C., M. Whitham, J. Komdeur, M. van der Velde, and I. T. Moore (2011). Testosterone, plumage colouration and extra-pair paternity in male North-American barn swallows. PLoS ONE 6(8):e23288.

Engen, S., B. E. Sæther, and A. P. Møller (2001). Stochastic population dynamics and time to extinction of a declining population of barn swallows. Journal of Animal Ecology 70(5):789–797.

Evans, D. R., K. A. Hobson, J. W. Kusack, M. D. Cadman, C. M. Falconer, and G. W. Mitchell (2020). Individual condition, but not fledging phenology, carries over to affect post-fledging survival in a Neotropical migratory songbird. Ibis 162(2):331–344.

Evans, K. L., R. B. Bradbury, and J. D. Wilson (2003). Selection of hedgerows by Swallows *Hirundo rustica* foraging on farmland: The influence of local habitat and weather. Bird Study 50(1):8–14.

Evans, K. L., J. D. Wilson, and R. B. Bradbury (2007). Effects of crop type and aerial invertebrate abundance on foraging barn swallows *Hirundo rustica*. Agriculture, Ecosystems and Environment 122(2):267–273.

Falaschi, M., R. Manenti, W. Thuiller, and G. F. Ficetola (2019). Continental-scale determinants of population trends in European amphibians and reptiles. Global Change Biology 25(10):3504–3515.

Finn, D. S., and N. L. R. Poff (2008). Emergence and flight activity of alpine stream insects in two years with contrasting winter snowpack. Arctic, Antarctic, and Alpine Research 40(4):638–646.

Fiske, I. J., E. M. Bruna, and B. M. Bolker (2008). Effects of sample size on estimates of population growth rates calculated with matrix models. PLoS ONE 3(8):e3080.

Gallardo, J. C., F. J. Vilella, and M. E. Colvin (2019). A seasonal population matrix model of the Caribbean Red-tailed Hawk *Buteo jamaicensis jamaicensis* in eastern Puerto Rico. Ibis 161(2):459–466.

García-Pérez, B., K. A. Hobson, G. Albrecht, M. D. Cadman, and A. Salvadori (2014). Influence of climate on annual survival of Barn Swallows (*Hirundo rustica*) breeding in North America. Auk 131(3):351–362.

Gerber, L. R., K. E. Buenau, and G. Vanblaricom (2004). Density dependence and risk of extinction in a small population of sea otters. Biodiversity and Conservation 13:2741–2757.

Grüebler, M. U., F. Korner-Nievergelt, and J. Von Hirschheydt (2010). The reproductive benefits of livestock farming in barn swallows *Hirundo rustica*: Quality of nest site or foraging habitat? Journal of Applied Ecology 47(6):2010.

Grüebler, M. U., F. Korner-Nievergelt, and B. Naef-Daenzer (2014). Equal nonbreeding period survival in adults and juveniles of a long-distant migrant bird. Ecology and Evolution 4(6):756–765.

Grüebler, M. U., M. Morand, and B. Naef-Daenzer (2008). A predictive model of the density of airborne insects in agricultural environments. Agriculture, Ecosystems and Environment 123(1-3):75–80.

Grüebler, M. U., and B. Naef-Daenzer (2010). Brood overlap and male ornamentation in the double-brooded barn swallow. Behavioral Ecology 21(3):513–519.

Halupka, L., A. Dyrcz, and M. Borowiec (2008). Climate change affects breeding of reed warblers *Acrocephalus scirpaceus*. Journal of Avian Biology 39(1):95–100.

Halupka, L., and K. Halupka (2017). The effect of climate change on the duration of avian breeding seasons: A meta-analysis. Proceedings of the Royal Society B: Biological Sciences 284(1867):20171710.

Harriman, V. B., R. D. Dawson, L. E. Bortolotti, and R. G. Clark (2017). Seasonal patterns in reproductive success of temperate-breeding birds: Experimental tests of the date and quality hypotheses. Ecology and Evolution 7(7):2122–2132.

Healy, K., T. H. G. Ezard, O. R. Jones, R. Salguero-Gómez, and Y. M. Buckley (2019). Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. Nature Ecology and Evolution 3(8):1217–1224.

Henderson, I., C. Holt, and J. Vickery (2007). National and regional patterns of habitat association with foraging Barn Swallows *Hirundo rustica* in the UK. Bird Study 54(3):371–377.

Hepp, G. R., R. A. Gitzen, and R. A. Kennamer (2020). Relative Importance of Vital Rates to Population Dynamics of Wood Ducks. Journal of Wildlife Management 84(2):320–330.

Hoffmann, M., C. Hilton-Taylor, A. Angulo, M. Böhm, T. M. Brooks, S. H. M. Butchart, K. E. Carpenter, J. Chanson, B. Collen, N. A. Cox, W. R. T. Darwall, et al. (2010). The impact of conservation on the status of the world's vertebrates. Science 330(6010):1503–1509.

Holmes, R. T., T. W. Sherry, and P. P. Marra (1992). Multiple brooding and productivity of a neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. The Auk 109(2):321–333.

Husby, A., L. E. B. Kruuk, and M. E. Visser (2009). Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. Proceedings of the Royal Society B: Biological Sciences 276(1663):1845–1854.

Imlay, T. L., F. Angelier, K. A. Hobson, G. Mastromonaco, S. Saldanha, and M. L. Leonard (2019a). Multiple intrinsic markers identify carry-over effects from wintering to breeding sites for three Nearctic-Neotropical migrant swallows. Auk 136(4):1–15.

Imlay, T. L., and M. L. Leonard (2019). A review of the threats to adult survival for swallows (Family: Hirundinidae). Bird Study 66(2):251–263.

Imlay, T. L., J. Mills Flemming, S. Saldanha, N. T. Wheelwright, and M. L. Leonard (2018). Breeding phenology and performance for four swallows over 57 years: relationships with temperature and precipitation. Ecosphere 9(3):e02166.

Imlay, T. L., D. Nickerson, and A. G. Horn (2019b). Temperature and breeding success for cliff swallows (*Petrochelidon pyrrhonota*) nesting on man-made structures: Ecological traps? Canadian Journal of Zoology 97(5):429–435.

Jacobs, A. C., L. L. Reader, and J. M. Fair (2013). What determines the rates of double brooding in the western bluebird ? Condor 115(2):386–393.

Jamieson, S. E. (2011). Pacific Dunlin *Calidris alpina pacifica* show a high propensity for second clutch production. Journal of Ornithology 152(4):1013–1021.

Johns, M. E., P. Warzybok, R. W. Bradley, J. Jahncke, M. Lindberg, and G. A. Breed (2018). Increased reproductive investment associated with greater survival and longevity in Cassin's auklets. Proceedings of the Royal Society B: Biological Sciences 285(1885):20181464.

Kociolek, A. V., A. P. Clevenger, C. C. St. Clair, and D. S. Proppe (2011). Effect of road networks on bird populations. Conservation Biology 25(2):241–249.

Kusack, J. W., G. W. Mitchell, D. R. Evans, M. D. Cadman, and K. A. Hobson (2019). Effects of agricultural intensification on nestling condition and number of young fledged of barn swallows (*Hirundo rustica*). Science of the Total Environment 709:136195.

Lahlah, N., Y. Chabi, M. Bańbura, and J. Bańbura (2006). Breeding biology of the House Martin *Delichon urbica* in Algeria. Acta Ornithologica 41(2):113–120.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62(1):67–118.

Lenske, A. (2018). Using automated radio-telemetry to link food availability, reproductive success, and habitat use of Barn Swallows (*Hirundo rustica erythrogaster*). [M.Sc. thesis]. Peterborough, CAN: Trent University.

Liu, Y., E. S. C. Scordato, R. Safran, and M. Evans (2018). Ventral colour, not tail streamer length, is associated with seasonal reproductive performance in a Chinese population of Barn Swallows (*Hirundo rustica gutturalis*). Journal of Ornithology 159(3):675–685.

Manlik, O., R. C. Lacy, and W. B. Sherwin (2018). Applicability and limitations of sensitivity analyses for wildlife management. Journal of Applied Ecology 55(3):1430–1440.

Matthysen, E., F. Adriaensen, and A. A. Dhondt (2001). Local recruitment of great and blue tits (*Parus major, P. caeruleus*) in relation to study plot size and degree of isolation. Ecography 24(1):33–42.

McClenaghan, B., K. C. R. Kerr, and E. Nol (2019). Does prey availability affect the reproductive performance of barn swallows (*Hirundo rustica*) breeding in Ontario, Canada? Canadian Journal of Zoology 97(11):979–987.

McElreath, R. (2020). Statistical Rethinking: A Bayesian Course with Examples in R and Stan. 2nd edition. CRC Press, Boca Raton.

McHugh, N. M., B. L. Bown, and J. E. Clark (2018). Use of field margins managed under an agri-environment scheme by foraging Barn Swallows *Hirundo rustica*. Bird Study 65(3):329–337.

McKim-Louder, M. I., J. P. Hoover, T. J. Benson, and W. M. Schelsky (2013). Juvenile Survival in a Neotropical Migratory Songbird Is Lower than Expected. PLoS ONE 8(2):e56059.

McMahon, B. J., A. Helden, A. Anderson, H. Sheridan, A. Kinsella, and G. Purvis (2010). Interactions between livestock systems and biodiversity in South-East Ireland. Agriculture, Ecosystems and Environment 139(1-2):232–238.

Meehan, T. D., A. L. Harvey, N. L. Michel, G. M. Langham, and A. Weinstein (2018). A Population Model Exploring Factors Influencing Black Oystercatcher *(Haematopus bachmani*) Population Dynamics. Waterbirds 41(2):115–221.

Mills, L. S., and M. Lindberg (2002). Sensitivity Analysis to Evaluate the Consequences of Conservation Actions. In Population Viability Analysis (S. R. Beissinger and D. R. McCullough, Editors). University of Chicago Press, Chicago, USA, pp. 338–366.

Møller, A. P. (1989). Population dynamics of a declining swallow *Hirundo rustica* population. Journal of Animal Ecology 58(3):1051–1063.

Møller, A. P. (1994). Sexual selection and the Barn Swallow. Oxford University Press, Oxford, UK.

Møller, A. P. (2001). The effect of dairy farming on barn swallow *Hirundo rustica* abundance, distribution and reproduction. Journal of Applied Ecology 38(2):378–389.

Møller, A. P. (2008). Climate change and micro-geographic variation in laying date. Oecologia 155(4):845–857.

Møller, A. P. (2013). Long-term trends in wind speed, insect abundance and ecology of an insectivorous bird. Ecosphere 4(1):6.

Møller, A. P., E. Flensted-Jensen, K. Klarborg, W. Mardal, and J. T. Nielsen (2010). Climate change affects the duration of the reproductive season in birds. Journal of Animal Ecology 79(4):777–784.

Møller, A. P., and F. De Lope (1999). Senescence in a short-lived migratory bird: age-dependent morphology, migration, reproduction and parasitism. Journal of Animal Ecology 68(1):163–171.

Monroe, A. P., K. K. Hallinger, R. L. Brasso, and D. A. Cristol (2008). Occurrence and Implications of Double Brooding in a Southern Population of Tree Swallows. The Condor 110(2):382–386.

Musitelli, F., A. Romano, A. P. Møller, and R. Ambrosini (2016). Effects of livestock farming on birds of rural areas in Europe. Biodiversity and Conservation 25(4):615–631.

Naef-Daenzer, L., M. U. Grüebler, and B. Naef-Daenzer (2011). Parental care trade-offs in the inter-brood phase in Barn Swallows *Hirundo rustica*. Ibis 153(1):27–36.

Nagy, L. R., and R. T. Holmes (2005a). To Double-Brood or Not? Individual Variation in the Reproductive Effort in Black- Throated Blue Warblers (*Dendroica caerulescens*). The Auk 122(3):902–914.

Nagy, L. R., and R. T. Holmes (2005b). Food limits annual fecundity of a migratory songbird: An experimental study. Ecology 86(3):675–681.

Nebel, S., J. Casey, M.-A. Cyr, K. J. Kardynal, E. A. Krebs, E. F. Purves, M. Bélisle, R. M. Brigham, E. C. Knight, C. Morrissey, and R. G. Clark (2020). Falling through the policy cracks: implementing a roadmap to conserve aerial insectivores in North America. Avian Conservation and Ecology 15(1):23.

Nebel, S., A. Mills, J. D. McCracken, and P. D. Taylor (2010). Declines of Aerial Insectivores in North America Follow a Geographic Gradient. Avian Conservation and Ecology 5(2):1.

Newton, I. (2007). Weather-related mass-mortality events in migrants. Ibis 149(3):453–467.

O'Brien, E. L., and R. D. Dawson (2013). Experimental dissociation of individual quality, food and timing of breeding effects on double-brooding in a migratory songbird. Oecologia 172(3):689–699.

Ogden, L. J. E., and B. J. M. Stutchbury (1996). Constraints on double brooding in Neotropical migrant, the Hooded Warbler. The Condor 98(4):736–744.

Oli, M. K. (2004). The fast-slow continuum and mammalian life-history patterns: An empirical evaluation. Basic and Applied Ecology 5(5):449–463.

Orłowski, G., and J. Karg (2013). Partitioning the effects of livestock farming on the diet of an aerial insectivorous passerine, the barn swallow *hirundo rustica*. Bird Study 60(1):111–123.

Osawa, T. (2015). Importance of Farmland in Urbanized Areas as a Landscape Component for Barn Swallows (*Hirundo rustica*) Nesting on Concrete Buildings. Environmental Management 55(5):1160–1167.

Paananen, T., J. Piironen, P. C. Bürkner, and A. Vehtari (2020). Implicitly adaptive importance sampling. preprint arXiv:1906.08850v2.

Pasinelli, G., J. P. Runge, and K. Schiegg (2011). Source-sink status of small and large wetland fragments and growth rate of a population network. In Sources, Sinks and Sustainability (J. Liu, V. Hull, A. T. Morzillo and J. A. Wiens, Editors). Cambridge University Press, Cambridge, UK, pp. 216–238.

Peck, G. K., and R. D. James (1987). Breeding birds of Ontario: Nidiology and distribution. Volume 2. Royal Ontario Museum, Toronto, CAN.

Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton (2014). The biodiversity of species and their rates of extinction, distribution, and protection. Science 344(6187):e1246752.

Podolsky, A. L., T. R. Simons, and J. A. Collazo (2007). Modeling Population Growth of the Ovenbird (*Seiurus aurocapilla*) in the Southern Appalachians. The Auk 124(4):1359–1372.

Province of New Brunswick (2017). New Brunswick Census of Agriculture Report 2016. Fredericton,New Brunswick. 16pp.

QGIS (2020). QGIS Geographic Information System. QGIS Association.

Raja-aho, S., T. Eeva, P. Suorsa, J. Valkama, and E. Lehikoinen (2017). Juvenile Barn Swallows *Hirundo rustica* L. from late broods start autumn migration younger, fuel less effectively and show lower return rates than juveniles from early broods. Ibis 159(4):892–901.

Robinson, R. A., C. A. Morrison, and S. R. Baillie (2014). Integrating demographic data: Towards a framework for monitoring wildlife populations at large spatial scales. Methods in Ecology and Evolution 5(4):1361–1372.

Saether, B.-E., and O. Bakke (2000). Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate. Ecology 81(3):642–653.

Sæther, B.-E., T. H. Ringsby, E. Røskaft, B.-E. Saether, and E. Roskaft (1996). Life History Variation, Population Processes and Priorities in Species Conservation: Towards a Reunion of Research Paradigms. Oikos 77(6):217–226.

Safran, R. J. (2004). Adaptive site selection rules and variation in group size of barn swallows: Individual decisions predict population patterns. American Naturalist 164(2):121–131.

Safran, R. J. (2006). Nest-site selection in the barn swallow, *Hirundo rustica* : What predicts seasonal reproductive success? Canadian Journal of Zoology 84(11):1533–1539.

Saino, N., M. Romano, R. Ambrosini, D. Rubolini, G. Boncoraglio, M. Caprioli, and A. Romano (2012). Longevity and lifetime reproductive success of barn swallow offspring are predicted by their hatching date and phenotypic quality. Journal of Animal Ecology 81(5):1004–1012.

Sánchez-Bayo, F., and K. A. G. Wyckhuys (2019). Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232:8–27.

Schaub, M., O. Gimenez, A. Sierro, and R. Arlettaz (2007). Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. Conservation Biology 21(4):945–955.

Schaub, M., J. von Hirschheydt, and M. U. Grüebler (2015). Differential contribution of demographic rate synchrony to population synchrony in barn swallows. Journal of Animal Ecology 84(6):1530–1541.

Schaub, M., B. Ullrich, G. Knötzsch, P. Albrecht, and C. Meisser (2006). Local population dynamics and the impact of scale and isolation: A study on different little owl populations. Oikos 115(3):389–400.

Schifferli, L., M. U. Grüebler, H. A. J. Meijer, G. H. Visser, and B. Naef-Daenzer (2014). Barn Swallow *Hirundo rustica* parents work harder when foraging conditions are good. Ibis 156(4):777–787.

Shields, W. M. (1984). Factors Affecting Nest and Site Fidelity in Adirondack Barn Swallows (*Hirundo rustica*). The Auk 101(4):780–789.

Sicurella, B., M. Caprioli, A. Romano, M. Romano, D. Rubolini, N. Saino, and R. Ambrosini (2014). Hayfields enhance colony size of the Barn Swallow *Hirundo rustica* in northern Italy. Bird Conservation International 24(1):17–31.

Sillett, T. S., and R. T. Holmes (2005). Long-term demographic trends, limiting factors, and the strength of density dependence in a breeding population of a migratory songbird. In Birds of two worlds: the ecology and evolution of temperate-tropical migration (R. S. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, USA, pp. 426–436.

Simons, L. S., and T. E. Martin (1990). Food limitation of avian reproduction: an experiment with the cactus wren. Ecology 71(3):869–876.

Smith, A. C., M.-A. R. Hudson, V. Aponte, and C. M. Francis (2019). North American Breeding Bird Survey- Canadian Trends Website, Data-version 2017. [Online.] Accessed at https://wildlife-species.canada.ca/breeding-bird-survey-results/P004/A001/?lang=e&m=s&r=BARS&p=L

Snapp, B. D. (1976). Colonial breeding in the Barn Swallow (*Hirundo rustica*) and its adaptive significance. The Condor 78(4):471–480.

Spiller, K. J., and R. Dettmers (2019). Evidence for multiple drivers of aerial insectivore declines in North America. The Condor 121(2):1–13.

Stanton, R. L., C. A. Morrissey, and R. G. Clark (2018). Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. Agriculture, Ecosystems and Environment 254:244–254.

Stearns, S. C. (1992). The evolution of life histories. Oxford University Press, New York, USA.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller (2004). Status and Trends of Amphibian Declines and Extinctions Worldwide. Science 306(5702):1783–1786.

Tarof, S. A., P. M. Kramer, J. R. Hill, J. Tautin, and B. J. M. Stutchbury (2011). Brood size and late breeding are negatively related to juvenile survival in a Neotropical migratory songbird. The Auk 128(4):716–725.

Tate, P. (1986). The Swallow. Shire Publications, Ltd, Aylesbury, UK.

Taylor, L. U., B. K. Woodworth, B. K. Sandercock, and N. T. Wheelwright (2018). Demographic drivers of collapse in an island population of Tree Swallows. Condor 120(4):828–841.

Team, R. C. (2020). R: A language and environment for statistical computing. [Online.] Available at https://www.r-project.org/.

Teglhøj, P. G. (2017). A comparative study of insect abundance and reproductive success of barn swallows *Hirundo rustica* in two urban habitats. Journal of Avian Biology 48(6):846–853.

Templer, P. H., A. F. Schiller, N. W. Fuller, A. M. Socci, J. L. Campbell, J. E. Drake, and T. H. Kunz (2012). Impact of a reduced winter snowpack on litter arthropod abundance and diversity in a northern hardwood forest ecosystem. Biology and Fertility of Soils 48:413–424.

Thompson, B. C., G. E. Knadle, D. L. Brubaker, and K. S. Brubaker (2001). Nest Success Is Not an Adequate Comparative Estimate of Avian Reproduction. Journal of Field Ornithology 72(4):527–536.

Tilman, D., M. Clark, D. R. Williams, K. Kimmel, S. Polasky, and C. Packer (2017). Future threats to biodiversity and pathways to their prevention. Nature 546(7656):73–81.

Tinbergen, J. M., and M. W. Dietz (1994). Parental Energy Expenditure During Brood Rearing in the Great Tit (*Parus major*) in Relation to Body Mass, Temperature, Food Availability and Clutch Size. Functional Ecology 8(5):563–572.

Townsend, A. K., T. S. Sillett, N. K. Lany, S. A. Kaiser, N. L. Rodenhouse, M. S. Webster, and R. T. Holmes (2013). Warm Springs, Early Lay Dates, and Double Brooding in a North American Migratory Songbird, the Black-Throated Blue Warbler. PLoS ONE 8(4):e59467.

Turner, A. (2004). Family Hirundinidae (swallows and martins). In The Birds of the World vol.9 (J. Del Hoyo, A. Elliott and D. Christie, Editors). Lynx Edicions, Barcelona, pp. 602–685.

Vehtari, A., A. Gelman, and J. Gabry (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing 27(5):1413–1432.

Verhulst, S., M. Tinbergen, and S. Daan (1997). Multiple breeding in the Great Tit. A trade-off between successive reproductive attempts? Functional Ecology 11(6):714–722.

Walker, L. E., J. M. Marzluff, and D. A. Cimprich (2016). Source-sink population dynamics driven by a brood parasite: A case study of an endangered songbird, the black-capped vireo. Biological Conservation 203:108–118.

Weggler, M. (2006). Constraints on, and determinants of, the annual number of breeding attempts in the multi-brooded Black Redstart *Phoenicurus ochruros*. Ibis 148(2):273–284.

White, G. C., and K. P. Burnham (1999). Program MARK: Survival estimation from populations of marked animals. Bird Study 46:120–138.

White, T. C. R. (2008). The role of food, weather and climate in limiting the abundance of animals. Biological Reviews 83(3):227–248.

Wilson, S., and K. Martin (2012). Influence of life history strategies on sensitivity, population growth and response to climate for sympatric alpine birds. BMC Ecology 12:e9.

Winkler, D. W., M. K. Luo, and E. Rakhimberdiev (2013). Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). Oecologia 173(1):129–138.

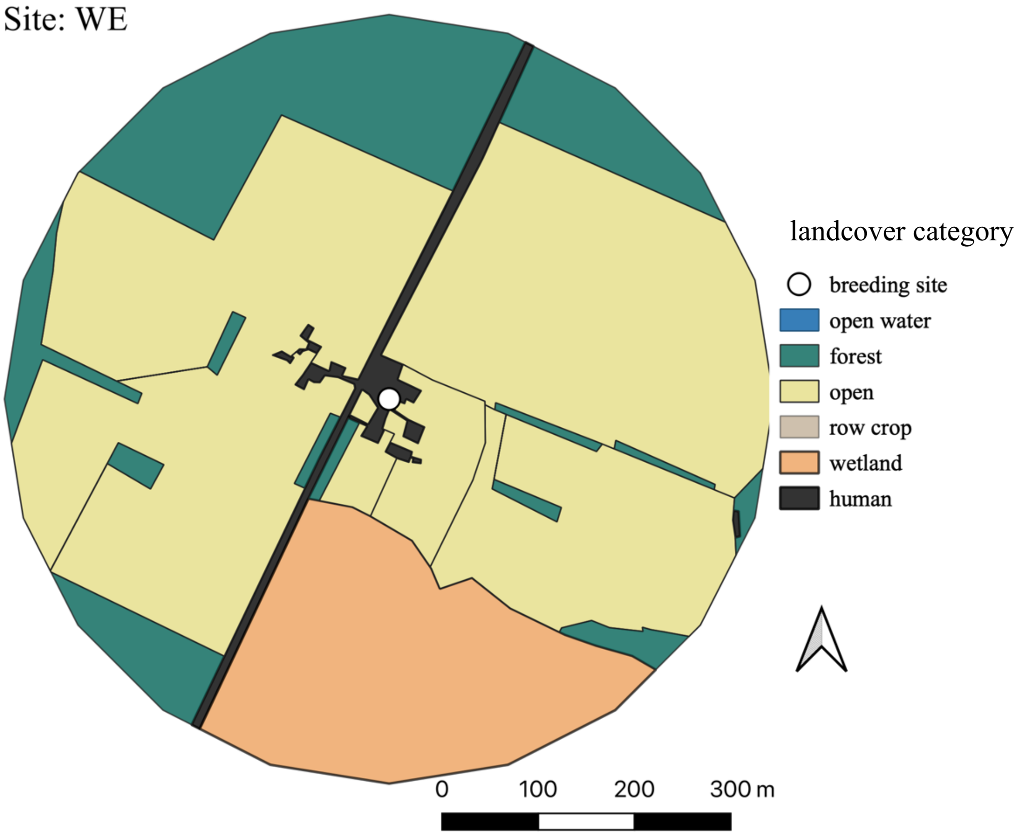
Wisdom, M. J., L. S. Mills, and D. F. Doak (2000). Life stage simulation analysis: Estimating vital-rate effects on population growth for conservation. Ecology 81(3):628–641.

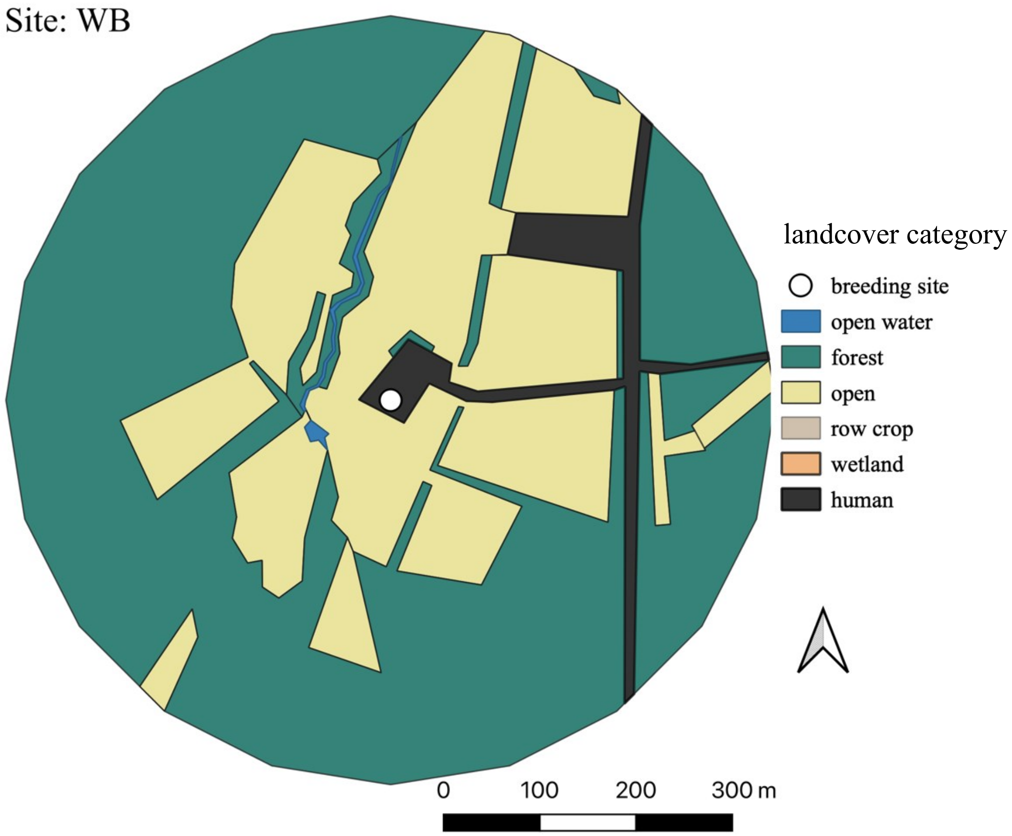
Woodworth, B. K., N. T. Wheelwright, A. E. M. Newman, and D. R. Norris (2017). Local density regulates migratory songbird reproductive success through effects on double-brooding and nest predation. Ecology 98(8):2039–2048.

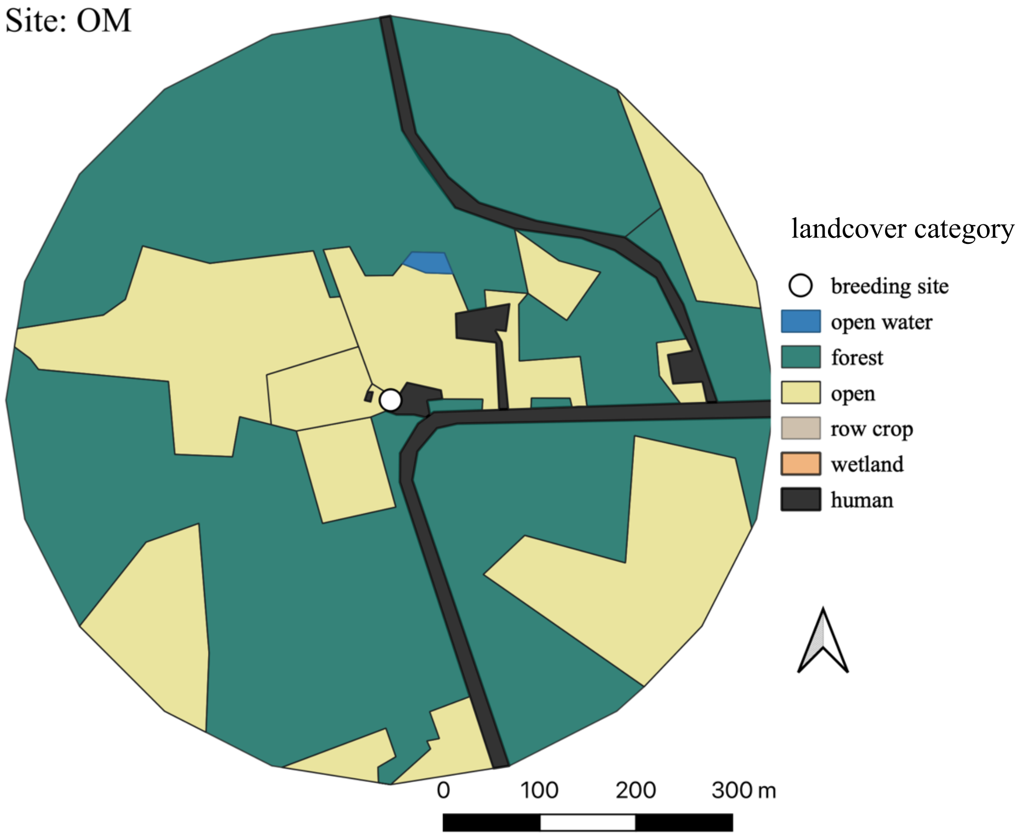
Zabala, J., X. Lambin, J. Soufflot, P. Soufflot, D. Chenesseau, and A. Millon (2020). Proximate causes and fitness consequences of double brooding in female barn owls. Oecologia 192(1):91–103.

Zabel, F., R. Delzeit, J. M. Schneider, R. Seppelt, W. Mauser, and T. Václavík (2019). Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. Nature Communications 10:2844.

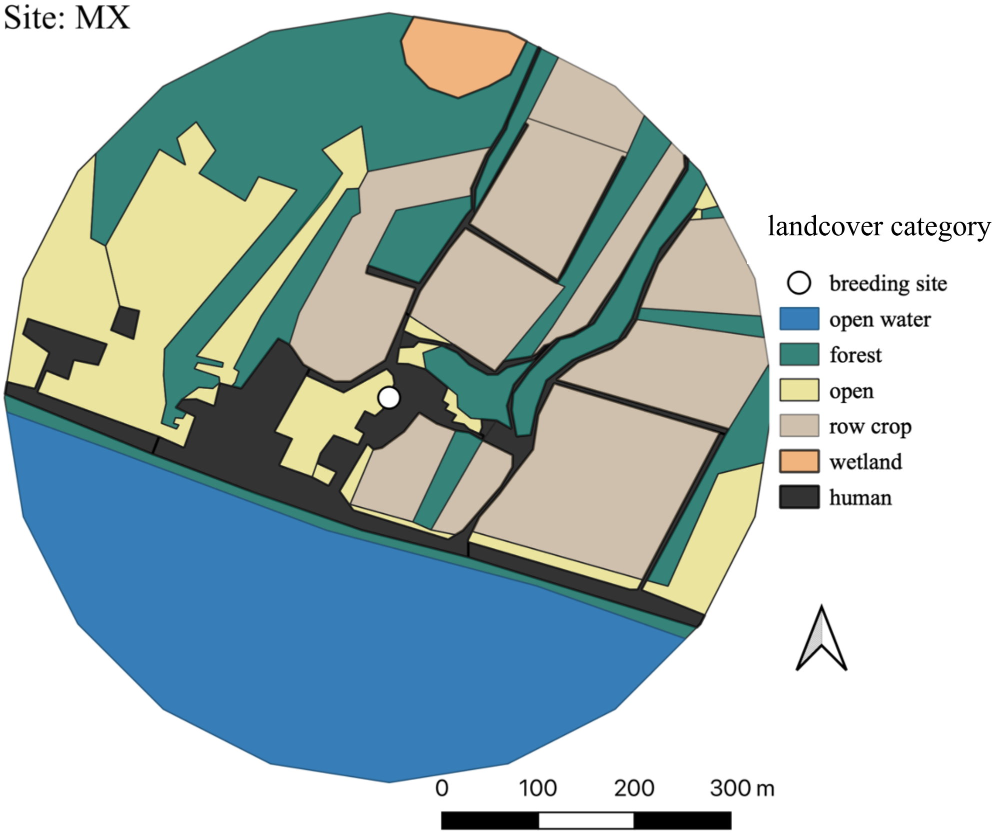
## Appendix A: Landcover Maps

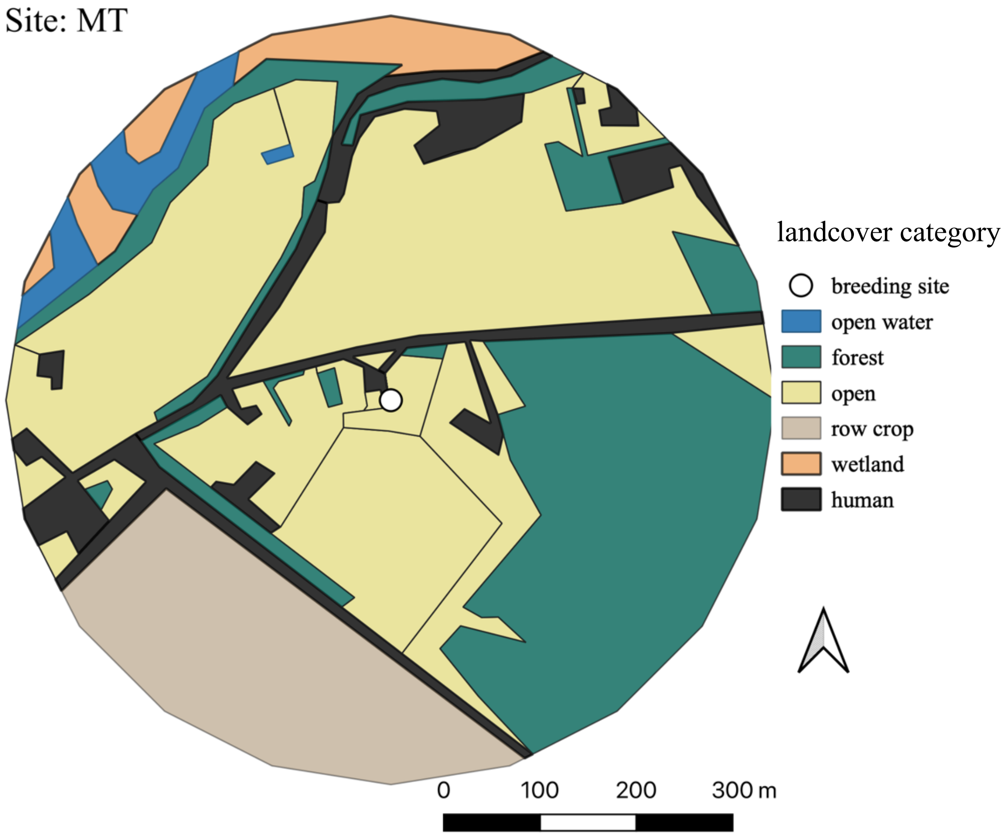


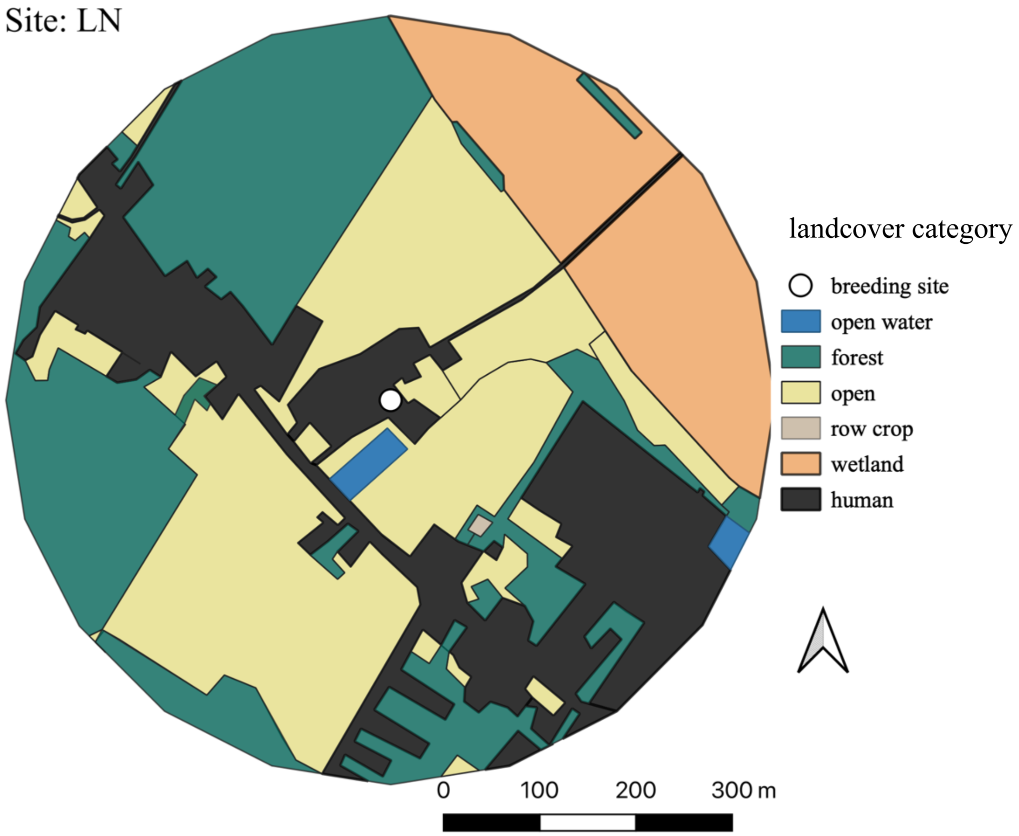

Site: WB
landcover category
○ breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

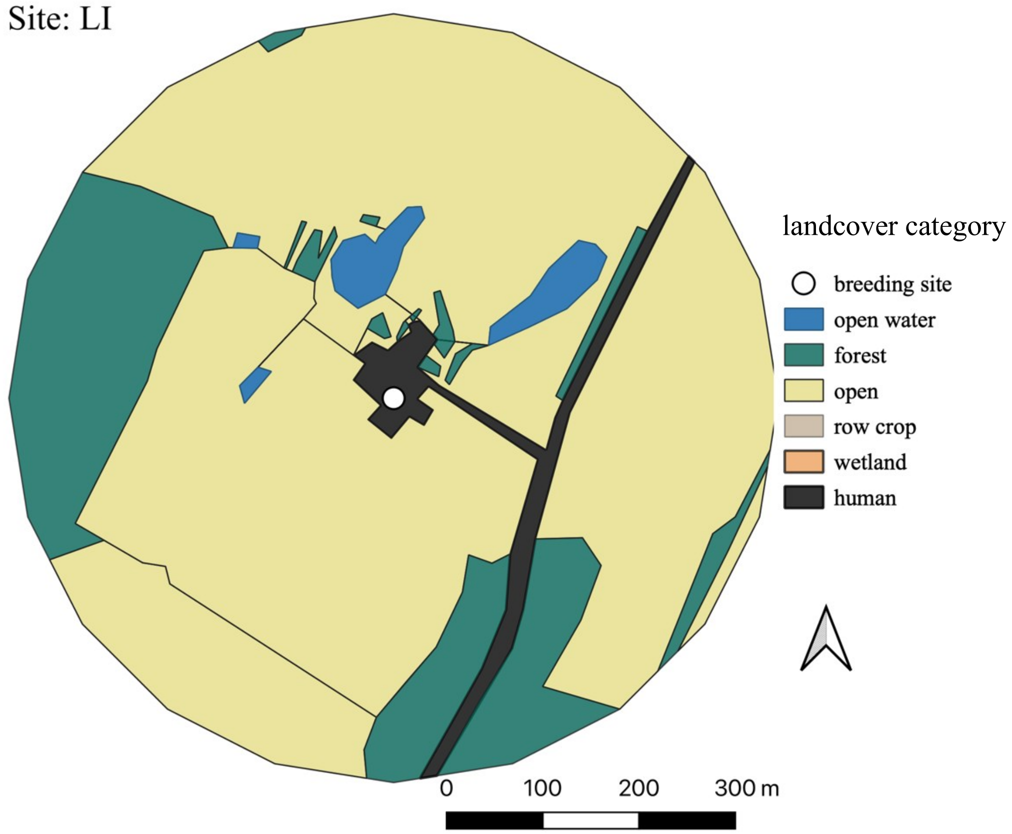

Site: OM
landcover category
○ breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

Site: MX

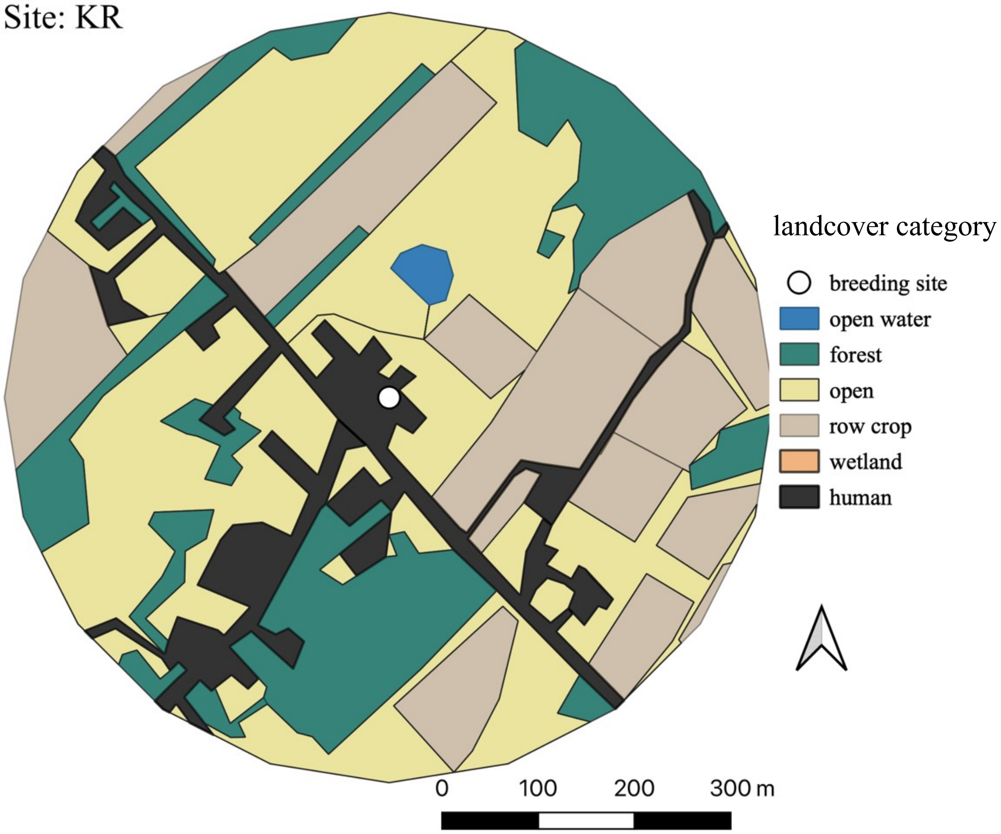

landcover category
○ breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

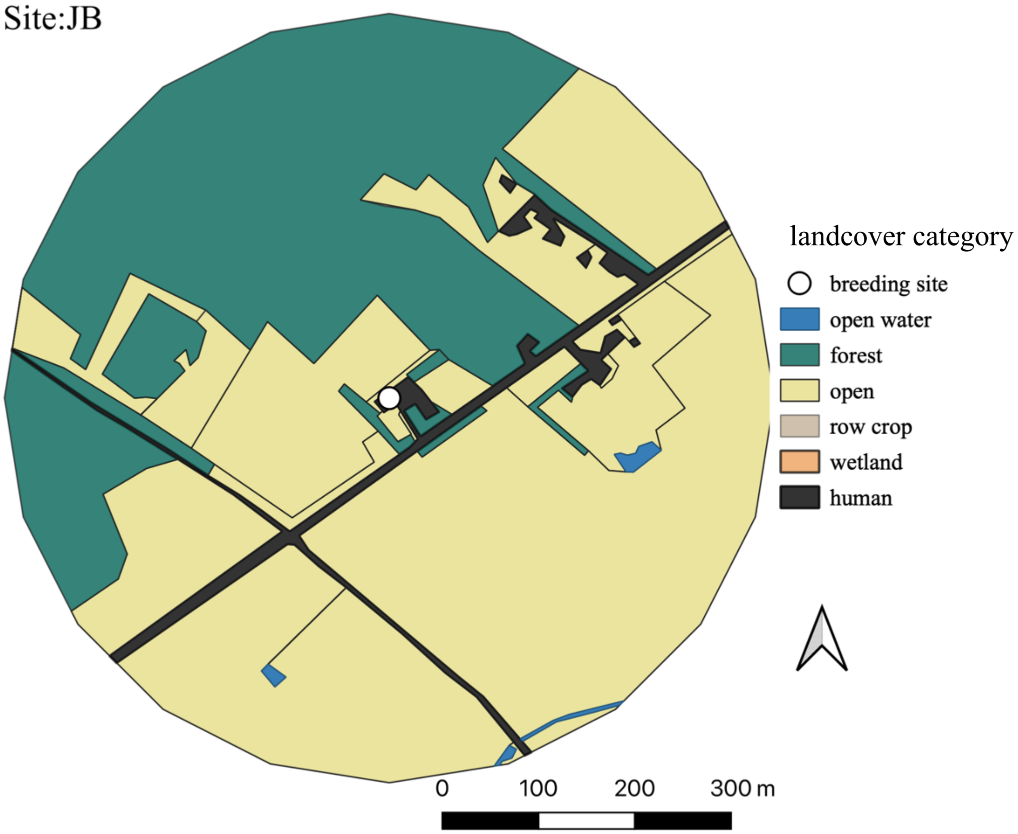

Site: MT
landcover category
○ breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

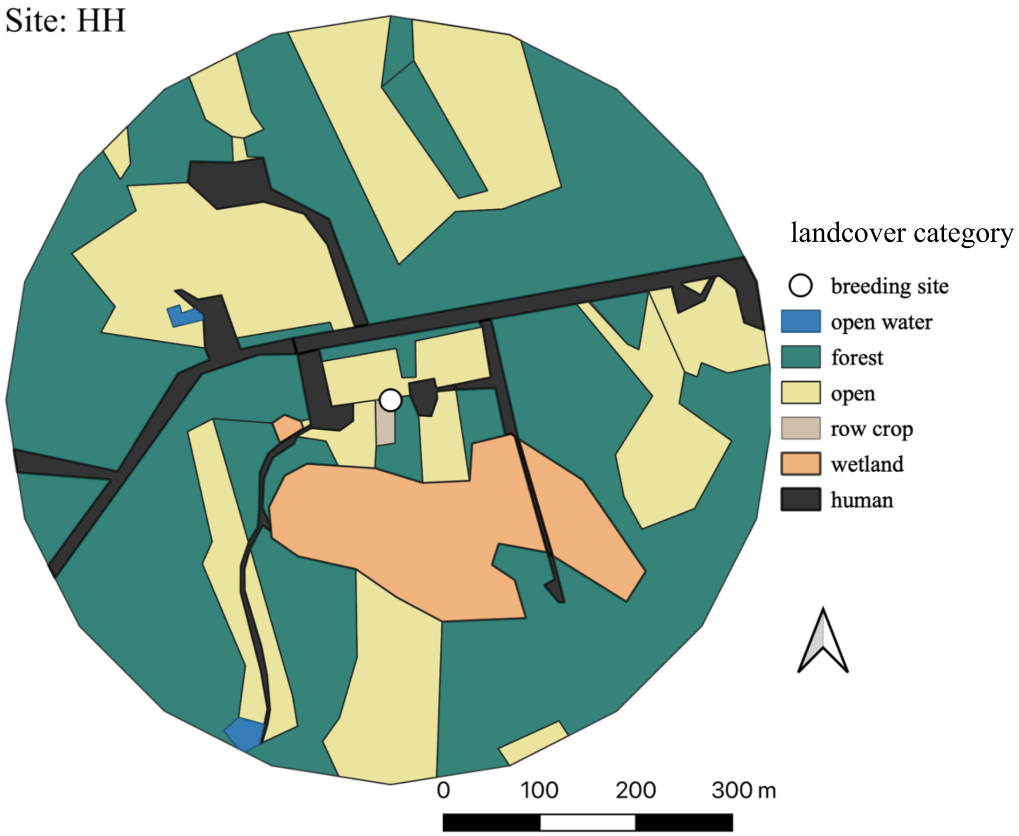

Site: LN
landcover category
breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

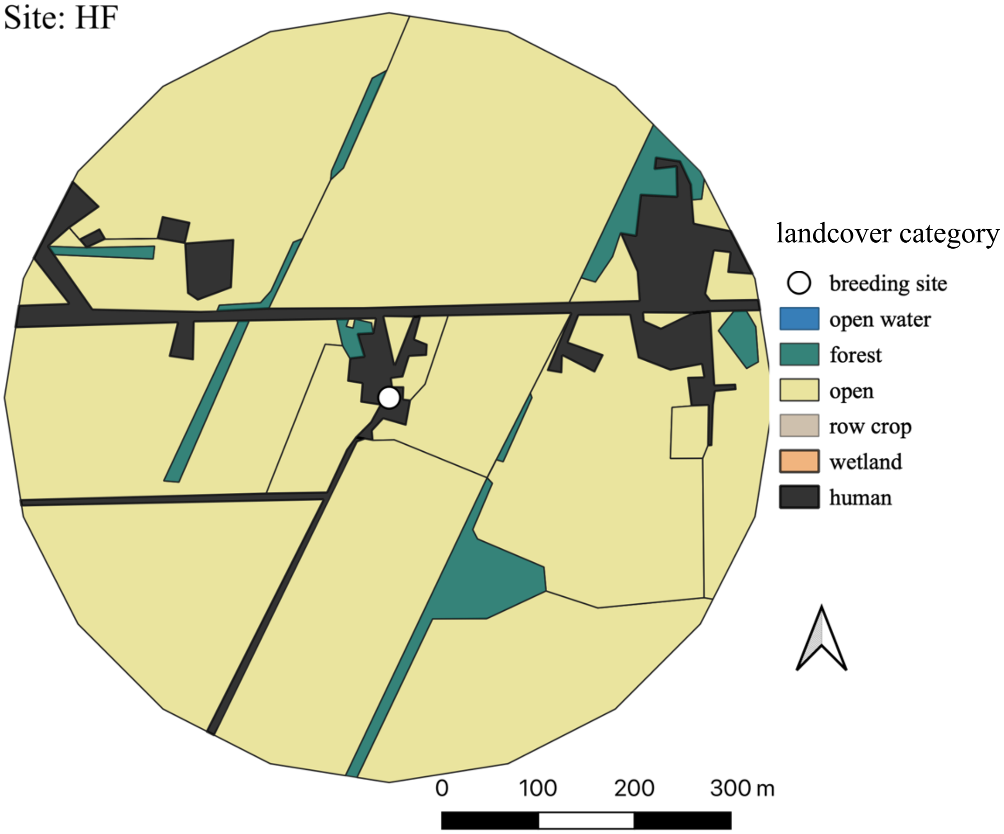

Site: LI
landcover category
○ breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

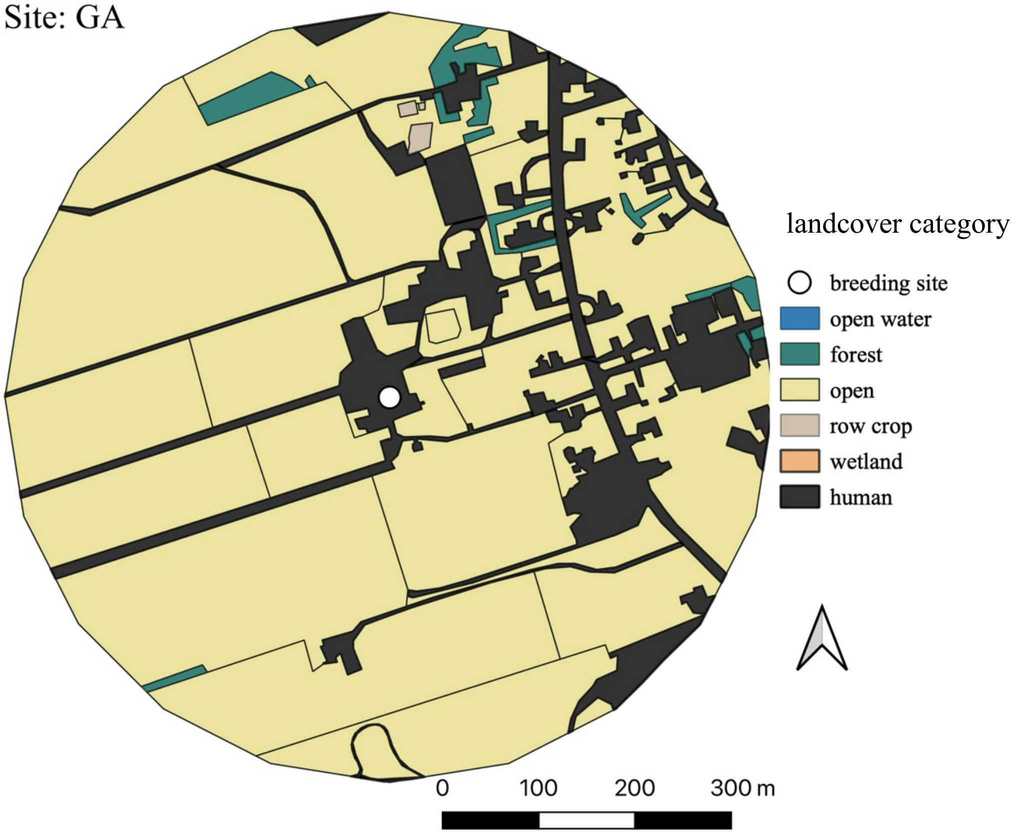
Site: KR


landcover category
breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m


Site:JB
landcover category
breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

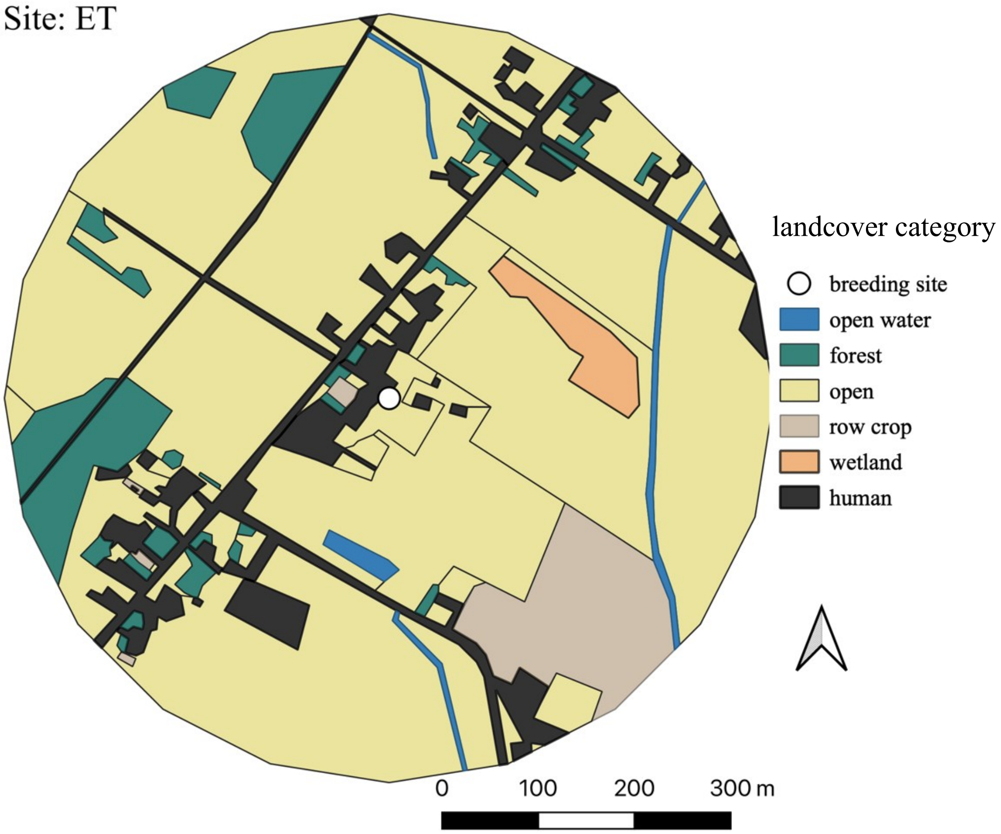

Site: HH
landcover category
breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m


Site: HF
landcover category
breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

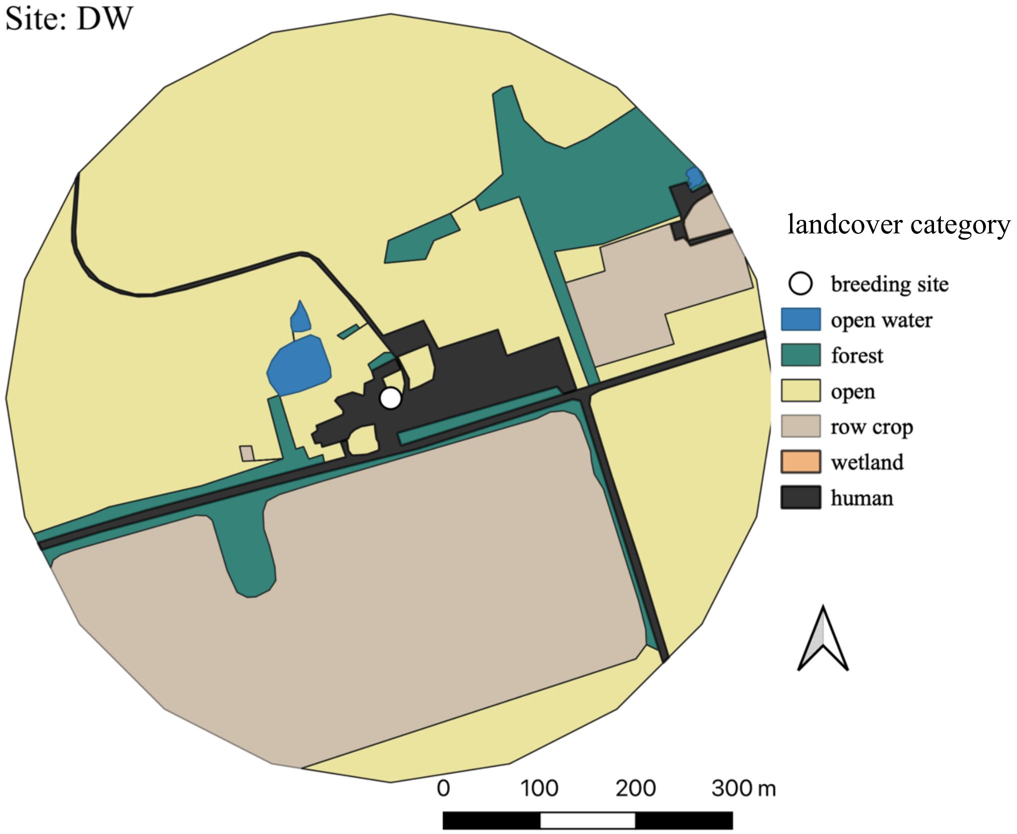


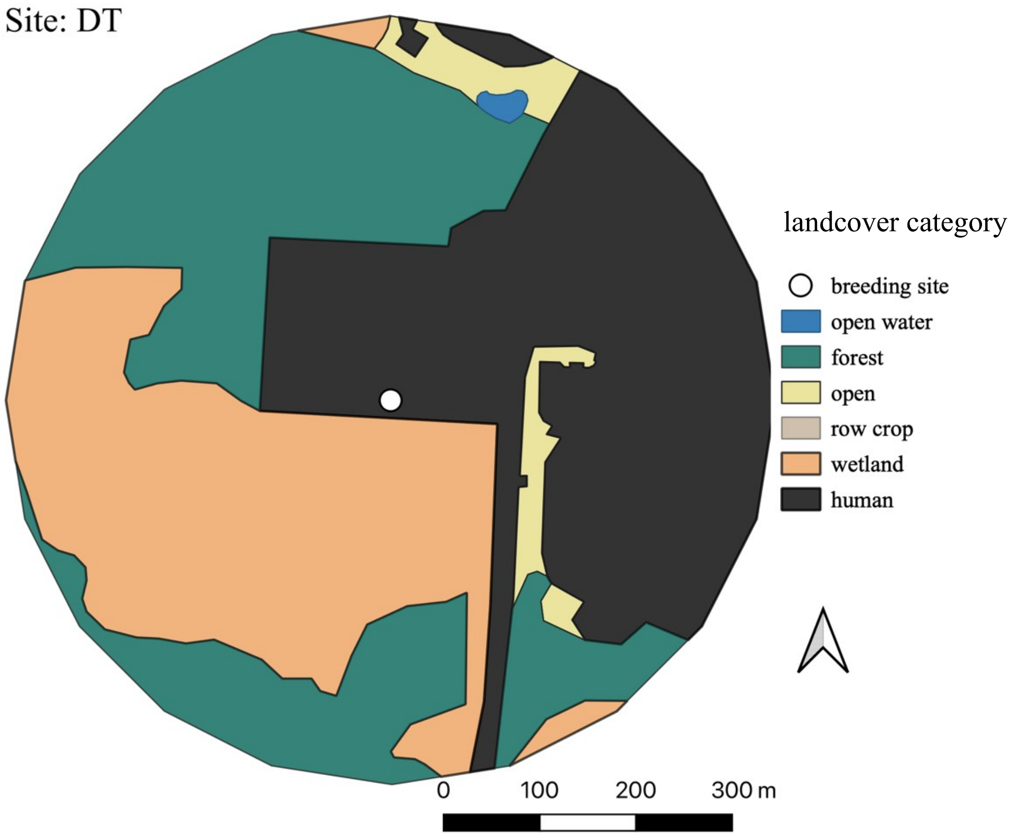
Site: GA

landcover category
○ breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m


Site: ET

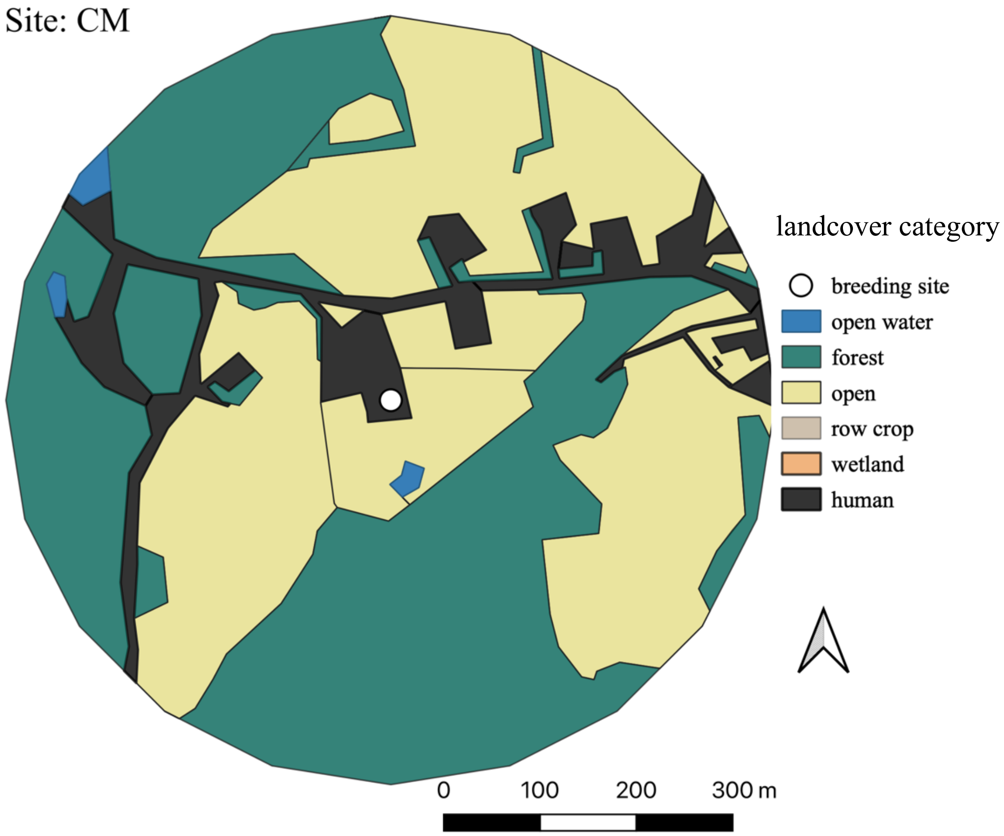
landcover category
breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m


Site: DW
landcover category
breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

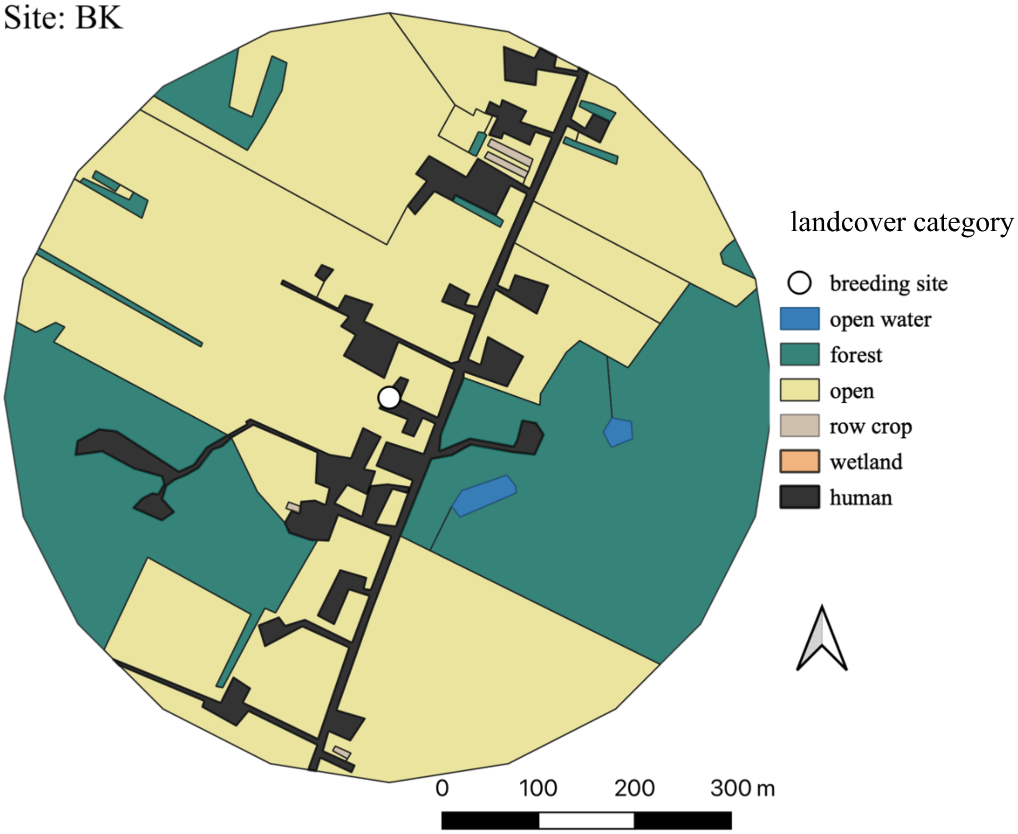


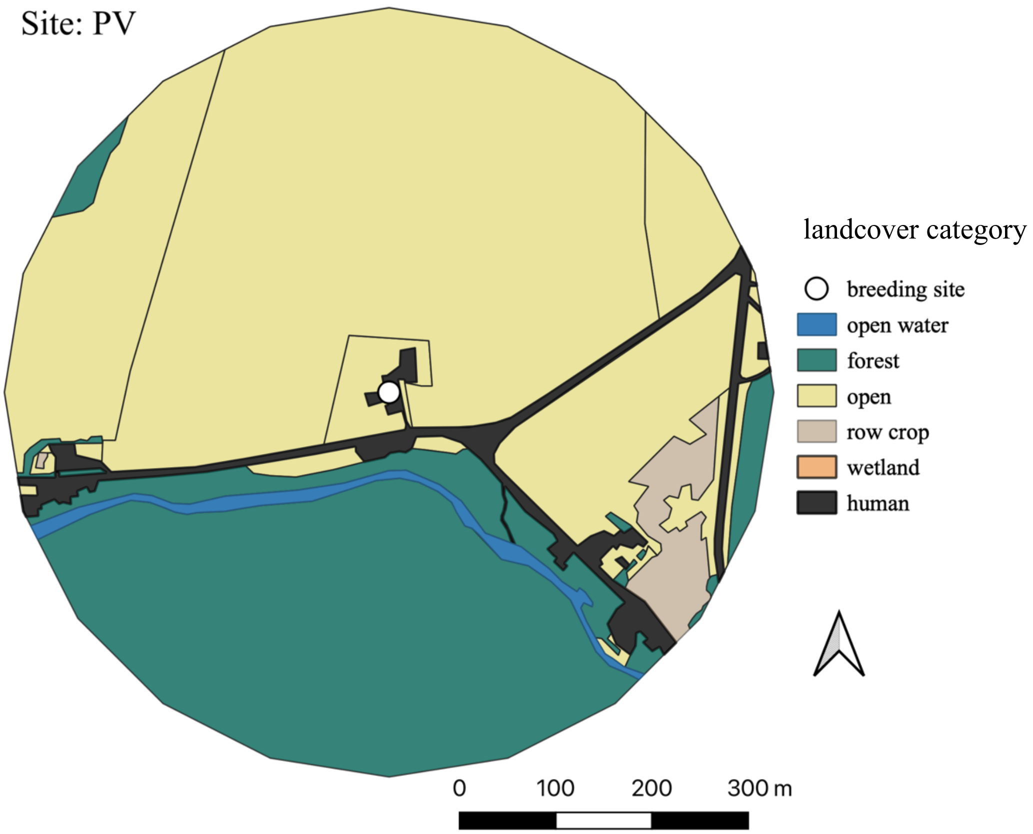
Site: DT

landcover category
○ breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m


Site: CM
landcover category
breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

Site: BK


landcover category
○ breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m


Site: PV
landcover category
○ breeding site
open water
forest
open
row crop
wetland
human
0
100
200
300 m

## Appendix B. Hierarchical Model Equations and Posterior Predictive Checks

Model: Full

$$MB \sim Binomial(n, p_{ybs})$$

$$logit(p_{ybs}) = \alpha_0 + \alpha_{0,bs} + \alpha_{0,y} + \beta_1 ROOF_b + \beta_2 WEATHst1_{bs} + \beta_3 WEATHst2_{bs} + \beta_4 WETLAND_{bs} + \beta_5 HUMAN_{bs} + \beta_6 WOODED_{bs} + \beta_7 OPEN_{bs} + \beta_8 LIVE_{bs} + \beta_9 WEATHyr1_y + \beta_{10} WEATHyr2_y$$

$$\alpha_{0,bs} \sim Normal(\alpha_{0,s}, \sigma_{0,bs})$$

$$\alpha_{0,s} \sim Normal(0, \sigma_{0,s})$$

$$\alpha_{0,y} \sim Normal(0, \sigma_{0,y})$$

$$\alpha_0 \sim Normal\ (0,1.5)$$

$$\beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \beta_6, \beta_7, \beta_8, \beta_9, \beta_{10} \sim Normal(0,1.5)$$

$$\sigma_{0,bs}, \sigma_{0,s}, \sigma_{0,y} \sim Exponential(1)$$

$$where\ b = 1 \ldots 60, s = 1 \ldots 18, y = 1 \ldots 5$$

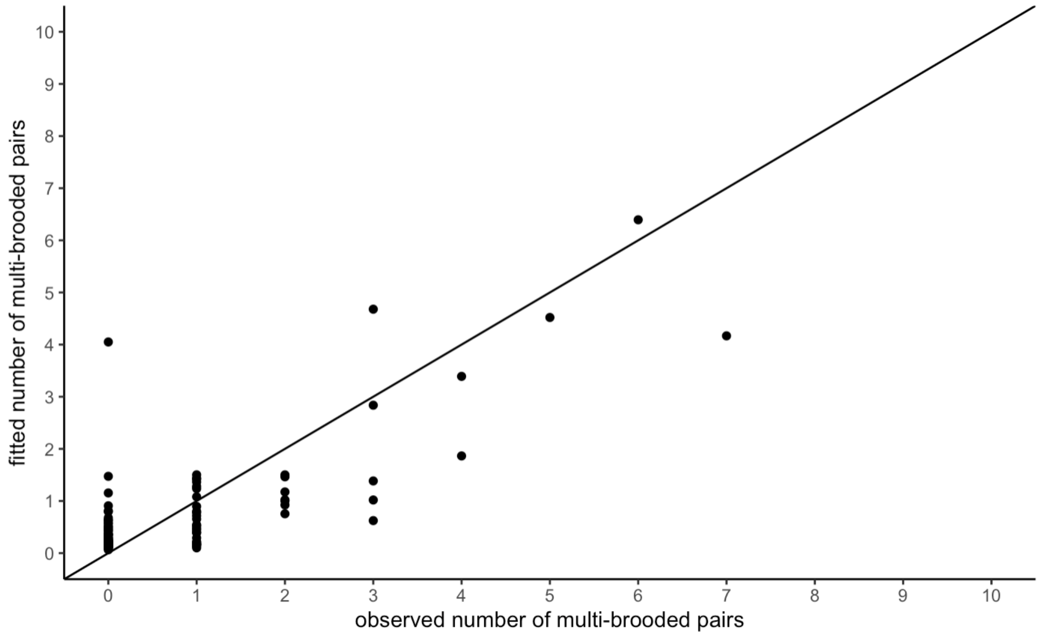


**Figure B1-** Posterior predictive check given the full model, predicting the probability of multiple brooding. If the model was perfect, the observed versus fitted number of multi-brooded pairs would align with the trend line.

Model: Intercept Only

$$MB \sim Binomial(n, p_{ybs})$$

$$logit(p_{ybs}) = \alpha_0 + \alpha_{0,bs} + \alpha_{0,y}$$

$$\alpha_{0,bs} \sim Normal(\alpha_{0,s}, \sigma_{0,bs})$$

$$\alpha_{0,s} \sim Normal(0, \sigma_{0,s})$$

$$\alpha_{0,y} \sim Normal(0, \sigma_{0,y})$$

$$\alpha_0 \sim Normal(0,1.5)$$

$$\sigma_{0,bs}, \sigma_{0,s}, \sigma_{0,y} \sim Exponential(1)$$

$$where\ b = 1 \ldots 60, s = 1 \ldots 18, y = 1 \ldots 5$$

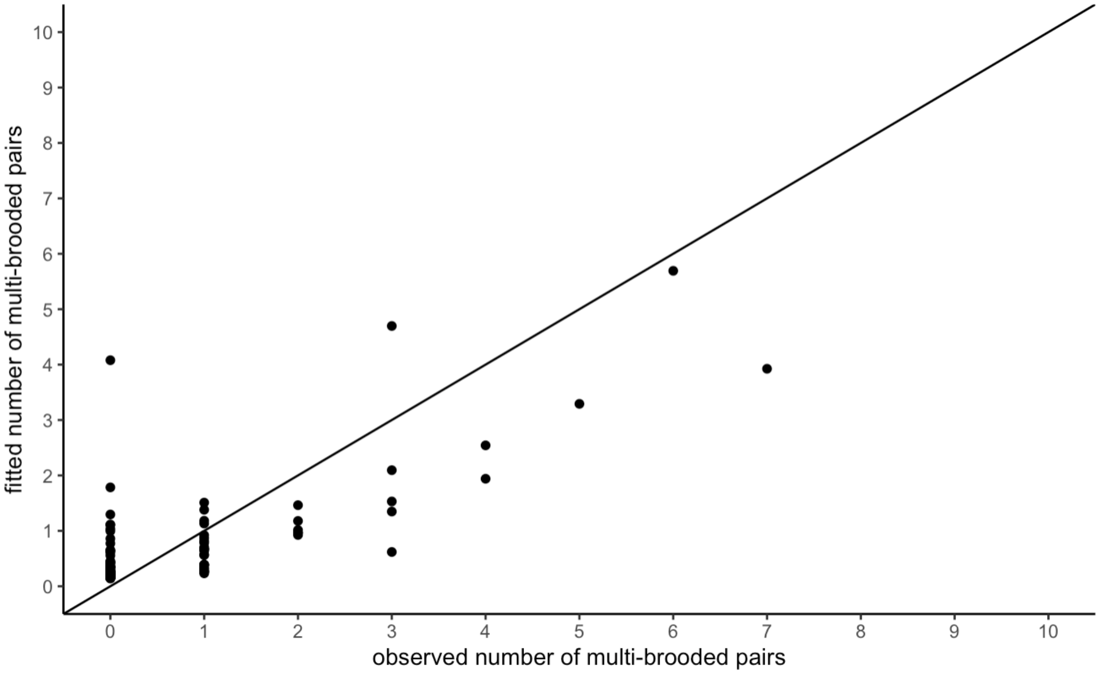


**Figure B2-** Posterior predictive check given the intercept only model, predicting the probability of multiple brooding. If the model was perfect, the observed versus fitted number of multi-brooded pairs would align with the trend line.

Model: Intercept with building level factors

$$MB \sim Binomial(n, p_{ybs})$$

$$logit(p_{ybs}) = \alpha_0 + \alpha_{0,bs} + \alpha_{0,y} + \beta_1 ROOF_b$$

$$\alpha_{0,bs} \sim Normal(\alpha_{0,s}, \sigma_{0,bs})$$

$$\alpha_{0,s} \sim Normal(0, \sigma_{0,s})$$

$$\alpha_{0,y} \sim Normal(0, \sigma_{0,y})$$

$$\alpha_0 \sim Normal(0,1.5)$$

$$\beta_1 \sim Normal(0,1.5)$$

$$\sigma_{0,bs}, \sigma_{0,s}, \sigma_{0,y} \sim Exponential(1)$$

$$where\ b = 1 \ldots 60, s = 1 \ldots 18, y = 1 \ldots 5$$

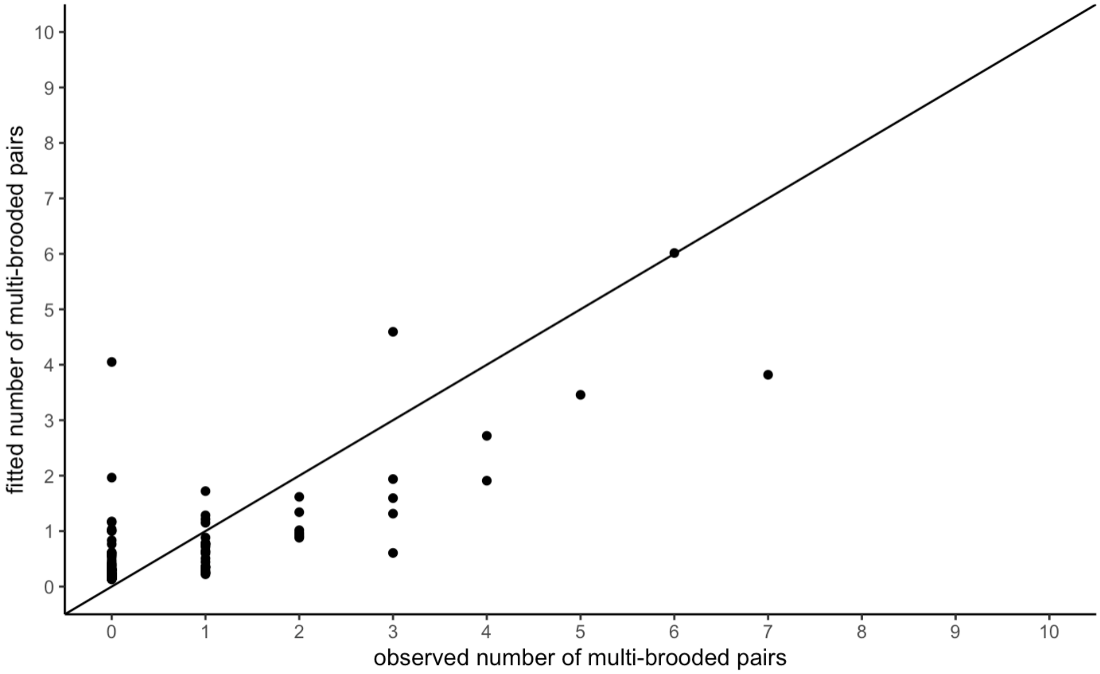


**Figure B3-** Posterior predictive check given the intercept model with building level factors, predicting the probability of multiple brooding. If the model was perfect, the observed versus fitted number of multi-brooded pairs would align with the trend line.

Model: Intercept with site level factors (best model)

$$MB \sim Binomial(n, p_{ybs})$$

$$logit(p_{ybs}) = \alpha_0 + \alpha_{0,bs} + \alpha_{0,y} + \beta_2 WEATHst1_{bs} + \beta_3 WEATHst2_{bs} + \beta_4 WETLAND_{bs} + \beta_5 HUMAN_{bs} + \beta_6 WOODED_{bs} + \beta_7 OPEN_{bs} + \beta_8 LIVE_{bs}$$

$$\alpha_{0,bs} \sim Normal(\alpha_{0,s}, \sigma_{0,bs})$$

$$\alpha_{0,s} \sim Normal(0, \sigma_{0,s})$$

$$\alpha_{0,y} \sim Normal(0, \sigma_{0,y})$$

$$\alpha_0 \sim Normal(0{,}1.5)$$

$$\beta_2, \beta_3, \beta_4, \beta_5, \beta_6, \beta_7, \beta_8 \sim Normal(0{,}1.5)$$

$$\sigma_{0,bs}, \sigma_{0,s}, \sigma_{0,y} \sim Exponential(1)$$

$$where\ b = 1 \dots 60, s = 1 \dots 18, y = 1 \dots 5$$

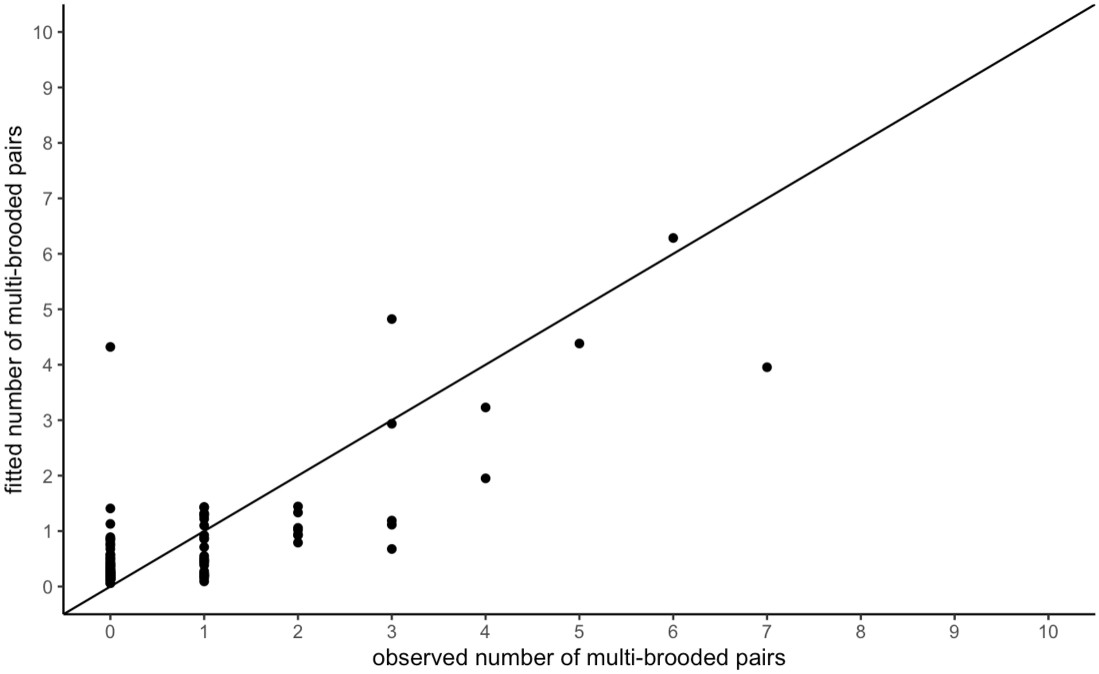


**Figure B4-** Posterior predictive check given the intercept model with site level factors, predicting the probability of multiple brooding. If the model was perfect, the observed versus fitted number of multi-brooded pairs would align with the trend line.

Model: Intercept with year level factors

$$MB \sim Binomial(n, p_{ybs})$$

$$logit(p_{ybs}) = \alpha_0 + \alpha_{0,bs} + \alpha_{0,y} + \beta_9 WEATHyr1_y + \beta_{10} WEATHyr2_y$$

$$\alpha_{0,bs} \sim Normal(\alpha_{0,s}, \sigma_{0,bs})$$

$$\alpha_{0,s} \sim Normal(0, \sigma_{0,s})$$

$$\alpha_{0,y} \sim Normal(0, \sigma_{0,y})$$

$$\alpha_0 \sim Normal(0,1.5)$$

$$\beta_9, \beta_{10} \sim Normal(0,1.5)$$

$$\sigma_{0,bs}, \sigma_{0,s}, \sigma_{0,y} \sim Exponential(1)$$

$$where\ b = 1 \ldots 60, s = 1 \ldots 18, y = 1 \ldots 5$$

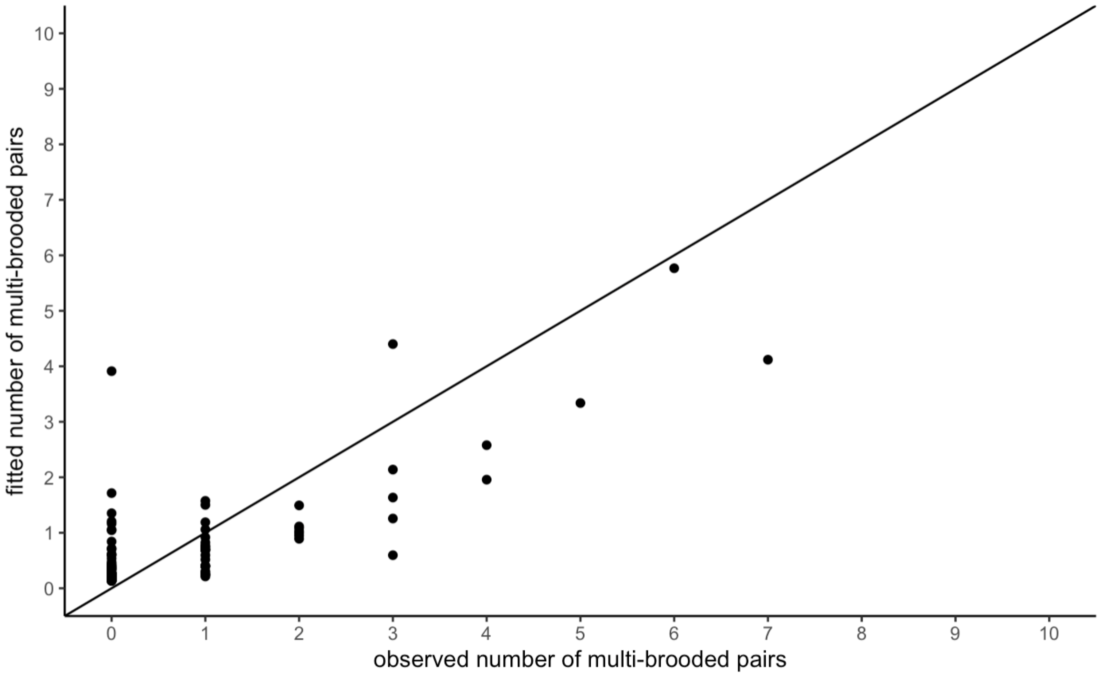


**Figure B5-** Posterior predictive check given the intercept model with year level factors, predicting the probability of multiple brooding. If the model was perfect, the observed versus fitted number of multi-brooded pairs would align with the trend line.