

# Examining the effects of local weather variation on the seasonal fecundity of passerines, using the Barn Swallow *Hirundo rustica* as a model

This thesis is being submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

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### Summary

Climate change will result in shifts in local weather conditions, with ramifications for important demographic processes such as seasonal fecundity. These may be mediated by the behavioural and strategic decisions associated with them. Despite predictions of increased wind speeds, few studies have examined the impact of wind, or the interactive effects of different weather variables, on seasonal fecundity. I test for these using the Barn Swallow *Hirundo rustica* as a model species. Twenty years of nest data from across Britain revealed interactive effects of both weather and land use on clutch size, hatching success and brood size.

Next, a model to describe seasonal fecundity based on a single population, that simultaneously considered weather-related carry-over effects from one stage to the next, revealed not all stages of seasonal fecundity were affected equally by weather. Conditions that promoted a positive response in one stage often resulted in a negative response in the following stage: for example conditions that promoted higher clutch sizes often resulted in reduced hatching success.

I next examined weather-related effects on female incubation behaviour; the sensitivity of which varied between hourly and daily time scales. There were weather related impacts, including from wind speed, on both female behaviour and the thermal environment of the nest.

Similarly, the mass of nestlings was more sensitive to weather than that of recent fledglings at both daily and lifetime scales. Nestling mass was negatively related to both temperature and rainfall, but this relationship was mediated by wind speed. Fledgling mass declined with temperature on days with high rainfall.

Overall, my results show that the interactive effects of weather can have important implications for seasonal fecundity. Wind speed typically has an overall negative effect on seasonal fecundity, through increasing the negative effects of rainfall or temperature; this may have implications for population trends and persistence of species such as the Barn Swallow, given predictions for increased wind speeds under future climate change.

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#### **Co-author contributions**

A version of Chapter 5: Contrasting sensitivity of nestling and fledgling Barn Swallow *Hirundo rustica* body mass to local weather conditions was published as:

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Richard Facey – conceived, designed, and wrote the manuscript. James Vafidis – helped with data collection and contributed to the analysis. Jeremy Smith – helped with data collection and contributed to the analysis. Rob Thomas and Ian Vaughan – Provided advice and guidance on the development of the manuscript.

# Table of Contents

SUMMARY	I
ACKNOWLEDGEMENTS	II
TABLE OF CONTENTS	IV
LIST OF FIGURES	VII
LIST OF TABLES	IX

CHAPTER 1: SEASONAL FECUNDITY AND THE EFFECTS OF WEATHER VARIATION	1
1.1 GENERAL INTRODUCTION	1
1.2 DEFINITIONS OF INDIVIDUAL FITNESS AND FECUNDITY	3
1.3 THE INFLUENCE OF WEATHER ON FECUNDITY IN BIRDS	5
1.4 THE EFFECT OF WEATHER ON THE COMPONENTS OF SEASONAL FECUNDITY	6
1.4.2 Incubation	8
1.4.3 Hatching	9
1.4.4 Nestling stage	11
<b>1.5 ECOLOGICAL TRAITS THAT APPEAR TO REDUCE SPECIES' SENSITIVITY TO WEATHER</b>	13
1.6 KNOWLEDGE GAPS AND AREAS REQUIRING MORE RESEARCH	15
1.6.1 Effects of Wind	15
1.6.2 Interactive effects of weather	16
1.6.3 Carry-over effects among the components of fecundity	17
1.7 THESIS STRUCTURE	18
1.8 MODEL SPECIES AND SYSTEM	20
1.8.1 Study Species	20
1.8.2 Data and Study Site	21

# CHAPTER 2: THE EFFECTS OF WEATHER AND LAND COVER ON BARN SWALLOW FECUNDITY AT A NATIONAL SCALE.....

ECUNDITY AT A NATIONAL SCALE 2	25
SUMMARY	25
2.1 INTRODUCTION	26
2.2 Methods	30
2.2.1 Nest Record Data	30
2.2.2 Weather and land use data	30
2.3 STATISTICAL ANALYSIS	31
2.4 RESULTS	35
2.5 DISCUSSION	44

#### CHAPTER 3: THE EFFECTS OF WEATHER ON THE SEASONAL FECUNDITY OF BARN

SWALLOWS	 50
SUMMARY	 
3.1 INTRODUCTION	 
3.2 METHODS	 

3.2.1 Study Site and Nest Monitoring	53
3.2.2 Weather data	54
3.3 STATISTICAL ANALYSIS	56
3.3.1 Stage 1: Effects of weather on the components of individual breeding attempts	s56
3.3.2 Stage 2: Effects of weather on Seasonal fecundity	60
3.4 RESULTS	62
3.4.1 Results from stage 1: the effects of weather on the individual components of	
fecundity	64
3.4.2 Results from stage 2: Sensitivity and combined effects of weather across	
breeding stages on seasonal fecundity	70
3.5 DISCUSSION	79

#### 

Summary	87
4.1 INTRODUCTION	89
4.2 Methods	
4.2.1 Temperature probe deployment	
4.2.2 Weather data	
4.3 STATISTICAL ANALYSIS	
4.4 RESULTS	
4.4.1 Hourly effects of weather on incubation behaviour	
4.4.2 Day-level effects of weather on incubation behaviour	103
4.4.3 Nocturnal nest temperature	103
4.5 DISCUSSION	106

#### 

SUMMARY	
5.1 INTRODUCTION	
5.2 Метнод	116
5.2.1 Nest monitoring	
5.2.2 Weather data	
5.3 STATISTICAL ANALYSIS	
5.4 RESULTS	120
5.4.1 The effects of weather on nestling mass	
5.4.2 The effects of weather on fledgling mass	123
5.5 Discussion	126

С	HAPTER 6: GENERAL DISCUSSION	
	6.1 Overview	
	6.2 THE IMPACTS OF WIND ON SEASONAL FECUNDITY	ERROR! BOOKMARK NOT DEFINED.
	6.3 THE INTERACTIVE EFFECTS OF WEATHER ON SEASONAL FECUNDITY	ERROR! BOOKMARK NOT DEFINED.
	6.4 TEMPORAL RESOLUTION OF WEATHER ON SEASONAL FECUNDITY	ERROR! BOOKMARK NOT DEFINED.

6.5 IMPLICATIONS FOR SEASONAL FECUNDITY AND BARN SWALLOW POPULATIONS ERROR! BOOKMARK
NOT DEFINED.
6.6 CONSIDERATIONS IN RELATION TO THE APPROACHES USED ERROR! BOOKMARK NOT DEFINED.
6.7 WIDER APPLICATIONS AND FUTURE DIRECTIONS ERROR! BOOKMARK NOT DEFINED.
6.7.1 Application of the seasonal fecundity model Error! Bookmark not defined.
6.7.2 Exploring heterogeneity and limits of responses to weather effectsError!
Bookmark not defined.
6.7.3 Understanding the weather-related causes of hatching failure Error! Bookmark
not defined.
6.8 GENERAL CONCULSIONS ERROR! BOOKMARK NOT DEFINED.

REFERENCES	
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# List of Figures

Figure 1.1: Conceptual model of seasonal fecundity in a multi brooding species with altricial young (adapted from Etterson <i>et al.</i> 2011)
Figure 1.2: Aerial view of Cardiff Riding School23
Figure 2.1: Frequency histograms of environmental variables included in the GAMM: a) total spring rainfall (mm), b) mean spring temperature (°C), c) mean spring wind speed (kph), and the proportion of land cover within 500m of the nest: d) grassland, e) freshwater, and f) built land use
Figure 2.2: Smoothed predictions of weather variables across Great Britain (all years combined) from the GAM to visualise geographical variation in weather
Figure 2.3: Predicted geographical variation in breeding parameters across the UK (all years combined) from the GAMMs to explain weather and land cover effects on: a) clutch size, b) hatching success, and c) brood size
Figure 2.4: Smoothed predictions of land cover use across Great Britain (all years combined) from the GAM to visualise geographical variation in land cover around each swallow nest
Figure 2.5: Fitted GAMM for the relationship between clutch size and: a) total spring rainfall (mm), b) the interaction between mean spring temperature (°C) and wind speed (kph), and c) the interaction between wind speed and the proportion of grassland within 500m of the nest
Figure 2.6: Fitted GAMM for the relationship between the hatching success and the interaction between a) winds speed and the proportion of grassland within 500m of the nest, b) temperature and the proportion of the built land cover within 500m of the nest and c) temperature and wind speed
Figure 2.7: Fitted GAMM for the relationship between brood size and: a) the proportion of grassland within 500m of the nest, and b) the interaction between total spring rainfall and mean spring wind speed
Figure 3.1: Boxplot of first and second breeding attempts, and plots of first egg date and average temperature during the pre-laying period, the start day of incubation and average temperature during incubation, day of hatching and average temperature during incubation, and day of hatching and mean ambient temperature during the chick stage 63
Figure 3.2: Model predictions for the effects of mean temperature, and wind speed, and total rainfall during the pre-laying period and the laying period

Figure 3.3: Fitted models (GEE-GLM) for the effects of on incubation duration, hatching
success, and the probability of a second brood being initiated in the Barn Swallow Hirundo
rustica

Figure 3.4: Fitted models (GEE-GLM) for the interactive effects of total rainfall and mean wind speed, and mean temperature and total rainfall during the first breeding attempt on the probability of a second brood being initiated in the Barn Swallow *Hirdundo rustica*... 69

Figure 3.5: Sensitivity of clutch size, incubation duration, hatching success, and brood	
survival under nine different weather scenarios	. 722

Figure 3.6: Sensitivity to weather of the number of fledglings produced in the first and
second brood, the probability of a second brood being initiated, and seasonal fecundity
overall
Figure 4.1: Example temperature trace from the nest of a Barn Swallow showing "on-bouts"
and "off-bout"

Figure 4.2: Modelled relationships (GAMMs) between time of day and a) off-bout duration, b) off-bout frequency and c) incubation constancy per hour, and d) nest temperature. 1000

Figure 5.1: Fitted relationships and 95% confidence interval for the short-term (within-day) negative effects on chick mass on the from the two-way interactions between a) mean ambient temperature and wind speed, and b) mean ambient temperature and total rainfall.

# List of Tables

Table 1.1: Examples of the range of terms and definitions used in studies of fecundity	4
Table 1.2: Total number of pairs breeding at the CRS during the period of study and the number subsequently included in the analyses for Chapter	23
Table 2.1: Parameter estimates, standard errors and p-values for GAMMs linking the thre components of fecundity to temperature, rainfall and wind seed and the proportion of lau use within 500m of each nest that was suburban/urban (built) and grassland on clutch siz hatching success, and brood size	e nd ze, 33
Table 3.1: Mean nest data for first and second breeding attempts, from 8 years of nest    monitoring of Barn Swallows    5	55
Table 3.2: Starting models for analysis of the effects of mean temperate, total rainfall (mr and mean wind speed on components of seasonal fecundity in the Barn Swallow <i>Hirundo rustica</i>	n), 59
Table 3.3: QIC values and results of likelihood ratio tests comparing starting models that included a "day" variable and one without, for each of the dependent variables analysed.	60
Table 3.4: Parameter estimates, standard errors and <i>p</i> -values for GEE-GLMs to explain the effects of temperature, rainfall and wind seed on the components of seasonal fecundity	е 68
Table 3.5: Predicted values for clutch size, incubation duration, brood survival, the number of fledglings produced for first and second breeding attempts, and the probability of a second brood in the Barn Swallow under twenty seven weather permerutations	er 76
Table 4.1: Mean values (± SD, range in parenthesis) for incubation behaviour, nest temperature, and weather variables at the level of hour and day. As temperature and wir speed values used in the analyses were means for the respective temporal scale, only the range is presented	nd
Table 4.2: Effects of rainfall, ambient temperature and wind speed on aspects on the incubation behaviour of female Barn Swallows Hirundo rustica at the level of hour and da	y)
Table 4.3: Effects of rainfall, temperature, and wind speed on the within-nest temperatur    of Barn Swallows Hirundo rustica at the level of hour and day	∙e )22 iv
	1/1

Table 5.2: Model outputs for daily effects of local weather on nestling and fledgling ma	ass.
	. 1222
Table 5.3: Model outputs for long-term (lifetime) effects of local weather on nestling a	nd
fledgling mass	12424

# Chapter 1: Seasonal fecundity and the effects of weather variation.

# 1.1 General Introduction

In order for individual organisms to maximize their lifetime fitness (i.e., lifetime reproductive success), life-history theory predicts that they should make strategic decisions that balance survival against current reproductive success (Searns 1992). The strategic behavioural decisions made by an individual bird (e.g., what to eat, when to breed, where to overwinter), are influenced by the local environmental conditions that it experiences (McNamara & Houston 1996). Individuals may make strategic decisions in response to short term environmental changes, such as changes in the weather within or among days, or over longer periods, such as across a season or as the result of climatic differences between years (Burger *et al.* 2012; Coe *et al.* 2015; Cuthill *et al.* 2000; Dawson *et al.* 2005; Vafidis *et al.* 2014).

In the short term, strategic decisions may, for example, include switching the mode or location of foraging activities; in bad weather, Barn Swallows *Hirundo rustica* provisioning chicks do not increase their energy expenditure to compensate for reduced foraging but instead increase their efforts when conditions are good, to allow their chicks to accrue body reserves (Schifferli *et al.* 2014). Likewise, under conditions that reduce chick provisioning, nestlings need to "decide" whether to invest energy into growth and development, or self-maintenance (Ambrosini *et al.* 2006 Dawson *et al.* 2005; Podlesak & Blem 2001; Sikamäki 1996). Longer-term decisions can include accruing body reserves due to longer term unpredictability in food supply (Vafidis *et al.* 2014), and decisions about whether to initiate multiple broods within a single breeding season (Nagy & Holmes 2005).

Individuals may also make strategic decisions in response to environmental variability, or by using current environmental conditions to predict those in the future. For example, European robins *Erithacus rubecula* achieved a higher mass at dusk on days when overnight temperature was likely to be lower (Thomas & Cuthill 2000). Increased daily gains in mass and fat reserves at dusk have also been linked to less predictable food supplies and temperatures during the preceding day, and with lower diurnal temperatures (Bednekoff *et* 

*al.* 1994; Cuthill *et al.* 2000; Ekman & Hake 1990). Longer term variation in the predictability of food may similarly require strategic responses. Vafidis *et al.* (2014) demonstrated that Eurasian reed warblers *Acrocephalus scirpaceus* occupying sub-optimal, dry scrub habitat on their wintering grounds maintained higher body reserves than those in their preferred wetland habitat – this was interpreted as a strategy to buffer against possible starvation due to the lower and less predictable food supply found in the dry scrub habitat. In these examples, individuals need to trade off the benefits of carrying greater body reserves, such as reduced short- and longer-term threats of starvation, against the disadvantages that higher body mass brings, such as increased flight costs, reduced foraging efficiency and increased predation rates (Blem 1975; Rogers 1987; Thomas 2000; Witter & Cuthill 1993).

Strategic decision making has to account for the complex and multifaceted nature of environmental change. Such changes occur across a wide range of spatial and temporal scales, affecting properties including average conditions and the frequency and magnitude of extreme events. Furthermore, multiple changes often co-occur (e.g., habitat degradation and climate change, Brook *et al.* 2008; Eglington & Pearce-Higgins 2012). Across much of Europe, recent decades have been a period of rapid warming with geographically variable changes in rainfall; while rainfall has increased by 10-40% in northern Europe, it has declined by 20% in southern Europe (Alcamo *et al.* 2007). Northern Europe is expected to experience more frequent periods of extreme weather, such as intense rainfall events, flooding and droughts (Alcamo *et al.* 2007; Kendon *et al.* 2014), as well as warmer spring and autumn temperatures (Xoplaki *et al.* 2005), and increased wind speeds (Vautard *et al.* 2010; Young *et al.* 2011).

A better understanding of strategic decision making is vital if we are to understand the responses of individuals and populations to these environmental changes, particularly as these responses can have longer term consequences. For example, decisions that affect nestling nutrition can have implications for nestling mass, which in turn can impact survival rates, recruitment, and even the condition and fledging success of their own, future offspring (Christensen-Dalsgaard *et al.* 2018; Magrath 1991; Mccarty & Winkler 1999; Tilgar *et al.* 2010). Despite the importance of considering behavioural responses to environmental change, models linking species' abundance and distribution to climate change have traditionally ignored these behavioural mechanisms, which is likely to impair the predictive power of these models under novel climatic conditions (Urban *et al.* 2016).

Understanding the impacts of climate change on the demographic processes that drive population trajectories is therefore important if we are to conserve biodiversity into the future. One approach is to use long term datasets recording demographic parameters along with contemporaneous climatic data (e.g., Morrison *et al.* 2013; Morrison *et al.* 2010), where such data exist. However, as the decisions made by individuals are influenced by their local environment (McNamara & Houston 1996), and as climate change will be manifested as changes to local weather, another approach is to use between- and withinbreeding season variation in weather as an analogue for longer-term climate change (e.g., Burger *et al.* 2012; Sabo *et al.* 2002; Salaberria *et al.* 2014). Fecundity is an important measure in determining lifetime fitness and is a primary driver of population dynamics and persistence (Etterson *et al.* 2011; Nagy & Holmes 2004, 2005; Sillett *et al.* 2000; Temple & Cary 1988; Bennett & Owens 1997). Therefore, a better understanding of the relationships between local weather, strategic decision making, and seasonal fecundity could provide important insights into the future impacts of long-term climate change on populations.

# 1.2 Definitions of individual fitness and fecundity

Within the literature, terms including *fecundity*, *annual fecundity* and *seasonal fecundity* are often used interchangeably (Table 1.1). Where a definition specifies a sex, it usually refers to the female (Table 1.1), likely due to the prevalence of extra-pair mating by males in many species of bird (Brouwer & Griffiths 2019) that makes identifying the number of young produced by individual males more challenging without genetic techniques. A unifying definition, again focusing on females, is provided by Etterson *et al.* (2011) who define fecundity as *'the number of offspring produced per female in a pre-defined period'*.

Within the context of this thesis, the focus is upon seasonal fecundity, defined as *the number of young fledged by an individual female in a single breeding season*. Seasonal fecundity is the result of a series of inter-related components (Etterson *et al.* 2011; Oppel *et al.* 2013) (Figure 1.1) but as it is concerned with only one breeding season, it does not include measures of the offsprings' post-fledging survival and subsequent recruitment into the breeding population. A change in any one or more of the constituent stages could affect seasonal fecundity, and determining which stage(s) drive changes in fecundity is a frequent research aim (e.g., Carro *et al.* 2014; Nagy & Holmes, 2004).

Table 1.1: Examples of the range of terms and definitions used in studi	es of fecundity.
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<u>Term</u>	Definition
Fecundity	Number of offspring produced per female in a pre-defined period (Etterson <i>et al.</i> 2011)
	The number of fledglings per pair per annum (Monadjem & Bamford 2009)
	The number of young that reach fledging age per female in a breeding season (Mattsson & Cooper 2007)
Annual Fecundity	Young fledged by an individual female in a year (Holmes, 2007) Annual number of eggs (Grüebler <i>et al</i> . 2010)
Seasonal Fecundity	The number of offspring produced by a female bird over a single breeding season (Oppel <i>et al.</i> 2013) Young fledged per female per breeding season (Pease & Grzybowski 1995)
(Breeding) Productivity	The number of fledglings per breeding attempt (Whitfield <i>et al.</i> 2008) Brood size (number of young ringed at 7-8 days of age) (Hušek
	et al. 2012) The number of young that survive the dependent stage per adult female within a breeding season (Mattsson & Cooper 2007)



Figure 1.1: Conceptual model of seasonal fecundity in a multi brooding species with altricial young (adapted from Etterson et al. 2011)

# 1.3 The influence of weather on fecundity in birds

The effects of climatic and local weather variation on seasonal fecundity have been the subject of much research. However, this research has often focused on local weather variation over medium to longer time scales (monthly to seasonally, e.g., Oppel *et al.* 2013), rather than the shorter timescales (hours to days, Coe *et al.* 2015) to which birds may respond immediately. In addition, research in this area has tended to focus on seasonal fecundity as a whole, or just one or two component parameters in isolation, for example using spring temperatures to explain variation in the timing of breeding (e.g., Burger *et al.* 2012). While there has been research examining the effects of short-term (daily or hourly) changes in weather conditions on the seasonal fecundity of birds, much has been framed within theoretical frameworks, such as optimal clutch size theory (e.g., Farnsworth & Simons 2001) or resource allocation (e.g., Dobbs 2006). Where studies have considered how

an individual's short-term responses to weather conditions affect components of fecundity, most have been framed in terms of determining fitness costs to breeding adults (survival, current and future breeding success, e.g., Stenseth *et al.* 2002; Hepp & Kennamer 2012) or offspring (phenotypic quality, survival, recruitment probability and future reproductive success, e.g., Ambrosini *et al.* 2006; Gorman *et al.* 2005). Fewer studies have examined short-term behavioural changes as adaptive, strategic, compensatory responses to short-term changes in weather.

# 1.4 The effect of weather on the components of seasonal fecundity

Weather may affect seasonal fecundity directly or indirectly. Indirect mechanisms include the effects of temperature, rainfall, and wind speed on the abundance and availability of food resources (Arbeiter *et al.* 2016; Dawson & Bortolotti, 2000; Grüebler *et al.* 2008; Pearce-Higgins *et al.* 2005). Such changes in food supply can in turn affect the behaviour and energetics of both parents and offspring, as well as the former's ability to invest in reproduction. Such changes are illustrated by the more rapid nest defence response of Eurasian reed warblers *Acrocephalus scirpaceus* to a perceived predator when provided with supplementary food, as compared to un-supplemented control birds (Vafidis *et al.* 2018). While males do incur costs during breeding (Bleu *et al.* 2016), these indirect weather effects may be expected to be stronger for females over all due to the demands of egg production, but perhaps expected to be strongest in species in which the female alone incubates the eggs, without mate provisioning, and solely care for young (Clutton-Brock 1991).

Direct weather effects may be mediated via alterations to the nest microclimate, the implications of which may vary between the stages of fecundity (see below and Chapters 3 and 4). For example, while higher nest temperatures can have a negative impact on developing embryos during incubation (Conway & Martin 2000; Scanes 2015), higher temperatures can increase survival and growth rates in nestlings as they are able to divert more energy into growth rather than thermoregulation (Dawson *et al.* 2005). Below I discuss weather effects on components of seasonal fecundity during some of the major

stages of a breeding attempt, namely the pre-laying/laying period, incubation, hatching, and the nestling phase.

#### 1.4.1 Pre-laying and Laying

Temperature can affect the timing of laying, typically with warmer spring temperatures leading to earlier laying (Dunn, 2004; Nooker *et al.* 2005; Saino *et al.* 2004). Such advancement of laying across recent decades is well-documented across a range of species (e.g., Pearce-Higgins *et al.* 2005; Visser *et al.* 2009; Winkler *et al.* 2002). This may be related to a combination of factors including food availability, lower energetic costs for females, and earlier stimulation of gonad development (Dunn, 2004; Nooker *et al.* 2005; Saino *et al.* 2004). However, rainfall and/or wind speed ("windiness") may have more influence on laying date, hatching date, and clutch intiation in some avian taxa, such as aerial insectivores, than temperature (Irons *et al.* 2017; Møller 2013).

Clutch size appears to be relatively insensitive to temperature, with a range of studies showing no relationship between temperature and clutch size across many species at both the level of breeding attempt (i.e., short-term) and season (long-term) (e.g., Spotless Starling Sturnus unicolor Salaberria et al. 2014; Red-Backed Shrike Lanius collurio Golawski 2008; Black-Headed Gull Chroicocephalus ridibundus Theyn & Becker 2006; Red Grouse Lagopus lagopus Fletcher et al. 2013; Great tit Parus major Vedder 2012). This is not universal, however; for example, Nol et al. (1997) found that Semipalmated Plovers Charadrius semipalmatus laid smaller clutches in years of lower-than-average temperature. While clutch size is frequently negatively correlated with laying date (Nooker et al. 2005, but see Winkler et al. 2002), it is likely that decisions regarding clutch size are based on energetic constraints on larger clutches later in the reproductive cycle, such as the higher energetic costs of incubating larger clutches (Morneo et al. 1991; Heaney & Monaghan 1996; Reid et al. 2000a; Visser & Lessells 2001). In the short-term, investment in reproduction can also involve adjustment of egg volume or mass and quality (i.e., increased concentrations of compounds such lysozyme and carotenoids that are important for embryo/offspring performance); both mass and/or volume, and quality havebeen shown to increase with temperature (Nooker et al. 2005; Saino et al. 2004; but see Golawski 2008, and Vedder 2012). Such temperature related increases in investment in eggs size or composition may have further benefits; for example, larger egg volume has been linked to

higher hatching rates (Saino *et al.* 2004). Rainfall has also been linked to changes in clutch size in both the short- and long-term. For example, while Theyn & Becker (2006) found no effect of temperature during laying on clutch size in Black-headed Gulls but laid larger clutches (typical clutch size 1-3 eggs) when laying occurred in wetter weather. . Likewise longer-term patterns of rainfall can have impacts on clutch size; higher pre-breeding season rainfall led to an increase in probability of three or four egg clutches (cf. 1–2 egg clutches) in the Montserrat Oriole *Icterus oberi* (Oppel *et al.* 2013). Such increases in clutch size in wetter weather may be due, as in the above two examples, to increased food abundance meaning females were in better condition prior to egg-laying (Theyn & Becker 2006; Oppel *et al.* 2013).

#### 1.4.2 Incubation

A range of factors including food abundance, clutch size and the perceived risk of nest predation can affect incubation behaviour and duration, but weather may also have a large effect (Ardia et al. 2010; Conway & Martin 2000a & b; Cooper & Voss 2013; Nagy & Holmes 2004; Zicus et al. 1995, Vafidis et al. 2018). Temperature appears to be particularly important during incubation as it affects a number of energetic aspects, such as rewarming of eggs, or the ability of incubating parents to forage and maintain their own condition (Bryan & Bryant 1999; Griffith et al. 2016; Jones 1989; Reid et al. 1999). In the short term, temperature has been linked to the onset of incubation, incubation duration, the maintenance of egg temperatures, and the behaviour of parent birds during incubation (Carroll et al. 2018; Haftorn 1988; Bryan & Bryant 1999; Cresswell 2004; Ardia et al. 2009; Camfield & Martin 2009; Conwayet et al. 2000a, 2000b; Ardia et al. 2010, Schulze-Hagen 1969; Ribault 1982; Coe 2015). Ardia et al. (2009) found that female Tree Swallows Tachycineta bicolor incubating in experimentally heated nest boxes maintained higher egg temperatures during incubation compared to control females. Similarly, Mueller et al. (2019) showed that heating the nests of Prothonotary Warblers Protonotaria citrea shortened incubation duration. Reduced incubation duration under warmer ambient temperatures may be the result of reduced energetic demands (e.g., slower cooling rates leading to less energy to rewarm eggs) or though mechanisms such as "ambient incubation" whereby ambient temperature is sufficiently high to facilitate embryo development, even in the absence of an incubating parent (Griffith et al. 2016). Contrary to this, Higgott et al. (2020) found evidence for increasing incubation duration with temperature in the Long-tailed Tit *Aegithalos caudatus,* although the cause of this increase was not clear.

Higher rainfall has also been shown to affect incubation behaviour, for example increasing nest attendance or resulting in shorter absences from the nest (Kovařík *et al.* 2009; Coe *et al.* 2015). In the Long-tailed Tit, incubation duration increases with the proportion of rainy days (Higgott *et al.* 2020). Rainfall has, however, been shown to have no effect on incubation behaviour in the Great Tit *Parus major* (Basso & Richner 2015; Schöll *et al.* 2020). While it is not clear what drives these interspecific differences in response, it may be due to energetics; despite both species laying similar sized clutches (Robinson 2005), the Great Tit is almost twice the mass of a Long-tailed Tit. Perhaps Great Tits are able to better weather periods of heavier or above average precipitation by having larger overall body reserves on which to draw? Or perhaps the cavities in which Great tits nest provide greater insulation overall compared to the nests of Long-tailed Tits, which nest in bramble and scrub?

Wind speed may also have an impact on incubation behaviour; increased air flow over the nest is likely to increase egg cooling rates and thus increase the energy required to re-warm eggs (Wang & Beissinger 2009; Gray and Deeming 2017; Heenan & Seymour 2012; Hilton *et al.* 2004). Heenan and Seymour (2012) estimated that, even at relatively low speeds, compensating for the convective heat loss by eggs caused by air flow through a nest could require almost double the heat production by the incubating parent. Consistent with this, Hidle *et al.* (2016) found that higher wind speeds increased incubation effort (expressed as the amount of mass lost during incubation) in the Common Eider *Somateria mollissima*.

#### 1.4.3 Hatching

The impacts of weather on hatching success can occur as early as egg formation, if weather affects foraging ability and thus the quality of the eggs laid by a female. For example, high temperatures during laying resulted in female Barn Swallows laying eggs which had a higher hatching success (Saino *et al.* 2004). Delays in the start of incubation can also affect

hatching success; Wang and Beissinger (2009) demonstrated that increases in rain or wind speed delayed the start of full incubation across a range of species, which in turn led to lower hatching success. Weather conditions during incubation can have an impact on hatching by affecting embryo development or viability. Optimal embryo development occurs within a narrow range of temperatures, between 36.0 and 40.2°C (Conway & Martin 2000, Scanes 2015), thus the mechanisms driving weather related impacts on hatching success are related to those discussed above for incubation behaviour and duration; weather conditions that promote the maintenance of more stable thermal nest environments (for example through higher nest attendance which would lead to a reduction in the fluctuation in temperature experienced by the embryo) are less likely to incur fitness consequences on developing embryos compared to weather conditions that force incubating parents to neglect their clutch for prolonged periods of time (Olson *et al.* 2006).

That said, the influence of weather on hatching success appears to be variable across species. For example, while Rodriguez & Barba (2016) found that temperature during incubation did not affect hatching success and Higgot et al. (2020) found only minor evidence for the impact of temperature and rainfall on hatching success over the same period. Nol et al. (1997) found reduced hatching success in years of lower-than-average temperatures. Wesołowski et al. (2002) and Martin et al. (2017) found that heavy rain in the short-term (days) can led to reduced hatching success. Equally, exposure to high temperatures, specifically prolonged exposure to temperatures above the ideal maximum for development during incubation, can lead to increases in abnormal development and embryo mortality (Conway & Martin 2000, Scanes 2015). These apparently contradictory and inconsistent effects of weather conditions on hatching success in different species and studies are likely to be partly the result of variation in life history traits between species (e.g., cavity versus open cup nesting, see below). Furthermore, the tolerance of embryos to egg-neglect changes with age (Cooper & Voss 2013), and incubating parents can alter their incubation behaviour, in part, in response to changes in weather (e.g., Coe et al. 2015, see Chapter 4).

#### 1.4.4 Nestling stage

Weather variation can impact on the nestling stage via direct mechanisms that alter energetic costs, demands or allocation by chicks (Sikamäki 1996; Dawson et al. 2005), or by indirect mechanisms, for example by altering prey availability and provisioning rates (Ritz et al. 2005; Grüebler et al. 2008). The balance between these two mechanisms likely determines the relationship between weather variables and the nestling phase. Temperatures have been shown to increase several traits associated with the nestling stage (hatching to fledging) including nestling survival, feather development, growth, and body mass (Podlesak & Blem 2001; Dawson et al. 2005; Ambrosini et al. 2006; Salaberria et al. 2014; Bourne et al. 2020). In many temperate habitats, warmer temperatures would be expected to have a positive effect on such characteristics, through increased food availability for insectivorous species, and reduced energetic costs of thermoregulation allowing chicks to allocate nutrition to growth rather than self-maintenance. This has been observed to an extent; for example, Tree Swallow nestlings from experimentally warmed nests had a greater survival rate, faster feather development and were heavier, compared to nestlings in unheated control nests (Dawson et al. 2005), likely due to a reduction in the chicks' energy demands. Podlesak & Blem (2001) found nestling mass, survival and growth rate were higher in a "warm" year, compared to a cold one. Similarly, de Zwann et al. (2019) found that nestling Horned Larks Eremophila alpestris delayed their development during cold temperatures, and Fernaz et al. (2012) found that in nestling Barn Swallows mass and feather development were lower during cold weather.

Extremes of high temperature can be particularly problematic and may result in negative effects on the nestling stage (Rodrigez & Barba 2016; Adreasoon *et al.* 2019; Imlay 2019). Rodrigez & Barba (2016) showed that nestling Great Tits from experimentally heated nests were lighter in mass at 15 days old than nestlings from unheated control nests; a similar relationship between mass and temperature has been found in Cliff Swallows *Petrochelidon pyrrhonota* (Imlay *et al.* 2019). Lower mass from high or regionally extreme temperatures may be the result of evaporative heat loss and dehydration and may be fatal. Extremely high temperatures therefore have the potential to be catastrophic for seasonal fecundity; for example, Bourne *et al.* (2020) showed that exposure to high temperatures in the southern Kalahari not only reduced survival probabilities of nestling Pied Babbler *Turdoides bicolor*, but no young survived when mean maximum temperatures exceeded 38°C.

Generally, rainfall appears to have a negative effect on nestling provisioning rates, survival, and fledging success likely through mechanisms such as reduced prey availability or through negative effects on chick thermoregulation, for example via chilling of wet chicks (e.g., Arlettaz et al. 2010; Conrey et al. 2016; Crombie & Arcese 2018; but see Oppell et al. 2013). Schöll and Hillie (2020) found that heavy and persistent rainfall during the nestling stage led to a reduction in the survival of Great Tit chicks to the extent that it not only led to brood reduction, but also to the loss of entire broods, as a result of negative impacts on food availability and chick thermoregulation. Similarly, rainfall has been shown to have a negative effect on nestling mass and growth rates across a range of species (e.g., Cirl Bunting Emberiza cirlus Evans et al. 1997; Pied Flycatcher Ficedula hypoleuca Siikamäki 1996; Eurasian Bittern Botaurus stellaris Kasprzykowski et al. 2014; Gambel's White-Crowned Sparrow Zonotrichia leucophrys gambelii and Lapland Longspur Calcarius lapponicus Pérez et al. 2016). However, as with temperature, rainfall effects are not consistent across all species. For example, Kruuk et al. (2015) found a positive association between chick mass and high levels of precipitation during the nestling phase in the Superb Fairy-wren Malurus cyaneus. Similarly, Vernasco et al. (2018) found that nestling Wood Thrush Hylocichla mustelina survival declined in drought years but this was mediated by the amount of mature forest cover. Drought years were also associated with lower nestling body condition, brood size, and delayed post-fledging dispersal. However, at a seasonal level, pre-breeding rainfall had no effect on re-nesting probability or nest survival in the Montserrat Oriole Icterus oberi (Oppel et al. 2013).

The effects of temperature can vary within a season. In a study of Spotless Starlings *Sturnus unicolor* nesting in the Mediterranean region, Salaberria *et al.* (2014) showed that while temperature had no effect on mass or tarsus length in nestlings from first broods (when temperatures were generally cooler), it had a negative effect on those in second broods (when temperatures were higher), despite them being reared in the same nest. The effect of temperature on nestling growth differed between first and second broods; while first brood nestlings had longer wings and bills with increasing temperature, second brood nestlings were found to have shorter wings and bills with increasing temperature. Similarly, the effects of rain on the nestling phase can vary temporally, either with chick age or the time scale at which rain is measured. Mainwaring and Hartley (2016) found evidence that

later-hatched nestlings showed larger mass changes during low levels of rainfall but in early-hatched nestlings mass change was greatest during higher levels of rainfall. At the level of season, rainfall can have a positive effect on nest survival, but daily nest survival can be negatively impacted by daily rainfall or individual rainfall events (e.g., Mountain Plover *Charadrius montanus*, Dreitz *et al.* 2012, Dunnock *Prunella modularis* Harrison & Whitehouse 2012, Lark Bunting *Calamospiza melanocorys* Skagen & Adams 2012). Similar impacts of rainfall have been found in Marabou Storks *Leptoptilos crumeniferus*, with higher non-breeding season rainfall being linked to earlier nesting the next year and higher nest success, but higher rainfall within the breeding season being associated with lower nest success. Rainfall effects are not, however, necessarily scale-dependent in all species; Wright *et al.* (2009) found a negative association between the numbers of fledglings produced (in relation to the number of eggs laid) and rainfall, both at the temporal level of brood and of season.

Wind is an important meteorological variable that is likely to affect the nestling phase of insectivorous birds, through changes in prey abundance and availability (Quinney *et al.* 1986; Dawson *et al.* 2000; Grüebler *et al.* 2008; Møller 2013), and by altering the nest microclimate and costs of thermoregulation (Salzman 1982; Bakken *et al.* 2002; Heenan & Seymour 2012; Gray & Deeming 2017). Comparatively few studies, however, have linked higher wind speeds to reduced nestling growth; for example in nestling Blue Tits *Cyanistes caeruleus* (Mainwaring & Hartley 2016), Black-legged Kittiwakes *Rissa tridactyla* (Christensen-Dalsgaard *et al.* 2018) and Eurasian Bittern (Kasprzykowski *et al.* 2014). In contrast to rainfall and temperature, and despite growing evidence of its influence on reproductive traits (Møller 2013; Irons *et al.* 2017), the impact of wind speed on the nestling phase has received less attention and is less well known (Irons *et al.* 2017; Mainwaring & Hartley 2013).

# 1.5 Ecological traits that appear to reduce species' sensitivity to weather

Understanding the implication of weather variation on seasonal fecundity and its individual components requires examining weather variation at differing temporal scales. As shown

above, the effects of weather vary between the component stages of seasonal fecundity. The exact nature of those impacts may be dependent on the inherent nature of the component (see above) but also on the life-history, breeding behaviour or ecology of the species concerned. Life-history traits such as mate provisioning are likely to buffer the (energetic) impacts of weather on reproduction. For example, mate-provisioning in the Red-backed Shrike *Lanius collurio* is thought to explain the lack of a relationship between ambient temperature or rainfall and clutch size or hatching success (Golaswki 2008). Behavioural plasticity will also help reduce or eliminate negative impacts of poor weather conditions or allow individuals to take advantage of good conditions. For example, experimental heating of Blue Tit nest boxes leads to earlier hatching as a result of increased nocturnal incubation by females prior to clutch completion (Vedder 2012). Here Blue Tits were likely using temperature as a cue indicating a perceived early food-peak and adjusted their incubation strategy in response (Vedder 2012).

The effects of weather on incubation behaviour and duration are likely to be dependent on a combination of behavioural plasticity by incubating parents, involving short-term behavioural adjustments to current weather conditions (Coe *et al.* 2015, see also Chapter 4), and their ecological or life history traits. The choice of nest type (e.g., cavity/burrow versus "open" nests) or nest structure can help to alleviate some impacts; for example Tree Swallow nests that contained more feathers and with deeper cups cooled at slower rates during breaks in incubation (Windsor *et al.* 2013). Parenting strategy (e.g., bi- versus uniparental incubation) will also play a part in determining the impacts of weather and hence the mechanisms that could be employed to mitigate for those impacts; species in which only one sex incubates (typically the female) would be expected to be more sensitive to weather as the female bears the whole of the energetic cost of incubation.

Similar relationships are observed for post-hatching stages of fecundity. Hatching asynchrony may reduce the effects of weather on food supply by spreading out the energetic requirements of the brood; or by providing a mechanism to reduce the energetic demands of the brood overall during times of reduced food availability, either "accidentally" (i.e., the youngest dying from starvation from being out-competed for scant resources) or deliberately (i.e., infanticide/ fratricide and consumption of smaller nestlings, e.g., O'Connor 1978). Before this fatal end point is reached, however, adverse effects of weather

can be combated by the differing allocation of resources, notably: i) by parents using honest signals to determine food requirements among nestlings, and thus share food more evenly, or through changes in the frequency, timing or type of food they provide (Dawson *et al.* 2000; Paiva *et al.* 2006); ii) nestlings "opting" either to invest in thermoregulation over growth or to prioritise the development of some tissues over others (Lepczyk & Karasov 2000; Metcalfe & Mongahan 2001; Schifferli *et al.* 2014; Honarmand *et al.* 2017); or iii) strategic mass regulation to accrue body reserves as a buffer against starvation during periods of interrupted food availability (Cuthill *et al.* 2000).

# 1.6 Knowledge gaps and areas requiring more research

From the review of the literature, I have identified three major gaps and priorities for research: i) the effects of wind on seasonal fecundity and its component parameters in passerines, ii) the need for a greater understanding of the interactive effects of within breeding attempt/season weather on seasonal fecundity and ii) an understanding of the weather-related carry-over effects from one component to the next.

#### 1.6.1 Effects of Wind

There is increasing evidence that wind speed can have important impacts on elements of seasonal fecundity (Hidle *et al.* 2016; Thyen & Becker 2006; Capp *et al.* 2017; Irons *et al.* 2017). In fact, wind may be more important than temperature in affecting some aspects of fecundity (Irons *et al.* 2017). Yet, despite trends and predictions towards increases in average wind speeds, or "windiness", as a result of climate change (Vautard *et al.* 2010; Young *et al.* 2011), the impact of wind on seasonal fecundity or its components has received much less attention than the impacts of temperature or rainfall. This is particularly true for passerines, where few studies have examined the effects of wind, especially compared to larger avian taxa such as water/seabirds and raptors (e.g., Christensen-Dalsgaard *et al.* 2018; Kasprzykowski *et al.* 2014; Kouba *et al.* 2015; Thyen & Becker, 2010).

Most studies that have considered the relationship between wind and fecundity have addressed indirect linkages via impacts on food activity/or abundance (e.g., Hussell &

Quinney 2008) As with temperature and rainfall, wind speed may have also direct effects on fecundity. In one of the few studies to look at the energetic impact of wind on passerines during incubation, Heenan and Seymour (2012) estimated that even relatively modest increases in wind speed could almost double the required heat transfer to the clutch by incubating parents of Spiny-Cheeked Honeyeater Acanthagenys rufogularis and Yellowthroated Miner Manorina flavigula. Similarly, in one of the only studies to directly address the effects of wind on incubation behaviour, Capp et al. (2017) found that White-Crowned Babblers left the nest for two and a half times as long under high wind speeds, compared to when there was no wind. Compared to other avian taxa, the effects of wind on the chick stage in passerines also remains understudied; of the few studies, Mainwaring and Hartley (2016) found that wind speed had mixed effects on nestling morphology in the Blue Tit; with high wind being positively related to fourth primary feather length but negatively related to tarsus length. Similarly, one of the few studies to examine the impact of wind on seasonal fecundity in passerines was that by Møller (2013) who found that Barn Swallows had lower reproductive success in winder summers, through reduced success of second broods. The comparatively small number of studies examining the impacts of wind mean there are still gaps in our knowledge with regard to the potential impacts of weather variation on seasonal fecundity and its parameters.

#### 1.6.2 Interactive effects of weather

While many studies have considered the impacts of multiple weather variables on elements of seasonal fecundity (e.g., Dreitz *et al.* 2012; Golaswki 2008; Mccarty & Winkler; 1999; Morganti *et al.* 2017), comparatively few have examined the potential for these variables to interact. Even fewer have examined how such interactive effects may differentially impact different components of seasonal fecundity. These possibilities are important to consider, because there is increasing evidence that the impact of one weather variable on a component of fecundity is modulated by its interaction with another (e.g., Carrol *et al.* 2018; Coe *et al.* 2015; Mainwaring & Hartley 2016; Irons *et al.* 2017). For example, Coe *et al.* (2015) found that incubation behaviour and nest temperature in Tree Swallows was dependent on the interactive effects of temperature and rainfall; females took fewer offbouts during warm and dry conditions but left the nest more often under cold and dry or warm and wet conditions. Those studies that have looked at the simultaneous effects of multiple weather variables have typically used one of two approaches – principal

component analysis (PCA, e.g., Arlettaz *et al.* 2010; Siikamäki 1996), or linear and generalized linear mixed-effects models (LMMs and GLMMs; Coe *et al.* 2015; Mainwaring & Hartley 2016; Irons *et al.* 2017). While both approaches are valid, the advantage of the latter is that it allows effects of weather variables to be tested both individually *and* interactively. By utilizing an LMM/GLMM framework, Mainwaring and Hartley (2016), for example, showed that the growth of Blue Tits had a negative relationship with temperature and wind speed but was positively correlated with rainfall, both as an *independent effect* but also *interactively* with other weather variables. This contrasts with a PCA approach which does not allow the disentangling of individual and interactive effects. A greater understanding of the associations among weather variables and their independent and interactive effects across additional species could shed more light on the complex effects of local and global environmental change.

#### 1.6.3 Carry-over effects among the components of fecundity

Further complexity is introduced by the links between the component stages of seasonal fecundity, meaning that any one component (e.g., hatching success) might respond to environmental variation both independently and as a result of cascading effects from one stage to the next. For example, weather related effects on the nest environment during incubation can affect nestling growth, immunity, fledging success, and phenotype (Ambrosini et al. 2006; Ardia 2013; Ardia et al. 2010; Kim and Monaghan 2006; Nord and Nilsson 2011). The impacts of the nest environment during the incubation and chick stages can carry over into later life too, and affect post fledging survival, lifespan, and future reproductive success (e.g., Berntsen & Bech 2016; Greño et al. 2008; Hepp & Kennamer 2012; Obërg et al. 2014; Rodríguez et al. 2016). Therefore, focusing on single breeding parameters might not be sufficient to determine the full effects of environmental variability on seasonal fecundity (Mattsson & Cooper 2007; Etterson et al. 2011). For example, such an approach may fail to consider the ability of individuals to buffer the effects of variation in a single environmental parameter on overall fecundity (Wiebe & Martin 1998). By the same token, connecting environmental variation solely to variation in seasonal fecundity many not be sufficiently sensitive to identify those component parameters that might be most affected by environmental change (Oppel et al. 2013), or may mask the importance of carry over effects from one fecundity stage or life stage to the next. Few studies have attempted to simultaneously account for other components of fecundity and weather beyond controlling for the effect of a particular component. For example, clutch size can affect incubation duration (Reid *et al.* 1999) and so it is often included in models to explain effects of environmental variation on incubation duration (e.g., MacDonald *et al.* 2013) or behaviour (e.g., Capp *et al.* 2018), to control for its effect, but without consideration given to the impact of environmental variation on clutch size *per se*.

# 1.7 Thesis structure

The aim of this thesis is to address the three knowledge gaps identified above, for which there is a comparative paucity of evidence:

- 1) To measure the effects of wind on the parameters of seasonal fecundity: I aim to increase our understanding of the potential impacts of wind speed on the component parameters of seasonal fecundity. My overarching hypothesis is that wind will have a negative effect on fecundity overall, with a similar effect size to both temperature and rainfall on the individual components of seasonal fecundity.
- 2) To test for possible interactive effects of weather on the components of fecundity. My overarching hypothesis is that weather variables will act interactively to affect the component parameters of fecundity, and as a result the seasonal fecundity metric as a whole.
- To account simultaneously for weather-related effects on a component of fecundity and weather-related carry-over effects from the one that proceeded it.

I will address these specific objectives by using the Barn Swallow *Hirundo rustica* as a model species to explore the impacts of local weather on the seasonal fecundity of short-lived passerines. This thesis comprises four data chapters. Chapter 1 takes a broad view, examining weather effects on parameters of seasonal fecundity at a large spatial range, while Chapter 2 examines more detailed interactions between weather and fecundity by focusing on a single, well studied, population. Chapters 3 and 4 both focus on specific parameters of fecundity to examine potential strategic decisions used to overcome weather related impacts.

# Chapter 2 – Effects of weather variation on seasonal fecundity of Barn Swallows at a UK scale

Two key components of the environment, namely land use and weather, have been shown to affect elements of seasonal fecundity (e.g., Newton 1998; Morrison *et al.* 2013). Differences in land management may alter the sensitivity of breeding birds to weather variation, with important implications for how the impacts of ongoing climate change can be mitigated. In this chapter, data on Barn Swallows from the British Trust for Ornithology's Nest Record Scheme spanning the years 1987 to 2018 were used to test for spatial and temporal variation in components of seasonal fecundity in relation to land use (derived from the UK Land Cover Map 2015, Rowland *et al.* 2017) and weather (HadUK-Grid, Met Office 2019).

#### Chapter 3 - Effects of weather variation on seasonal fecundity at a local scale

Using detailed nest record data on Barn Swallows, collected at a specific site (see study site below) between 2007 and 2014, this chapter describes the effects of short-term variation (days) in local weather on seasonal fecundity and its components. The effects of temperature, rainfall, and windspeed, and their interactions, on clutch size, incubation duration, hatching success, brood size, brood survival, and the probability of a second brood, are modelled using generalised estimating equations. Predictions from these models are then used to test the relative sensitivity of each component to different weather scenarios, and these findings are combined in a conceptual model of seasonal fecundity.

## Chapter 4 – The effects of local weather variation on the incubation behaviour of female Barn Swallows

In this chapter I investigate how ambient temperature, rainfall and wind influence the incubation behaviour of Barn Swallows. Data-loggers were used to record nest temperatures and incubation activity through the day and night of a subset of swallow nests in 2014, to quantify female incubation behaviour. I test three main predictions that: i) incubation behaviour will differ under varying weather conditions; ii) sensitivity to weather will be greater over a short (hourly) time scale as birds respond rapidly to current conditions, whereas over a longer (daily) time scale birds will compensate for shorter-term variation in weather conditions, and iii) diurnal weather conditions and consequent incubation behaviour will have carry-over effects into the nocturnal phase.

Chapter 5– the implications of local weather variation on nestling growth & development Using the seven-year data set (2007-2014), I investigate the combined and interactive effects of temperature, rainfall and wind speed on the mass and growth of individual chicks during the nestling stage (8-12 days post-hatching) and fledgling stage (20-35 days posthatching), representing the dependent and semi-/fully independent stages of development. I test the following predictions: i) nestling body mass is positively related to temperature but negatively related to wind speed and rainfall, at both daily and lifetime scales, due to impacts on, for example, aerial insect abundance and parental provisioning rates; and ii) fledgling mass is sensitive to weather in the short-term (daily scale), due to weather-related variation in insect abundance and activity, but is less sensitive to weather in the long-term (lifetime scale), as fledglings are expected to be less susceptible to food-limitation once they have completed their growth.

### 1.8 Model Species and System

#### 1.8.1 Study Species

The Barn Swallow is a socially monogamous, synanthropic trans-Saharan migrant, with a breeding distribution that spans the Palaearctic and Nearctic. The species is virtually ubiquitous as a breeding species in Britain and Ireland, with a population in the region of 705,000 pairs/territories (Balmer *et al.* 2013; Woodward *et al.* 2020). Nests are built of mud, and most are found in and around a variety of anthropogenic structures, especially those containing or associated with livestock, although some pairs breed in "natural" nest-sites such as caves and cliff faces. Clutch size is moderate at around four to five eggs, with approximately five weeks elapsing from the laying of the first egg to the young leaving the nest. Although flies (Diptera) feature heavily in their diet, Barn Swallows are foraging generalists, taking a wide range of flying invertebrates (Cramp & Simmons 1988; Turner 2010). It is a short-lived species, typically living for two or three years, although individuals can live much longer than this; the oldest recorded Barn Swallow was just over 11 years on its death (Robinson 2005).

Despite moderate declines across Europe since the 1980s the Barn Swallow is not a species of immediate conservation concern (Eaton *et al.* 2015). Within the context of Britain and

Ireland, the species has shown an overall shallow decline in breeding population, though there are marked regional differences, with increases in the north and west of Britain but declines evident in the southeast.

The species lends itself well to behavioural and ecological studies generally, and particularly those associated with climate and reproduction. Barn Swallows show a high level of site fidelity and nest re-use between years (Safran 2004; Shields 1984). Their open cup nests are generally easy to access and monitor and being a multi-brooded species, several breeding attempts can be monitored in a season. Adults and young are both easily caught for ringing, allowing individuals to be marked for study. In addition, as Barn Swallows are "income breeders", using current intake of food to produce eggs (Ward & Bryant 2006), foraging in seasonally productive habitats, studying the fecundity and behavioural decisions made by breeding adult Barn Swallows is not confounded by the need to account more widely for the impact of changes in breeding phenology and food abundance that can occur in other model systems (Ward & Bryant 2006; Turner 2010; Burger *et al.* 2012). As the Barn Swallow is one of the most studied bird species in the world, there is a large body of literature on the Barn Swallow on which to draw, when interpreting the results of the present study (see Turner 2010 for an overview).

#### 1.8.2 Data and Study Site

The data used here were obtained from two sources. For Chapter 2, the data used to explore seasonal fecundity at a national scale were obtained from the British Trust for Ornithology's (BTO) Nest Record Scheme (NRS). NRS data is collected by a network of dedicated volunteers across the United Kingdom, who find nests and record the contents throughout the breeding season (see Crick *et al.* 2003). There are particular challenges of analysing citizen science datasets involving large numbers of contributors (e.g., Cooper *et al.* 2013; Dickinson *et al.* 2010). NRS data vary widely between individual nests in terms of the number of visits made to each one and the interval between visits, and the nest data are not necessarily linked to ringing data (Crick *et al.* 2003). This latter point means, for example, that it is not possible to link specific females to specific breeding attempts with complete confidence. I therefore concentrate on three components of fecundity using NRS data in Chapter 1: clutch size, hatching success, and brood size. The strength of this analysis

is its national-scale overview, with a large sample size, spanning many years; for example, between 1,000 and 2,000 nest records for swallows have been submitted annually since 2000 (Robinson *et al.* 2020).

While it is possible to derive a value for seasonal fecundity from NRS data (Crick et al. 2003; Freeman & Crick 2003; Paradis et al. 2000; Morrison et al. 2015), more detailed data were collected to be used in Chapters 3 - 5. These data were obtained from a population of swallows that breed at the Cardiff Riding School (N 51° 29' 0.7292" W 3 ° 12' 21.258") (hereafter CRS, Figure 1.1). The reproductive biology of the swallow population at the CRS has been studied since 2006, where 17-22 pairs breed annually (Table 1.2). Nests were monitored every three to four days from April to September (inclusive) between 2006 and 2014. Nest visits began in late April, to record first egg date, clutch size, hatching date, brood size, and chick survival and fledging success. The data collected in 2006 were not of sufficient detail for inclusion here, and no adults were caught in 2007 so I have concentrated on data collected from 2008 onwards. Chicks were typically ringed at 8-12 days of age, with some attempts to re-catch them once they had fledged. Adults were caught and ringed, often at the same time as the chicks or fledglings, by placing a mist net in the entrance of the building containing the nest; adults were sexed based on the presence or absence of a brood patch. In addition, wing, tail, and tail fork length were measured to the nearest mm. Mass was recorded to the nearest 0.1g using an electronic balance (Satrue SA-500 http://www.satrue.com.tw/dp2.htm). All birds were caught and ringed under BTO permit A5411, following best practice guidelines (Jenni 1998, Redfern & Clark 2001). As well as being ringed with a uniquely numbered metal ring issued by the BTO, adults were also fitted with a unique combination of three plastic colour-rings as part of a study on adult survival. It was not possible to monitor all nests at the CRS in any one year due to accessibility issues; for example, the nest being out of reach in some of the taller buildings. While attempts were made each year to catch all breeding individuals, it was not always possible. Therefore, only nests where the female was caught or resignted were taken forward for the analyses undertaken in Chapter 3 and Chapter 4. Nests suffered a high level of predation in 2014 so only chicks from first broods are included in the analyses undertaken in Chapter 4 and no nest monitoring data from 2014 is included in Chapter 3.

Figure 1.2: Aerial view of Cardiff Riding School (centre) and its dog-legged paddocks. The allotments are sited to the north and west, the River Taff runs along its north border, and Pontcanna Playing Fields to the south (Google Maps 2021)



Table 1.2 Total number of Barn Swallow pairs (represented by females) breeding at the CRS during the period of study and the number subsequently included in the analysis for Chapter 3. Only breeding attempts where the female was caught, and the nest was accessible for monitoring were used in the analysis. Attempt refers to the total number of breeding attempts represented per year in the analysis; note that more than one breeding attempt could be made by each female in a year).

Year	Total Pairs in each year	Pairs represented	Number of Attempts Represented
2008	21	15	23
2009	20	14	23
2010	20	18	27
2011	22	14	24
2012	26	18	27
2013	17	11	18
Total	126	90	142

The CRS falls wholly within the City of Cardiff, situated approximately one kilometre north of the civic centre of the city. The site comprises 10 hectares of intensively horse-grazed improved pasture (c. 4-4.5 horses per hectare of available pasture), dominated by Rye Grass *Lolium sp.*, Creeping Buttercup *Ranunculus repens*, and Silverweed *Potentilla anserina*, with areas of Broad-leafed Dock *Rumex obtustifolis* and Elder *Sambucus nigra* scrub. Patches of Bramble *Rubus sp.* form the dominant boundary plant, along with Hawthorn *Crataegus monogyna*. A number of tree species including Sycamore *Acer psedoplantanus*, Ash *Fraxinus excelsior*, and Lime *T. x euopaea* can be found both within the boundary feature and within fields.

This combination of study site and species overcomes many of the resource and logistical challenges associated with the study of fecundity (Etterson *et al.* 2011). The swallow's open cup nests, discrete nature of the nest location and high nesting density mean that nests are easy to locate and efficient to monitor; eliminating issues associated with nest detection, and reducing the time and resources needed to monitor them. The small nature of the site meant that it was possible to locate all nests in a given year, allowing for a complete census of the number of individual females (i.e., pairs) breeding at the site each year. While, as described above, an intensive program of ringing (known in N. America as "banding") allowed individuals to be assigned to each breeding attempt. The discrete and relatively isolated nature of CRS from other areas of suitable nesting habitat meant that those areas that do exist were easily surveyed for females that may have temporarily or permanently emigrated from the main study site (fewer than three females across the study period). Being relatively short-lived, female swallows attempt to breed every year and are highly site faithful (Turner 2006) so are less likely to be absent from the breeding population in some years, as is often the case with more long-lived species.

# Chapter 2: The effects of weather and land cover on Barn Swallow fecundity at a national scale

### Summary

Declining migratory species are likely to be affected by changes in both climate and land use across their range, through demographic drivers of population size, including components of seasonal fecundity. Although the consequences of changing fecundity may be visible at national scales, they are likely to be the result of changes in factors such as land cover or weather acting at local (breeding location) scales. In this study I use 20 years of nest record data to examine how local land cover (within 500m of each nest) and weather affect clutch size, hatching success and brood size in the Barn Swallow Hirundo rustica; a species that has shown regional variation in population change across its British range. Specifically, I examine the interactive relationship between weather and land cover on these components of fecundity. Clutch size declined with increasing total spring rainfall and was affected by the interaction between mean spring wind speed and temperature; with larger clutches in calm, cool springs/locations compared to windy, cool springs/areas. The relationship between clutch size and wind was affected by the proportion of grassland within 500m of the nest, a potentially important habitat for breeding swallows; with clutch size increasing with the proportion of grassland in windier springs/areas, with the reverse true in calm springs. Hatching success showed more complex interactions between land cover within 500m of the nest and weather. Success declined with increasing temperature in windier springs, but increased with temperature in calmer springs. Similarly, brood size declined with total spring rainfall in winder springs/areas but increased with rainfall in calm springs/areas. Clutch size was predicted to be lowest in the south east of England, increasing further north and west, with the largest clutch sizes predicted in the north west Scotland and Wales; the difference across the country was 0.59 eggs. Hatching success was predicted to be highest in western areas (predicted highest mean 94%, Isles of Scilly) but declined in the north and north east (82%). There was no significant geographical variation in brood size detected, with brood size predicted to vary my just 0.09 chicks across the country. The results show that both local weather and land cover can affect different aspects of fecundity, and may have complex, interactive relationships. In addition, the relative stability of brood size across the country suggest that changes in seasonal fecundity are unlikely to to explain regional changes in swallow populations.
## 2.1 Introduction

Many summer migrant bird species have undergone large population declines within the UK and Europe, with this decline being more pronounced in long-distance compared to shortdistance migrants (Thaxter et al. 2010; Vickery et al. 2014). The breadth of the declines means that over 80% of the species classed as long-distance migrants are considered as species of conservation concern in the UK (Eaton et al. 2009, 2015). Such national-scale trends often disguise complex, finer-scale patterns, with geographical variation in both the speed and direction of population change at local or regional scales (Balmer et al. 2013; Morrision et al. 2013; Risely et al. 2012). For example, several species, such as House Martin Delichon urbica, and Willow Warbler Phylloscopus trochilus, have declined at the UK level, despite their populations remaining stable or increasing in Scotland, whilst Tree Pipit Anthus trivialis has increased nationally but shown stark declines in some regions (Balmer et al. 2013; Harris et al. 2020; Morrison et al. 2013). These geographical variations in population status may result from environmental factors that vary across a species' range, such as differences in land use, habitat quality and weather variation (Morrison et al. 2013; Högstedt1980; Dhondt et al. 1992; Seki & Takano 1998), the effects of which may differ according to life stage (e.g., nestling, juvenile or adult). As a consequence, understanding the drivers of national-scale population changes needs studies that encompass both the largest spatial scales and the local or regional scales to which individual birds or breeding populations respond (Anders & Marshall 2005; Weegman et al. 2017).

For migratory species, environmental changes across multiple locations – breeding, stopover and wintering sites – may impact populations across the annual cycle and play a role in national-scale declines (Morrison *et al.* 2013; Ockendon *et al.* 2012; Sanderson *et al.* 2006; Vickery *et al.* 2014). At a UK-scale, representing part of the breeding range of many Afro-Palearctic migrant species, changes in agricultural practice and climate are regarded as two of the major factors driving biodiversity declines over recent decades (Hayhow *et al.* 2019). Such changes could impact breeding birds via, for example, reduced food availability (e.g., Barton *et al.* 2002; Wilson *et al.* 1999), phenological mismatches (e.g., Both *et al.* 2006), or increased frequency of weather extremes (e.g., Conrey *et al.* 2016; Dreitz *et al.* 2012). Both climate and land-use change can have similar impacts on bird populations (Eglington & Pearce-Higgins 2012) and their interactions may mask or exacerbate the effects of each other (Clavero *et al.* 2011). For example, the negative effects of drought on the

survival of nestling Wood Thrush *Hylocichla mustelina* were buffered in locations with a large amount of mature forest cover (Vernasco *et al.* 2018).

In principle, local changes in land use and climate could affect bird populations via changes in adult or juvenile survival (e.g., Weegman et al. 2017), in dispersal/migration, or in breeding productivity (e.g., Vernasco et al. 2018). Breeding productivity is often the main driver of demographic change and population trends (Newton 1998; Sillett et al.; 2000; Temple & Cary 1988); declining or low fecundity can reduce recruitment to the breeding population and increase the risk of local extinction or increase reliance on immigration (Bennett & Owens 1997; Temple & Car 1988). Several elements of productivity, such as clutch size, brood size or fledging success, have been shown to vary geographically in national scale studies (e.g., Rotenberry & Wiens 1989; Young 1995; Dunn et al. 2000). Such variation might follow identifiable trends at national scales; for example Møller et al. (1984), found that the number of eggs laid per pair decreased with latitude in both the Barn Swallow Hirundo rustica and House Martin, whilst House Martins in eastern regions of the UK attempted more broods and had higher nesting success than in other part of the country (Kettel et al. 2020). Alternatively, there may be no obvious geographical trend; for example, along an inter-continental gradient across North America, Weegman et al. (2017) found little consistency between sites in important demographic parameters such as juvenile survival in the Tree Swallow Tachycineta bicolor. Despite their differences at national or continental scales, either scenario could arise from local variations in demographic parameters related to factors such as altitude, climate, and habitat type or quality (e.g., Sanz 1998, 2008; Morrison et al. 2014). Consequently, understanding how relatively smallscale environmental variation links to national-scale population trends may be key to identifying causes of long-term declines in migrants (Cox et al. 2020).

Changes in land use have been implicated in the decline in abundance and fecundity of several bird species across Western Europe (Newton 2004; Møller 2001; Chamberlain & Crick 1999). Through the 1970s and 80s, mixed farming declined throughout Britain, with a trend in the south-east towards primarily arable farming, and in the west and north towards primarily pastoral farming (Robinson & Sutherland 2002). Such changes could have implications for resource availability for migratory insectivorous birds. For example, aerial insect abundance is higher on pasture grazed by livestock, compared to other uses such as

silage or cereal production (Evans *et al.* 2007), and is generally lower in more intensively managed agricultural land (Barton *et al.* 2002). Farm scale cessation of grazing by livestock has been shown to reduce the abundance, clutch size, and the persistence of populations of aerial insectivores such as Barn Swallows compared to when stock was present (Ambrosini *et al.* 2002; Møller 2001). Other characteristics of land use management, such as the timing of interventions, may also play an important role. The decline in the Eurasian Skylark *Alauda arvensis* in the 1990s was shown to be steepest in areas associated with intensive agriculture, reflecting a large decline in the frequency or success of second broods (cf. changes in clutch or brood size; Chamberlain & Crick 1999), following the widespread adoption of winter-sown cereals (Sutherland and Robinson 2002). Therefore, landscape-scale changes in land use or management can have wide-ranging implications for population processes. In addition there is increasing evidence that both temporal and spatial variation in population trends are driven by the interactive effects of climate and habitat / land use change (Morrison *et al.* 2013; Vernasco *et al.* 2018).

Weather can influence several parameters that contribute to seasonal fecundity (see Chapter 1 for a review). Increases in spring temperatures have been shown widely to lead to earlier laying dates (e.g., Pearce-Higgins et al. 2005; Visser et al. 2009; Winkler et al. 2002), which in turn can lead to increases in productivity via an increased chance of renesting after the first breeding attempt (Morrison et al. 2019). For aerial insectivores, including many migrant species, increases in spring rainfall and wind speed may have more influence on laying date, hatching date, and clutch intiation than temperature (Irons et al. 2017; Møller 2013). The relationships between individual components of breeding performance and weather can be complex (see Chapters 3, 4, and 5). The different stages of a breeding attempt may vary in their sensitivity to weather variation as a whole, or to specific weather variables; clutch size for example has been shown to be relatively insensitive to temperature (Salaberria et al. 2014; Golawski 2008; Vedder 2012) but not to rainfall (Oppel et al. 2013; Theyn & Becker 2006). Weather variables may act interactively to affect either components of fecundity, or behaviours related to them. For example, interactions between weather variables (e.g., rainfall and temperature) have been shown to impact on incubation behaviour (Capp et al. 2017; Coe et al. 2015; Chapter 4) and nestling development (Mainwaring & Hartley 2016; Chapter 5). Finally, weather variables may interact with land use to affect components of fecundity. However, whilst there is some evidence for this interaction from small spatial scales (e.g., site- or regional-scale effects), very few studies have considered this possibility across large spatial extents (Eglington & Pearce-Higgins, 2012; Morrison *et al.* 2010; Vernasco *et al.* 2018). The benefit of national- or continental-scale studies is the ability to capture a wider range and combination of climatic and land use variation, which should allow more powerful analyses of their combined effects.

In this chapter, I examine how local weather and land cover affect three components of seasonal fecundity in the Barn Swallow - clutch size, hatching success and brood size using 20 years of nest records collected by volunteers on behalf of the British Trust for Ornithology (BTO). The records cover the whole of mainland Britain and include regions with populations that have experienced contrasting fortunes. At least until recently, the Barn Swallow population appeared to be relatively stable in the UK because declines in the south east of England were offset by increases in the west and the north (Robinson et al. 2003), with these differences believed to be driven by a polarisation in agricultural land cover (arable in the east to pastoral in the west, Evans & Robinson 2004). To examine these changes, I used local weather data (1km<sup>2</sup> resolution, Met Office 2018) and land cover data (Rowland et al. 2017) from across Britain to create models to describe geographical and temporal changes in the above parameters, and to explore the role of local weather and habitat variables in driving these changes. As the presence of livestock has been shown to increase the number of chicks and clutch sizes in swallows (e.g., Grüebler et al. 2010; Møller 2001) I predict that the three metrics will be positively correlated with land cover types associated with livestock but negatively affected by the amount of built land cover, which has been shown to negatively impact swallow breeding success (Teglhøj 2017). Secondly, as swallows are "income breeders" and defer breeding until conditions are "good" (Nooker et al. 2005; Turner 1982) | predict that clutch size will be less sensitive to weather variation than either hatching success or brood size; these latter metrics are potentially more sensitive to weather due to proximate impacts on the nest environment, female behaviour and foraging behaviour (Coe et al. 2015; Fernaz et al. 2012; Schifferli et al. 2014). Møller (1984) found that clutch size decreased with latitude; I predict a similar trend in clutch size here. Clutch size sets an absolute maximum to brood size, with incomplete hatching success potentially reducing this limit. Therefore, I predict a similar geographical trend in brood size to that of clutch size, but brood size will be more affected by weather; as discussed above, unfavourable weather can impact chick survival through indirect and direct effects, for example, reduced chick provisioning.

# 2.2 Methods

#### 2.2.1 Nest Record Data

Nest Record Scheme (NRS) data for Barn Swallows (here after 'swallows') spanning the years 1987 to 2018 were obtained from the British Trust for Ornithology (BTO). The NRS has been the primary method for monitoring nests in Britain and Ireland since 1939 (Crick et al. 2003). Data are collected by a network of volunteers who find and visit nests, recording the location as well as the contents and stage of development. As the number of times each nest was visited and the starting point (egg or chick stage) both varied from nest to nest, I concentrated this analysis on three components of fecundity which could be calculated reliably for the majority of nests: clutch size, hatching success, and brood size. A total of 53,511 records of individual nests was returned initially, covering 1987 - 2018. Traditionally, nest records were submitted to the BTO on physical "nest record cards", rather than electronically. The time period chosen for study represents a period where 25-100% of the records submitted each year were available electronically, resulting in 437-1199 records available electronically per year. Prior to 1987, <20% of submitted cards were digitised. Nest records stored only in paper format were not available for study here. The nest record data were filtered to retain those: i) with nest locations recorded to a precision of 100m, and ii) which had at least two visits made during the egg stage (clutch size analysis only) or chick stage (brood size analysis only), or at least one visit in each of the egg and chick stage (included in both analyses). This allowed me to calculate the minimum clutch size (here after "clutch size"), maximum brood size (number of chicks, here after "brood size). In addition, I calculated hatching success, expressing brood size as a proportion of clutch size. This resulted in a dataset of 18,065 nests taken forward for pairing with land cover and weather data.

#### 2.2.2 Weather and land use data

I calculated total rainfall (mm), mean temperature (°C) and mean windspeed (kph) during spring (April–June inclusive) for each nesting attempt based on the 1km<sup>2</sup> resolution HadUK-Grid Weather data (Met Office 2018) i.e., the spring weather within the 1km<sup>2</sup> cell where

each nest was located. There data are interpolated from a network of meteorological stations throughout Britain. Land use data were obtained from the 25m resolution Land Cover Maps 1990, 2000, 2007, 2015, and 2019 (here after "LCM"; Rowland *et al.* 2017).

As Barn Swallows forage up to 500m from their nests (Turner 1982, 2006), I calculated the proportion of each of the 21 land cover categories from the LCM within a 500m radius buffer around each nest location. I used the raster package (Hijmans 2020) in R to count the number of 25x25m pixels belonging to each land cover category within 500m (n = 1976 pixels per nest), which were then converted to proportions of each buffer.

Land cover categories representing habitats known to affect the productivity of swallows, either positively or negatively, were selected for further analysis, namely: "grasslands" ("improved", "calcareous", "neutral" and "acid" LCM categories combined), "built" ("urban" and "suburban" LCM categories combined, see below), "arable & horticulture", and "freshwater". Swallows are expected to use both "arable" and "grassland" land to forage, but initial exploration showed that the proportion of "arable & horticulture" and "grassland" were highly correlated (r = -0.62); of these two variables "grassland" was chosen to be used in further analysis as the presence of grazing livestock has been shown to be important for several aspects of the swallow's breeding biology (Grüebler et al. 2010; Møller 2001).

As the available LCM data did not include all years covered by the NRS, data analyses included nest records two years either side of the different LCM survey dates, this is consistent with the approach taken by Kettel *et al.* (2020). I therefore calculated land cover for nest records spanning 1998-1992, 1998-2002, 2005-2009, and 2013-2017. Therefore, land cover here should be seen as a proxy rather than absolute value. This provided 12673 nests that could be paired with both land cover and weather data.

#### 2.3 Statistical Analysis

All data analysis used R version 3.5.3 (R Development Core Team 2019). Generalised additive mixed-effects models (GAMMs) were fitted using the mgcv package (Wood 2019) to explore the effects of local weather, land cover, and their interactions, on clutch size,

hatching success and brood size. Each starting model contained the fixed effects of total rainfall, mean temperature, mean windspeed, and the proportions of grassland, built environment and freshwaters within a circle of 500m radius around each nest, along with all two-way interaction terms between the three weather variables (e.g., "rain x temperature"), and interaction terms for each weather variable and land cover (e.g., "rain x grassland", "rain x built") to test whether land management appears to affect the sensitivity of swallows to weather variation. The starting models for hatching success and brood size also contained clutch size as a fixed effect; clutch size sets the maximum brood size, and clutch size has been shown to affect hatching success (Reid et al. 2000). Longitude and latitude were also included as a two-dimensional smooth term using the default thin-plate regression spline method (Wood 2019) in all starting models, to account for additional spatial variation in clutch size, hatching success and brood size. Previous analysis of NRS data from 1966-2019 indicates that swallows show no long-term trends in clutch or brood size (Woodward 2020); I therefore fitted "year" as a random factor in all models to account for multiple nest records from the same year. Pair plots and variance inflation factor values (VIF) were used to assess co-linearity between variables; with variables being considered independent when showing a VIF of <3 (Zuur et al. 2010); none of the variables included in the models showed a VIF >3.

Final models were refined using stepwise deletion, starting with the interaction terms, until there was no further reduction in the AIC (Burnham & Anderson 2002). Model validation procedures followed Zuur *et al.* (2007) and Thomas *et al.* (2017), with residuals checked for normality and homoscedasticity. The overall explanatory power of the model was assessed using the adjusted  $R^2$ .

In addition, in order visualize spatial variation in the weather and land use variables, generalised additive models (GAMs) were fitted using the mgcv package (Wood 2019). In each model, the response variable was the weather or land use cover values generated for each nest location (see above). Year was included as a fixed effect to capture inter-annual variation, and longitude and latitude were included as a two-dimensional smooth term using the default thin-plate regression spline method (Wood 2019) to account for additional spatial variation. The predictions from these models were generated for each Ordnance Survey 20 km<sup>2</sup> National Grid square across Britain.

Table 2.1: Parameter estimates, standard errors (s.e.) and *p*-values for GAMMs linking the three components of fecundity to temperature (°C), rainfall (mm) and wind seed (km/h) and the proportion of land use within 500m of each nest that was suburban/urban (built) and grassland on clutch size, hatching success, and brood size. Statistically significant terms are shown in bold type.

Response	Fixed effect	Parameter Estimate	± s.e	<i>p</i> value
Clutch Size	Rainfall	<0.001	<0.001	0.003
	Temperature	-0.024	0.008	0.004
	Wind speed	-0.079	0.022	0.000
	Grassland	-0.102	0.030	0.001
	Wind speed x Grassland	0.027	0.007	<0.001
	Temperature x Wind speed	0.006	0.002	0.002
Hatching Success	Clutch size	0.117	0.023	<0.001
	Rainfall	0.002	0.002	0.223
	Temperature	0.205	0.109	0.061
	Wind speed	0.768	0.288	0.008
	Grassland	1.590	0.411	<0.001
	Water	-2.990	6.848	0.662
	Built	3.623	2.136	0.090
	Rainfall x Water	-0.018	0.006	0.005
	Temperature x Water	0.668	0.442	0.131
	Wind speed x Water	-0.263	0.722	0.716
	Rainfall x Grassland	-0.001	0.001	0.329
	Wind speed x Grassland	-0.345	0.093	<0.001
	Temperature x Built	-0.277	0.141	0.049
	Rainfall x Built	0.003	0.003	0.332
	Wind speed x Built	-0.181	0.217	0.405
	Rainfall x Wind speed	<0.001	<0.001	0.206
	Temperature x Wind speed	-0.049	0.023	0.035
Brood Size	Clutch size	0.229	0.002	<0.001
	Rainfall	<0.001	<0.001	0.007
	Temperature	-0.001	0.002	0.673
	Wind speed	0.009	0.005	0.070
	Grassland	0.032	0.016	0.042
	Water	-1.005	0.515	0.051
	Wind speed x Water	0.105	0.056	0.061
	Temperature x Water	0.058	0.032	0.067
	Rainfall x Grassland	<0.001	<0.001	0.069
	Rainfall x Wind speed	<0.001	<0.001	0.009

Effective degrees of freedom (e.d.f.), *F*- and *p*-values for the two-dimensional smoother (latitude x longitude) in the above GAMMs. Models where the smoothed term was significant are shown in bold.

Response	e.d.f.	F value	<i>p</i> -value
Clutch size	2.00	40.6	<0.001
Hatching success	4.688	13.54	<0.001
Brood size	2.737	0.967	0.495



Figure 2.1: Frequency histograms of environmental variables included in the GAMMs (Table 2.): a) total spring rainfall (mm), b) mean spring temperature (°C), c) mean spring wind speed (kph), and the proportion of land cover within 500m of the nest: d) grassland, e) freshwater, and f) built land use.

#### 2.4 Results

Geographical variation in weather variables, predicted from the GAM, as well as summary statistics can be found in Table 2.1. Mean clutch size was  $4.50 \pm 0.82$  eggs (s.d., range 1 - 10), mean hatching success was  $0.87 \pm 0.26$  (0 - 1), and mean brood size was  $4.17 \pm 0.99$  chicks (1-10) see also Figure 2.3. The explanatory power of the models varied considerably ( $R^2$  for clutch size = 0.011, hatching success = 0.007, brood size = also 0.505). Mean ( $\pm$  s.d.). Geographical variation in land cover based on predictions based on values around nests can be seen in Figure 2.4, while the mean value of the proportion of each land cover class found within 500m of a nest were (all years combined): Grassland 0.42  $\pm$  0.28 (range = 0.0-1.0), built 0.07  $\pm$  0.14 ( $\pm$  range = 0.0-0.98), arable 0.32  $\pm$  0.29 (range = 0.0-1.0), and freshwater 0.02  $\pm$  0.07 (range = 0.0-0.81). Care should be taken when viewing Figure 2.4 as the predictions are based on values around each nest, and therefore likely influenced by geographical variation in the number of nest records. Pertinently, mean spring wind speed was a significant predictor of all three response variables, at least in interaction with other variables.

Although the model had a low  $R^2$  (GAMM;  $R^2 = 0.011$ , Table 2.), clutch size was sensitive to wind, both in interaction with spring temperature and the proportion of grassland within 500m of the nest site. Larger clutches were predicted from breeding swallows experiencing calm, cool springs (7oC, 4.8 eggs) compared to those swallows experiencing windy, cool springs (4.1 eggs); the reverse was true if mean spring temperature was higher (14oC), when calmer weather resulted in lower clutch sizes (4.3) compared to winder springs (4.8). The interaction between wind speed and the proportion of grassland within 500m of the nest was weak; under light winds, clutch size decreased by 0.03 eggs with every 10% increase in the proportion of grassland, whereas clutch size declined by 0.05 eggs for the same increase in grassland under stronger winds (Figure 2.5). Clutch size was relatively insensitive to rainfall; the negative relationship with total spring rainfall equating to a decrease of 0.2 eggs with every 500 mm increase in rainfall during spring (Figure 2.5). Clutch size showed a statistically significant, non-linear relationship with longitude and latitude (Table 2.1). Clutch size showed a statistically significant, non-linear relationship with longitude and latitude (Table 2.1). Clutch size was predicted to be lowest in the southeast of England (predicted mean clutch 4.30 eggs), increasing further north and west, with the largest clutch sizes predicted in northwest Scotland and Wales (4.89 eggs, Figure 2.3)



c) Wind Speed



Figure 2.2: Smoothed predictions of weather variables across Great Britain (all years combined) from the GAM to visualise geographical variation in weather. Predicted values are interpolated based on a 20 x 20 km grid, with nest locations indicated by blue dots. Predictions are derived from the spring weather values for each 1km square containing a swallow nest record. White = highest predicted values, black = lowest predicted values. a) mean spring temperature (mean based on values from each 1km square containing a nest record = 11.5  $\pm 1.13$  °C, range 6.81 - 14.08 °C), b) total spring rainfall (mean 181.47  $\pm 71.4$  mm, range 62.47 -634.91 mm), and c) mean spring wind speed (mean 4.03  $\pm 0.80$  kph-1, range 1.67 - 8.05 km -1).



b) Hatching success





c) Brood size



Figure 2.3: Predicted geographical variation in breeding parameters across the UK (all years combined) from the GAMMs to explain weather and land cover effects on: a) clutch size, b) hatching success, and c) brood size (see Table 2.1). Predicted values are interpolated based on a 20 x 20 km grid, with nest locations indicated by blue dots. White = higher values, black = lower values. All weather and land cover variables were held at their mean: mean spring wind speed = 4.044 km -1, mean spring temperature =  $11.45^{\circ}$ C, total rain = 185.59mm, and proportion of land cover within 500m of the nest, grassland = 0.427, arable = 0.27, built = 0.11.



Figure 2.4: Smoothed predictions of land cover use across Great Britain (all years combined) from the GAM to visualise geographical variation in land cover around each swallow nest. Predicted values are interpolated based on a 20 x 20 km grid, with nest locations indicated by blue dots. Predictions are derived from the proportions of each land cover within a 500m radius of a swallow nest record. White = highest predicted values, *black = lowest predicted values*. Note that these do not represent actual land cover distributions but are visualizations of the geographical smoothers used in the GAMM analyses of clutch size, hatching success, and brood size.



Figure 2.5: Fitted GAMM for the relationship and 95% confidence intervals (dotted lines) between clutch size and: a) total spring rainfall (mm), b) the interaction between mean spring temperature (°C) and wind speed (kph), and c) the interaction between wind speed and the proportion of grassland within 500m of the nest. With the exception of (a), black lines indicate low mean spring wind speed (1.6 kph) and blue lines represent high speed (8.1 kph). All other variables were held at their mean values: average spring wind speed = 4.04 kph (a only), proportion of grassland within 500m of the nest = 0.421 (a and b only), mean spring temperature 11.52°C (a and c only), and rain = 181.48 mm (b and c only).

Similarly, hatching success was sensitive to weather, and the interactions between weather and land cover (GAMM;  $R^2 = 0.007$ , Table 2.1). Hatching success was also sensitive to wind speed, with high wind speed typically having a negative effect on hatching success. Hatching success declined with increasing proportion of grassland within 500m of the nest when mean wind speeds were high (8.05 kph); declining by 0.01 for every 10% increase in grassland up to 40% grassland cover, after which hatching success declined by 0.02 with every 10% increase in grassland cover. Hatching success was, however, predicted to increase by the same amount (0.01) with increasing grassland cover for breeding pairs experiencing springs characterised by low mean wind speeds (1.67 kph) (Figure 2.6). Hatching success of 0.85, compared to a clutch of two eggs was expected to have a hatching success of 0.85, compared to a clutch of six eggs with a hatching success of 0.90.

Hatching success had a negative relationship with the proportion of built land cover within 500m of the nest under high mean spring temperatures (14 °C) but the effect was small, with just a 0.06 difference in hatching success between 0 and 100% built land cover within 500m of the nest. The effect size of the positive relationship of low mean spring wind speed and built cover was larger; hatching success differed by 0.09 between the two extremes of built land cover (Figure 2.6). Hatching success had a negative relationship with mean spring temperature when mean spring wind speed was high, but a positive relationship when mean spring wind speed was low (Figure 2.6). The model predicted a small but positive relationship between hatching success and the proportion of freshwater within 500m of the nest; hatching success increased by 0.092 between a nest with 0% freshwater cover and one with 80% freshwater cover. However, under low temperatures the relationship between hatching success and freshwater was negative and more pronounced – with a hatching success between the two extremes of freshwater cover being 50% lower under high freshwater cover than no freshwater cover (Figure 2.6). Some care should be taken with the interpretation of these results, however. The model as a whole had low explanatory power ( $R^2$  = 0.007) and the number of sites with a freshwater cover of >0.1 was extremely low (Figure 2.1); indeed, the mean proportion of freshwater cover within the dataset was 0.015%. Under mean temperature conditions, hatching success was predicted to be 0.89 with no freshwater within 500m of the nest, and 0.91 with 80% freshwater cover.

Hatching success had a negative relationship with the proportion of grassland within 500m of the nest in windier springs (14 kph); but was unrelated to grassland extent in less windy springs (1.61 kph). Hatching success declined with spring temperature under windy conditions (14.0 kph; Figure 2.6) but was broadly unaffected by temperature in less windy conditions (1.61 kph); increasing by only 0.03 for every 1°C in mean spring temperature (Figure 2.6). The term describing this geographical variation in hatching success (i.e., the smoothed longitude and latitude term) was significant (Table 2.1). Hatching success was predicted to be highest in western areas – particularly the west coast of Scotland (including the Outer Hebrides), southwest England, and west Wales (predicted mean hatching success = 94%) – and decreasing in the north and north east, being lowest in the north east of Scotland (including Orkney; 82%; Figure 2.3).

Brood size (GAMM;  $R^2 = 0.505$ , Table 2.1) was sensitive both land cover, and importantly showed sensitivity to wind; at least in its interaction with total spring rainfall. At a low spring wind speed (1.61 kph) brood size had a weak but positive relationship with rainfall – equating to a brood size 0.57 chicks larger for every 500mm increase in total spring rainfall – whereas the same increase in total spring rainfall resulted in 0.37 fewer chicks per brood in springs with high winds (14.0 kph, Figure 2.7). Brood size increased on average by 0.22 chicks for every additional egg laid. Similarly, brood size had a positive but negligible relationship with grassland cover (Figure 2.7). The geographical variation in hatching success (i.e., the smoothed longitude and latitude term) was statistically non-significant (Table 2.); with brood size varying little (4.06 – 4.15 chicks) across Britain (Figure 2.3).



Figure 2.6: Fitted GAMM for the relationship, and 95% confidence intervals (dotted lines), between the hatching success and the interaction between a) winds speed and the proportion of grassland within 500m of the nest, b) temperature and the proportion of the built land cover within 500m of the nest and c) temperature and wind speed. Blue lines represent high wind speed (8.05 kph, a & c only) and temperature (14.08 °C, b only). Black line represent low wind speed (1.67 kph, a & c), and temperature (6.81 °C, b). All other variables held at their mean: temperature = 11.5 °C (a only), rainfall = 181.47 mm (a-c), wind = 4.07 kph (b only), built = 0.07 (a & c), grassland = 0.42 (b & c), freshwater = 0.02 (a-c)



Figure 2.7: Fitted GAMM for the relationship, and 95% confidence intervals (dotted lines), between brood size and: a) the proportion of grassland within 500m of the nest, and b) the interaction between total spring rainfall and mean spring wind speed. For b) black lines represent low values for wind speed (16.67 kph, b only) and blue lines represent high values for wind speed (8.05 kph). All other variables were held at their mean values: rainfall = 185.59 mm (a only), and temperature 11.45°C (a & b), wind = 4.039 kph (a only), and proportion of grassland within 500m of the nest = 0.427 (b only) and water = 0.015 (a & b).

### 2.5 Discussion

In this Chapter I used data spanning three decades across Britain to examine the relationship between three demographic parameters contributing to seasonal fecundity (namely clutch size, hatching success, and brood size) and two major classes of variables (namely land cover and local weather conditions) that were hypothesized to influence these demographic parameters. All three breeding parameters were affected by the interaction between at least one weather variable and land cover within 500m of the nest, although hatching success showed more complex interactions between land cover within 500m of the nest and weather than either clutch size or brood size. Mean spring wind speed, in interaction with landcover, had an influence on all three breeding metrics but this tended to be negative. This chapter provides evidence of complex and often stuble interativer effects between weather and land use on important metrics of productivity.

The results provide evidence that all three demographic metrics were at least to some extent correlated with weather variation, and that the relationships with weather varied according to the land cover surrounding swallows' nests. This is consistent with the findings of Eglington & Pearce-Higgins (2012), who found that climate and land use had a similar magnitude of impacts on population trends in farmland birds. Pertinently to the aims of this thesis, clutch size, hatching success, and brood size were all sensitive to weather, although this was generally in interaction with one or more weather or land cover variables (Table 2.2). The effect of wind was generally negative on each of the three breeding metrics studied here, suggesting that increasing wind speeds as a result of climate change (IPCC 2014) may have negative effects on the breeding biology of aerial insectivores. The three models developed in the present study explained some variation in clutch size, hatching success and brood size; though the amount of variation in clutch size and hatching success explained by weather and land cover was very small. The  $R^2$  was highest for the model of brood size (0.503), but it is likely that clutch size, as an independent variable in this model, may explain much of this value as the number of chicks is strongly influenced by the number of eggs laid ( $R^2$  with clutch size in model = -8995.40 vs  $R^2$  without clutch size in model = -411.56). The results of this study suggest that both climate and land use changes may be drivers of national pattern of population decline in recent years, though effect sizes on the three components of fecundity studied here are generally low; this is discussed further below.

Before discussing the results in more detail, it is important to highlight some of the study's limitations. Firstly, the data were insufficiently detailed for most nests to differentiate between first and second breeding attempts by the same female/pair, as it was not generally clear, when multiple nests were recorded from the same site, how many pairs were present, or if the breeding attempt was a replacement clutch. Secondly it was not possible to determine first eggs dates as in most cases as it was not clear how far into clutch initiation or incubation the visits had taken place. First and second broods can be affected differently by weather (Salaberria et al. 2014) and show geographic variation (Møller 1984). Thirdly the value of grassland to swallows is partly dependent on the presence or absence of livestock grazing grassland (Henderson et al. 2010), as well as other management aspects; such data were not available for this study and so the effects of livestock farming should be considered in addition to the effect of grassland cover considered here. It would have also been interesting to be able to capture some level of variation in weather. However, for some of the weather variables included (i.e., rainfall and wind) the mean is strongly correlated with the variance. Therefore, variance could not be easily incorporated into the models as additional variables due to a high level of covariance (i.e., VIF >3) and I opted to examine "typical" (i.e., mean) spring weather.

Grassland cover within 500m of the nest appeared in the final model of clutch size in an interaction term with wind speed, but overall, land cover in general had little effect on clutch size. This relatively insensitivity of clutch size to land use could be the result of the relatively conservative size of swallow clutches; despite ranging from one to ten eggs, 84% of clutches in the dataset analysed had a clutch size of 4 or 5 eggs. Swallows are income breeders, using their current intake of food to produce each egg (Ward & Bryant 2006). Food intake is likely to be influenced by land cover; for example invertebrate abundance has been shown to be up to three and a half times greater on pasture compared to arable fields (Evans *et al.* 2007), and the abundance of foraging swallows is higher over pasture than arable field (Ambrosini *et al.* 2002; Evans *et al.* 2007). The model of clutch size suggests that, at the level of the individual pair, providing that a landscape contains at least some grassland a female swallow can find sufficient prey to allow for broadly comparable (if slightly smaller) clutch sizes, compared to pairs in more grassland dominated landscapes. However, as discussed above the presence or absence of livestock is an important

determinant of whether grassland *per se* is important to swallows as a foraging resource the comparatively small effects of grassland cover may be an artifact of diverse management including both grazed and non-grazed grassland types. Not all grassland is agricultural (e.g., public parks, playing fields and golf courses), and some areas of agricultural grassland may be maintained without livestock, for example to produce hay, silage or haylage for harvest (rather than to feed farm stock *in situ* as growing grass), or as a break crop in a rotation. The type of livestock may also influence its importance to swallows, with cattle grazed fields more likely to contain foraging swallows compared to fields grazed by horses or sheep (Henderson *et al.* 2010). Increases in the intensity of management can lead to declines in invertebrate numbers and diversity (Wilson et al. 1999), and hence the value of the grassland for foraging swallows.

Weather conditions showed some apparent effects on clutch size, in interaction with grassland cover, but the effect size was small; clutch size decreased slightly in calm springs as the proportion of grassland within 500m of the nest increased (Figure 2.5c) but clutch size increased slightly with the proportion of grassland in windier springs. Wind speed can change the distribution of invertebrates within the landscape, with invertebrates congregating along boundary features in windier conditions (Grüebler *et al.* 2008). As pastoral fields are typically smaller than arable fields (Robinson & Sutherland 2002), this may increase prey availability in grassland dominated landscapes in high winds, compared to landscapes with less grassland cover, or at least fewer linear features. A similar mechanism may account for the positive interactive effects of wind speed and temperature; however the negative combined effect of low wind speed and low temperature may be the result of insects becoming more dispersed in the landscape under calm, warm conditions and more challenging for swallows to catch (Grüebler *et al.* 2008).

Hatching success showed complex interactions between weather variables, and between land cover and weather, but it is unlikely that these are affecting the process of hatching *per se.* It is more likely that local weather and land cover variation are impacting hatching via the eggs stage as a whole, affecting factors such as egg quality, embryo development during incubation and survival to hatching (see Chapter 3 and Chapter 4). Increased rain or wind speed have been shown to influence the behaviour of incubating adults (Capp *et al.* 2017; Coe *et al.* 2015) and may delay or interrupt the start of full incubation in aerial

insectivores, resulting in reduced hatching success (Wang & Beissinger 2009); interestingly, this appears to be the reverse of the results presented here. The positive relationship between hatching success and spring temperature in calm spring conditions may stem from a combination of factors such as reduced energetic demands on incubating females, as a result of fewer negative impacts on the nest environment (see Chapter 4). In addition, increasing temperatures have been shown to increase proxies of egg quality such as egg mass and the quantity of antioxidants that increase hatching success (Siano et al. 2004). The result of higher hatching success under high winds speed and low temperature therefore seems contradictory; embryo development or survival would be expected to be impaired at low temperatures combined with high temperatures, due to increased cooling rates increasing energetic demands on an incubating female during conditions when prey is less active or abundant. The mechanism underlying this relationship is unclear. One possible explanation, that would need additional research, is that it may perhaps represent a strategic decision by females. For example as birds use current conditions to predict future need (Cuthill et al. 2000; Thomas & Cuthill 2002), females may decide to invest more in egg quality during poor conditions (low temperature with high winds), perhaps to increase the chances of hatching success (Siano et al. 2014), especially if environmental conditions suggest they may only be able to raise a single brood. Similarly, the mechanism linking hatching success with the interaction between the proportion of grassland within 500m of the nest and mean spring wind speed is unclear – especially the negative relationship between high wind speed and the proportion of grassland within 500m of the nest. Hatching success also declined with an increase in built cover within 500m of the nest when mean spring temperatures were high. Typically swallow nests in buildings experience higher than ambient (i.e., outdoor) temperatures, and this can be exacerbated by the structure that the nest is built on or in (Imlay et al. 2019); high temperatures can lead to embryo morality and perhaps this may be increased by the "urban heat island" effect. As described earlier, the relationship between the proportion of freshwater and rainfall on hatching success should be viewed with some caution given the paucity of data from nests surrounded by large areas of freshwater habitat. However, there was a slight decline in hatching success when comparing mean freshwater cover to no freshwater cover. Again, this may be reflective of insect availability affecting either egg quality or female incubation behaviour and thus embryo survival; while freshwater habitats do provide a source of prey for swallows, prey availability over freshwater is likely to be more temporally variable compared to terrestrial environments, for example due to big emergence events of mayflies (order Ephemeroptera).

While the proportion of grassland cover within 500m of the nest had a significant and positive effect on brood size, the effect size was negligible; a mere 0.014 chick increase for every 10% increase in grassland cover. This suggests that at least some other land cover types, such as arable, are able to provide for similar size broods as grasslands. Brood size declined with increasing total spring rainfall and high mean spring wind speed; as these represent poor conditions for foraging swallows, it is probably that parents are unable to support larger broods in these conditions (Fernaz *et al.* 2012; Grüebler *et al.* 2008; Schifferli *et al.* 2014). Interestingly, the proportion of built cover within 500m of the nest was not a significant predictor of brood size, despite previous evidence that pairs breeding in more built-up areas have lower breeding success (Teglhøj 2017).

All three-breeding metrics varied with both longitude and latitude, although this was only statistically significant for clutch size and brood size. Clutch size was typically larger in the north and west and smaller in the east (Figure 2.5). This does not mirror the proportion of grassland within 500m of the nest, which was typically highest in Wales and the southwest, lower in Scotland and northern England, but lowest in the Southeast of England (Figure 2.4). Interestingly the spatial pattern of clutch size nearly mirrors that of arable land use. The collinearity of grassland and arable land cover prevented me from testing explicitly for the effects of arable on these metrics here, but this spatial pattern is perhaps indicative that arable is poor habitat for swallows during egg laying. The extent of pasture (or inversely, arable) land use may be more relevant at the population level than at the level of the individual nest, affecting population density and persistence (Møller 2001; Ambrosini et al. 2002, 2012) compared to individual-level metrics; indeed Eglington & Pearce-Higgins (2012) found that changes in land-use intensity better explained the decline in farmland bird populations than trends in weather (climate). While I have not explicitly looked at temporal change in land use here, the results presented here suggest that factors affecting density of pairs may be more relevant to swallow populations. Indeed, the density of swallows tends to be lower in the arable east compared the more pastoral west and north of Britain (Robinson et al. 2003). Hatching success was lowest in eastern Scotland and northern England, and highest in Wales and southern England. The reasons for this are unclear, as none of the potential causes for "site specific" effects seem to apply at a wider geographical scale. Indeed, it may simply be an artifact, as the relationship between

hatching success and the two-dimensional smoothed effects of longitude and latitude was not statistically significant and therefore does not necessarily need an ecological explanation. The spatial variation in brood size was significant, with an apparent decrease in brood size with latitude. Although the negative effects of higher wind speed on brood size was independent of location, it makes sense that regions with typically windier springs – such as the north of England, and Scotland which were predicted to have the highest mean spring wind speeds (Figure 2.3c) – would likely host smaller broods. However, it should be borne in mind that the effect of latitude is small with a difference of just 0.11 of a chick between the most geographically distant sites, similar to the effect (-0.2 chicks) of high wind speed in interaction with high proportions of grassland within 500m of the nest. These results suggest that finer scale weather effects, such as at the level of the site/individual farm, discussed above may be more relevant to hatching success and brood size.

The results of this chapter demonstrate that clutch size, hatching success, and brood size show varying degrees of sensitivity to weather; but the strength and (in some cases) direction of these relationships are affected in part by land use. In the next chapter I use detailed data from a single population of swallows, where surrounding land use has remained unchanged during the study period (2006-2014); such an approach eliminates the potential confounding effects of land use and location when studying the impacts of weather on seasonal fecundity and its constituent parameters.

# Chapter 3: The effects of weather on the seasonal fecundity of Barn Swallows

# Summary

Seasonal fecundity is an important driver of population growth and persistence. Local environmental factors, such as changes in weather, can have important impacts upon fecundity, with both short-term and longer-term consequences. In this chapter I use eight years of nest record data for a population of Barn Swallows Hirundo rustica to explore the impacts of temperature, rainfall, and wind speed on the components of seasonal fecundity; namely clutch size, incubation duration, hatching success, chick survival, and the probability of initiating a second brood. All components were affected by at least one weather variable, and the results demonstrated some complex interactive effects between weather variables as drivers of seasonal fecundity. Wind speed, a variable that has received little attention in the study of breeding biology, affected all components of seasonal fecundity except incubation duration. Predictive models using scenarios based on the minimum, mean and maximum values of the three weather variables revealed that seasonal fecundity could be three to four times higher in years with 'good' versus 'poor' weather. High values for all fecundity components were not necessary to achieve a high seasonal value overall, highlighting the importance of disaggregating the components of seasonal fecundity to assess weather effects.

### 3.1 Introduction

Global climate is changing rapidly (IPCC 2014); likely consequences at local and regional scales in northwest Europe are changes in weather patterns, such as increases in the intensity of summer rainfall (Kendon et al. 2014), warmer spring and autumn temperatures (Xoplaki et al. 2005), and increased wind speeds (Vautard et al. 2010; Young et al. 2011). To persist in the face of climate change, organisms must either change their distributions to track geographical shifts in suitable environmental conditions (Chen et al. 2011; Kelly & Goulden 2008; Parmesan & Yohe 2003), evolve adaptations to the changing conditions (Grant & Grant 1993) or exhibit sufficient phenotypic plasticity to adjust to changing conditions (Pearce-Higgins et al. 2014). Phenotypically plastic responses so far appear to be much more common than evolutionary responses, at least over short to medium term timescales of environmental change (Pearce-Higgins et al. 2014). Examples of such phenotypic plasticity include changes in the timing of annual events such as leaf bud burst in trees (Vitasse et al. 2009) or behavioural changes such as earlier spring arrival dates in migratory birds (Both and Visser 2001; for an overview see Parmesan 2006). As behavioural decisions made by an individual may be influenced by the environmental conditions that they experience (McNamara & Houston 1996), the anticipated changes in local weather are likely to impact on strategic decisions relating to key demographic factors such as survival, reproductive behaviour, and seasonal fecundity.

Seasonal fecundity, i.e., the number of offspring produced per female per breeding season, is a key driver of population persistence and growth (Newton 1998), resulting from several successive but distinct components (Etterson *et al.* 2011; Oppel *et al.* 2013; see Figure 1.1 and discussion in Chapter 1). The sequential nature of the components means that the decisions made by breeding birds early in the breeding season could have consequences that cascade through the season, or even carry-over into future years. These consequences may be at the level of the number of breeding attempts, for example failure or successful completion of a breeding attempt may affect the decision of whether to re-nest (Nagy & Holmes, 2005). Alternatively, consequences may be specific to components within a breeding attempt. For example, increased clutch size is associated with reduced incubation duration (Engstrand & Bryant 2002) and with lower hatching success in species which lay larger broods (Reid *et al.* 2000). Similarly, decisions about breeding behaviour can have

consequences beyond the current reproductive attempt. For example, offspring experiencing sub-optimal developmental temperatures as a consequence of parental decisions during incubation may have lower reproductive success later in life (Hepp & Kennamer 2012). To fully understand how seasonal fecundity changes in response to environmental variation, it is therefore necessary to investigate these processes both individually and in terms of how they link together and interact to produce cascading effects of environmental change on seasonal fecundity.

Weather can have a range of direct and indirect effects on the constituents of seasonal fecundity, both within and across seasons. Direct effects mainly relate to energetics and the nest microclimate, whilst indirect effects may be mediated through factors such as food availability (see Chapter 1). Within an individual breeding season, conditions during the egg and nestling stages can be important: in swallows, ambient temperatures prior to laying and during incubation and nestling phases may impact nestling phenotypic quality (Ambrosini et al. 2006). Across seasons, weather may affect timing of breeding; for example, total rainfall in the previous summer impacted the timing of breeding in Marabou Stork Leptoptilos crumenifer (Monadjem & Bamford 2009). The apparent effects of weather may also vary according to the temporal scale over which they are observed (Skagen & Adams 2012). For example, nest survival in the Lark Bunting Calamospiza melanocorys has been shown to increase with rainfall across the breeding season, even though individual rain storms can cause short-term reductions in daily nest survival (Skagen & Adams 2012). Therefore, the impacts of weather might not be fully appreciated by focusing on individual components of seasonal fecundity (Mattsson & Cooper 2007; Etterson et al. 2011), or by solely focusing on weather averaged across the whole breeding season, or by focussing on only a single aspect of weather.

In the present study, I use six years of detailed nest records from a swallow population to test whether seasonal fecundity and its component parameters are influenced by weather. The swallow is a socially monogamous, multi-brooded species (Cramp 1988), and as an income breeder (relying on current food intake rather than body reserves for egg formation), it is expected to be particularly sensitive to weather, altering its breeding behaviour in relation to prevailing or anticipated conditions (Turner 1982). This chapter comprises two parts. In the first, I explore how daily weather variation affects the components of seasonal fecundity. Based on previous studies, I predict that weather will have different effects on individual components (e.g., clutch size has often been shown to increase with temperature, whereas incubation duration may decrease). The effects of wind speed on fecundity have rarely been considered in the literature (although see Chapter 1), but I predict that it will complement temperature and rainfall and provide a more complete explanation of variation in fecundity. In the second part of the chapter, the individual components of fecundity are combined into an overall model, and parameterised using empirical data, to examine how whole-season fecundity is affected by weather. The latter involves making predictions for different weather scenarios, revealing just how variable seasonal fecundity can be in relation to weather experienced during the breeding season. Overall, it was predicted that seasonal fecundity will vary markedly between breeding seasons with 'good' versus 'poor' weather conditions; with the highest fecundity under "good" conditions, representing relatively average conditions for summer in the region of study (South Wales), and the lowest fecundity under "poor" conditions, namely extremes of weather.

# 3.2 Methods

#### 3.2.1 Study Site and Nest Monitoring

Swallow nests were monitored at Cardiff Riding School, Cardiff, Wales, UK (see Chapter 1 for details). Nests were visited every three to four days between April and September inclusive, 2007–2014, continuing from the start of breeding activity each year until no further breeding attempts were initiated. Regular nest checks were made to record first egg date, clutch size, hatching date, brood size and number of fledglings, in addition to derived parameters such as hatching success (Table 3.1). Typically, 14–22 pairs nested at the study site in each year, with the same pair normally remaining faithful to the same nest site both within and between years.

For broods where hatching was not observed, the age of nestlings was estimated based on feather development (Turner 2006) and by comparison with chicks of known age; it was possible to examine all chicks within four days of hatching in all years. As it was not always possible to observe the exact fledging date, a chick was considered to be a fledgling 20 days

after hatching, based on the mean duration of the swallow's nestling period in the UK (Robinson 2015). A second breeding attempt was considered to be any breeding attempt by the same female that followed a successful first breeding attempt. Breeding attempts that resulted from re-nesting after a failed attempt were considered replacement broods (n = 7 attempts), rather than second broods, and these replacement broods were not considered in the analysis of second broods. To enable individual identification of breeding adults, and to assign them to a particular breeding attempt, breeding adults were ringed with (i) a combination of three coloured plastic leg rings, and (ii) a uniquely numbered metal ring (using 2 plastic rings on one leg, and 1 plastic and 1 metal ring on the other leg). To minimise the risk of desertion, adults were caught using mist-nets erected near the nest once the chicks were at least eight days of age. No cases of nest desertion were observed. All birds were caught and ringed by – or under the supervision of – the author, under British Trust for Ornithology permit A5411, following best practice guidelines (Jenni 1998; Redfern & Clark 2001).

#### 3.2.2 Weather data

Daily temperature and rainfall data (24-hour resolution) were obtained from the Meteorological Office (Met Office www.metoffice.gov.uk) weather station in Bute Park, Cardiff (51°29'16.7"N 3°11'17.0"W, 9m asl); approximately 1km from the study site. No wind speed data were available from the Bute Park station, so these were obtained from a second weather station approximately 18.7km to the south-east (St Athan; 51°24'18"N, - 3°26'24", 49m asl). As temperature and rainfall data from the two stations were highly correlated, linear regression models were fitted (n = 529 days; temperature  $R^2 = 0.915$ ; rainfall  $R^2 = 0.761$ ) and used to predict values missing for Bute Park (temperature n = 550 days missing days; rainfall n = 366). The three weather variables were weakly correlated with each other (r = 0.005 to 0.026), allowing them to be analysed as independent variables in models of the relationships between weather conditions and breeding parameters.

Mean temperature (°C, mean of minimum and maximum), total rainfall (mm) and mean wind speed (kph) were calculated for the following stages for each breeding attempt: 1) the 10 days prior to clutch initiation, a timeframe chosen to cover the period of rapid yolk formation (Saino *et al.* 2004); 2) laying period; 3) egg stage (date of first egg to date of hatching); 4) nestling stage, considered to be the 20 days between hatching and fledging;

and 5) the entire first breeding attempt. The weather variables for the egg laying period were calculated from the day prior to the first egg, to the day of the penultimate egg, assuming one egg is laid every 24 hours (e.g., Romanoff & Romanoff 1949, Perrins 2008) and that egg formation starts the day prior to an individual egg being laid (2-6 days in total). Incubation duration was considered to be the time elapsed from the day of the final egg being laid, until the day of hatching (11–21 days). In some broods, chicks died between hatching and fledging; the timing of any chick deaths was calculated as the mid-point between the visits immediately before and after the death. Where more than one chick died in a brood but between different nest visits, the mid-point between the last and penultimate visit was used.

	First Breeding Attempts	Second Breeding Attempts
First egg day <sup>1</sup>	53.56 ± 22.77 (24 – 134)	98.41 ± 14.90 (62 – 132)
Clutch Size	4.6 ± 0.84 (2 – 6)	4.2 ± 0.68 (3 – 6)
Incubation Duration (days)	16.33 ± 1.85 (12 - 21)	15.98 ± 1.72 (11 – 20)
Hatching day <sup>2</sup>	73.04 ± 22.10 (76 – 155)	111.6 ± 15.63 (76 – 150)
Hatching Success <sup>3</sup>	0.92 ± 1.4 (0.5 - 1)	0.93 ± 1.3 (0.5 – 1)
Brood size	4.22 ± 1.6 (2 – 6)	3.89 ± 0.82 (2 – 6)
Nestling survival <sup>4</sup>	0.89 ± 0.24 (0 – 1)	0.90 ± 02.5 (0 - 1)
Number Fledglings <sup>5</sup>	3.77 ± 1.38 (0 – 6)	3.51 ± 1.15 (0 – 6)

Table 3.1: Mean nest data (±S.E.; range in parentheses) for first (n=74) and second (n =57) breeding attempts, from 6 years of nest monitoring of Barn Swallows.

 $^{1,2}$  Day after the first of April (where April 1<sup>st</sup> = day 1).

<sup>3</sup> Proportion of eggs successfully hatching.

<sup>4</sup> Proportion of chicks in a brood reaching 20 days of age.

<sup>5</sup> Number of chicks surviving to 20 days.

#### 3.3 Statistical Analysis

The purpose of this study was to examine the effects of weather variation on seasonal fecundity. Therefore, data analysis comprised two stages: i) analysing the effects of the three weather variables, as individual terms, and all possible two-way interactions, on individual components of seasonal fecundity. This was to elucidate the main weather effects on each response variable. These models were then used to generate predictions to explore the sensitivity of each component through the use of sensitivity plots and, ii) populate an overall model of seasonal fecundity, developed to combine its constituent stages to allow an evaluation of their contributions to seasonal output and its sensitivity of the response variable overall was explored through sensitivity plots and a number of case studies based on the results of the overall seasonal fecundity mode. All analyses for i) were undertaken using "R" statistical software, version 3.2.2 (R Development Core Team, 2015), while ii) was fitted in Microsoft Excel (2013).

# **3.3.1 Stage 1: Effects of weather on the components of individual breeding attempts**

For the first stage, five components of seasonal fecundity (dependent variables) were regressed onto the same set of independent variables, namely mean daily temperature (°C), total rainfall (mm) and mean daily wind speed (kph). The dependent variables were: (i) clutch size, (ii) incubation duration, (iii) hatching success, (iv) chick survival and (v) probability of a second brood being initiated (Table 3.2). Models were fitted as generalised linear models using generalised estimating equations (GEE-GLM) implemented using the R Package "geepack" (Højsgaard *et al.* 2006) and using an "exchangeable" correlation structure to account for repeat occurrences of the same female within or between years. Generalised estimating equations were preferred to mixed-effects models due to the large number of small clusters (Vaughan *et al.* 2007): the majority of the 73 females in the study were represented by one or two breeding attempts (n = 60). A binomial error term was used in models for chick survival, hatching success and probability of a second brood, a

Poisson error term was used in the model for clutch size, and a Gaussian error term for the model for incubation duration.

All starting models contained the three weather variables, and all possible two-way interactions between them, for the relevant periods in the nesting cycle. In some cases, models also contained variables representing previous stages in the breeding cycle, or weather variables during the preceding stage, to account for potential cascading effects on fecundity (Table 3.2). Co-linearity among explanatory variables was assessed using pairwise plots and variance inflation factor (VIF) values; with variables being considered independent when showing a VIF of <3 (following Zuur *et al.* 2010).

To explore for seasonal effects a measure of time of year was to be included in each starting model. These "day" variables (first egg day, first day of incubation day and day of hatching for the laying-, hatching- and incubation- models respectively), however, showed high collinearity (VIF >3) with their respective temperature variables (Figure 3.1). The significance of each "day" variable was assessed by comparing the two versions of each starting model (one including and the other excluding a numeric "day" variable) with a likelihood ratio test. In all cases there was no significant difference between the two model structures and, in all bar-one case (probability of a second brood), the Quasi-Information Criteria (QIC, see below) was lower for the starting models without the "day" variable (Table 3.3). Indeed, with the exception of the model explaining probability of a second brood, the "day" variable was the first to be removed during initial exploration of model structure (see below). For the probability of the second brood, initial exploration showed that the QIC increased when either the "day" or "temperature" term was removed. Because of the above, especially given the high collinearity with temperature, all starting models taken forward for refinement did not include a "day" term. This may seem to reduce the ability of the models to look for seasonal effect, however, only 25% of first breeding attempts (n = 20) overlapped temporally with second breeding attempts (Figure 3.1) suggesting that the inclusion of a day variable would largely describe within-breeding attempt seasonal differences, for example between early-first and late-first breeding attempts, rather than across the season as a whole. Breeding attempt was not highly colinear (VIF >3) with neither the "temperature" nor the "day" variables and can be considered a proxy for seasonality at least in females that have more than one brood.

Models were refined using backwards stepwise deletion until there was no further decrease in the Quasi-Information Criteria. QIC fulfils a similar function to Akaike's information criterion (AIC) but is adjusted for analyses based on GEEs.

From the final models for clutch size, incubation duration, hatching success and brood survival I derived a series of predictions. The predictions were generated for weather scenarios representing all the possible permutations of low (minimum value), average (mean value) and high (maximum value) mean daily temperature, wind speed and rainfall; this is resulted in a total of 27 weather permutations. Predictions were generated separately first and second breeding attempts. For rainfall, the "high" value represented twice that of the mean. Any non-weather-related variables (e.g., breeding attempt or clutch size) in the models were held at their mean values for first or second breeding attempt, or where applicable, the predicted value from an earlier model was used. The predicted value for each parameter (e.g., clutch size) under the permutation that contained average values for weather (i.e., representing an average year) was used as a reference to examine the sensitivity of each of the parameters to weather. Sensitivity was expressed as the percentage difference between the predicted value under a given permutation and that of the reference value, the value obtained under a the "all mean" permutation. This provided a measure of positive or negative sensitivity compared to an average, or "typical", year. The results were then visualised used a sensitivity plot. Such an approach allows a greater exploration of the effects of the terms retained in the final model (compared to exploring main-effects from the GEE-GLMs) on the response variable by allowing multiple values to vary simultaneously.

Response	Sample size	Weather Predictors	Non-weather Predictors
Clutch Size	143	Pre-laying Temperature	Breeding Attempt
		Pre-laying Rainfall	
		Pre-Laying Wind speed	
		Laying Temperature	
		Laying Rainfall	
		Laying Wind speed	
		Pre-laying Temperature x Pre-laying Rainfall	
		Pre-laying Temperature x Pre-Laying Wind speed	
		Pre-laying Rainfall x Pre-Laying Wind speed	
		Laying Temperature x Laying Rainfall	
		Laying Temperature x Laying Wind speed	
		Laying Rainfall x Laying Wind speed	
Incubation Duration	137	Egg stage Temperature	Breeding Attempt
		Egg stage Rainfall	Clutch Size
		Egg stage Wind speed	
		Egg stage Temperature x Egg stage Rainfall	
		Egg stage Temperature x Egg stage Wind speed	
		Egg stage Rainfall x Egg stage Wind speed	
	107		
Hatching Success	137	Egg stage Temperature	Breeding Attempt
		Egg stage Wind speed	Incubation Duration
		Egg stage Temperature X Egg stage Rainfall	
		Egg stage Temperature x Egg stage wind speed	
		Egg stage Rainfall X Egg stage wind speed	
Fledging Success	132	Chick stage Temperature	Breeding Attempt
		Chick stage Rainfall	Brood Size
		Chick stage Wind speed	Hatching Success
		Chick stage Temperature x Chick stage Rainfall Chick stage Temperature x Chick stage Wind speed	
		Chick stage Rainfall x Chick stage Wind speed	
			Number of Eledalings from first
Probability re-nesting	75	1st Breeding Attempt Temperature	brood
		1st Breeding Attempt Rainfall	
		1st Breeding Attempt Wind speed	
		1st Breeding Attempt Temperature x 1st	
		Breeding Attempt Rainfall	
		1st Breeding Attempt Temperature x 1st	
		Breeding Attempt Wind speed	
		1st Breeding Attempt Rainfall x 1st Breeding	
		Attempt Wind speed	

Table 3.2: Starting models for analysis of the effects of mean temperature (°C), total rainfall (mm), and mean wind speed (km/h) on components of seasonal fecundity in the Barn Swallow *Hirundo rustica* 

Model	OIC model 1	OIC model 2	d f	w <sup>2</sup>	D
MOUEI			u.i.	<u> </u>	F
Clutch size	-598	-600	1	2.00	0.16
Incubation duration	157	155	1	0.95	0.33
Hatching success	90.5	88.1	1	0.59	0.44

77.6

77

1

1

0.57

2.46

0.45

0.12

Table 3.3: QIC values and results of likelihood ratio tests comparing starting models that included a "day" variable (model1) and one without (model2), for each of the dependent variables analysed.

#### 3.3.2 Stage 2: Effects of weather on Seasonal fecundity

78.7

76.9

Chick Survival

Probability of a 2<sup>nd</sup> brood

To determine how weather affected seasonal fecundity, the predictions generated from the models created during stage 1 were combined in a model that described seasonal fecundity overall. The model was fitted in Microsoft Excel (2013) and used a similar approach to Freeman and Crick (2003), who combined components of seasonal fecundity to predict the number of fledglings produced per breeding attempt (F.BA):

$$F.BA = CS \times HS \times (1-EFR)^{EP} \times (1-NFR)^{NP}$$
 (equation 1)

Where CS is clutch size, HS is hatching success and EP is the length (in days) of the egg phase, where EP = (CS + incubation duration) - 1, with the subtraction of a day accounting for the Barn Swallow's tendency to start incubating on the day that the last egg in a clutch was laid (Turner 2006). Calculating the duration of the egg phase in this manner recognises that both clutch size and incubation duration can alter the length of the egg phase independently of each other. NP is the nestling phase (in days), calculated from the day of hatching to the day of fledging. EFR and NFR are the daily failure rates of whole nests during the egg phase (EFR) and nestling phase (NFR), calculated using the Mayfield method (Mayfield 1961, 1975). In the current study there were too few egg stage and nestling stage failures (n = 5) to explore weather effects on egg failure rate (EFR) and nest failure rate (NFR). Instead, these were fixed as the mean values from the first and second broods (based on all years) under each weather scenario.

Mayfield (1961) studied a population in which all losses (bar one) of individual nestlings occurred during the hatching period, and thus were accounted for by hatching success. Therefore, Mayfield assumed nestling survival to be the same as nest success, i.e., all individuals that hatched went on to survive until fledging. In contrast, in the present study, there were instances where some or all the nestlings in a brood died at different points after hatching but prior to fledging (range = 2 - 19 days after hatching). Additionally, I determined hatching success differently from Freeman and Crick (2003); whereas they used Nest Record Scheme data (see Chapter 2) to calculate the ratio between the maximum brood size and clutch size, I was able to determine both the minimum and maximum brood size of each breeding attempt and thus determine hatching success (maximum brood size) separately. As I was able to calculate this latter metric, equation 1 was modified to account for the results of the chick survival (S<sub>ch</sub>) model, thus:

$$F.BA = (CS \times HS \times (1-EFR)^{EP} \times (1-NFR)^{NP})S_{ch} \qquad (equation 2)$$

To account for multi-brooding, I expanded equation 2 with reference to the conceptual model provided by Etterson *et al.* (2011, see Figure 1.1) to represent overall seasonal fecundity, i.e., the total number of offspring produced per pair in a season (SF):

$$SF = FBA_1 + (P_2 \times F.BA_2)$$
 (equation 3)

Where P<sub>2</sub> is the probability of a second brood being initiated. While some pairs in the study population attempted three breeding attempts in one season, the number was small (only four, or 2.7%, of the 147 breeding attempts across all years) and so the model was limited to two breeding attempts. Sensitivity of FBA for first and second attempts, and SF were calculated in the same way as described above for the individual parameters.

Following a similar procedure as described under stage 1, the sensitivity of fecundity at the level of brood and season to weather was explored using sensitivity plots. Again, sensitivity
was expressed as the percentage difference between the predicted value under a given permutation and that of the reference value (the value generated under mean values). Sensitivity at the level of breeding attempt were generated by combining the predictions for each of the 27 permutations separately as described in equation 2 above. The process was repeated, but with reference to equation three, to test the sensitivity of seasonal fecundity overall.

The actual predicted values generated from the 27 permutations generated in stage one were also combined in a "look up" table, with calculated values for first and second breeding attempts and seasonal fecundity calculated using equations 2 and 3 respectively. A series of case studies were used to explore the potential effects of changes in local weather variation on seasonal fecundity. These case studies were based on the results of the sensitivity plots.

## 3.4 Results

Mean values of the breeding / demographic parameters for first and second broods are presented in Table 3.1. The explanatory power of the models varied considerably ( $R^2$  = 0.081 - 0.414), but all contained at least one weather variable, and - with the exception of incubation duration - all contained at least one interaction term (Table 3.4). With the exception of the final model to explain incubation duration, wind speed was included in all final models suggesting this variable has important implications. All predicted values for clutch size, incubation duration, hatching success and brood survival fell within the range of the study population (Table ) and those expected for this species (Robinson 2005). The results from stage 1 describe the main relationships as described by the GEE-GLMS. The results from stage 2 present these in a more holistic pattern with the use of sensitivity plots.

a) Breeding Attempt



Figure 3.1: While showing some overlap overall, the majority of first and second breeding attempts were seasonally distinct (a) and thus "attempt" was included in models taken forward for refinement. However, as illustrated here temperature showed high collinearity (VIF >3) with "day" variables that would act as proxies for seasonal effects for other parameters (b-f), and so models containing "day" were not taken forward for refinement (see Data Analysis and Table 3.3). For "Day" variables (see Table 3.1) on the y-axis day 1 = 1<sup>st</sup> April. Panels b-f represent the relationship between b) first egg date, and the probability of a second brood being initiated, c) first egg date and average temperature during the pre-laying period, d) the start day of incubation and average temperature during incubation, e) day of hatching and average temperature during incubation, and f) day of hatching and mean ambient temperature during the chick stage. For panels b-f, open circles represent first breeding attempts, open triangles represent second breeding attempts.

#### b) Probability of a second brood

# **3.4.1** Results from stage 1: the effects of weather on the individual components of fecundity

#### **Clutch size**

Clutch size was affected by weather during both the pre-laying and laying period (GEE-GLM;  $R^2 = 0.414$ , Table 3.4; Fig 3), with wind speed both during the pre-laying and laying period having impacts on clutch size. Pre-laying temperature had a small negative effect on clutch size with just 0.28 fewer eggs laid for every 10°C increase when pre-laying rainfall was low (0 mm), but this increased to 1.8 fewer eggs for every 10°C increase in temperature when pre-laying rainfall was high (91mm) (Figure 3.2a). Low wind speeds (6.23 km/h) increased clutch size (1.3 eggs for every 10°C increase in mean-pre-laying temperature) but high pre-laying wind speeds (12.4 km/h) resulted in a decline in clutch size (-1.6 eggs for every 10°C increase). Clutch size increased if pre-laying rainfall was low (10mm increase in rainfall resulted in 0.03 more eggs) but declined if under high pre-laying wind speeds (0.1 fewer eggs were laid per 10mm increase in rainfall). During laying, a 10°C increase in temperature resulted in 1.19 fewer eggs per clutch, while 0.7 fewer eggs were laid for every 10kph increase in wind speed during laying.

#### Incubation duration

Incubation duration was largely unaffected by weather, with the exception of a significant negative effect of egg-stage temperature (GEE-GLM;  $R^2 = 0.081$ , Table 3.4). Incubation duration decreased by 2 days for every 10°C increase in mean egg-stage temperature (Table 3.2a).

#### **Hatching Success**

Egg stage temperature had a significant (p = 0.028), positive effect on hatching success (GEE-GLM;  $R^2 = 0.075$ , Table 3.4). However, the interaction between temperature and rainfall was also retained in the final model; when this relationship was considered the slope of the relationship between hatching success and temperature became negative with increasing rainfall (Table 3.3 and Table 3.4).

#### Chick Survival (proportion of the brood surviving to fledging)

Chick survival increased with rainfall in a relationship that was modulated by wind speed (GEE-GLM;  $R^2 = 0.235$ , Table 3.4), being higher under dry (0mm) but windy conditions (survival = 0.9) compared to dry, calm conditions (survival = 0.5, Table 3.4). Under high wind speed conditions (12.6 kph) chick survival decreased with rainfall but the effect was weak (-0.01 for every 10mm increase in rainfall) compared to the positive effect under calm conditions (0.11 for 10mm of rainfall). Under calm conditions, chick survival rate exceeded 0.9 once total rainfall had exceeded 35mm, and all chicks were predicted to survive once total rainfall had exceeded 70mm.

#### Probability of a second brood

Some caution should be applied when interpreting this model given the lack of a "day" variable effect included in the model, however the probability of a second brood being initiated was sensitive to weather during the first breeding attempt (GEE-GLM; *R*<sup>2</sup> = 0.389, Table 3.4). Females experiencing calm (7.3 km/h) but wet conditions during their first breeding attempt were less likely to initiate a second brood. Once total rainfall had exceeded approximately 200mm the probability of initiating a second brood being initiated was virtually zero. In windy (11.4 kph) first attempt, the probability of a second brood being virtually 1 over approximately 160 mm of rainfall. Similarly, the relationship between temperature and a second brood initiation depended on rainfall. Under dry conditions (34.0 mm), the probability of a second brood declined above a mean temperature of 14°C and was virtually zero by 17°C (Figure **Error! Reference source not found.**3.4). Conversely, when rainfall during the first breeding attempt was high (278 mm), the probability of a second attempt increased from zero below 12°C, reaching virtually 1 by approximately 16°C.









#### C) Interaction between rainfall and mean wind speed during the pre-laying period







d) Mean temperature during egg-laying



Figure 3.2: Model predictions, and 95% confidence intervals (dotted lines), for the effects of mean temperature, and wind speed, and total rainfall during the pre-laying period (a-c) and the laying period (d & e). For panels a-c only; black lines represent low values (temperature =  $9.27^{\circ}$ C, rain = 0.0 mm, wind speed = 6.23 km/h) and grey value high values ( $21.1^{\circ}$ C / 49.9 mm / 12.39 km/h). Mean values in all models; pre-laying =  $14.29^{\circ}$ C / 25 mm / 8.85 km/h; Laying phase;  $19.3^{\circ}$ C / 13.5 mm / 12.39 km/h.

#### a) Incubation Duration



#### b) Hatching success



c) Chick Survival



Figure 3.3: Fitted models (GEE-GLM), and 95% confidence intervals (dotted lines), for the effects of on incubation duration, hatching success, and the probability of a second brood being initiated in the Barn Swallow *Hirundo rustica*. Mean temperature during the egg stage was the only variable within the model to explain incubation duration (a). The model for hatching success is based on a first brood; attempt was a not significant term in the model (see Table 3.4). Egg stage weather (b only); black lines low rain = 0mm, grey line high rain = 120mm, incubation duration = 16 days, clutch size = 4.2. Chick stage weather (c only); black line low wind = 7.28kph, grey lines high wind = 12.6kph.

Table 3.4: Parameter estimates, standard errors (s.e.) and *p*-values for GEE-GLMs to explain the effects of temperature (°C), rainfall (mm) and wind seed (kph<sup>-1</sup>) on the components of seasonal fecundity. Statistically significant terms are shown in bold type.

Response	Parameter	Parameter Estimate	± s.e	p value
	Pre-laying Temperature	0.084	0.025	0.001
	Pre-laying Rainfall	-0.004	0.003	0.180
	Pre-Laying Wind speed	0.174	0.044	0.000
Clutch Size	Laying Temperature	-0.028	0.005	0.000
	Laying Wind speed	-0.019	0.004	0.000
	Pre-laying Temperature x Pre-laying Rainfall	0.001	0.000	0.000
	Pre-laying Temperature x Pre-Laying Wind speed	-0.010	0.003	0.001
	Pre-laying Rainfall x Pre-Laying Wind speed	-0.001	0.000	0.011
Incubation	Egg stage Temperature	-0.225	0.067	0.001
Hatching Success	Breeding Attempt	0.116	0.149	0.439
	Clutch Size	-0.025	0.032	0.437
	Incubation Duration	0.049	0.077	0.520
	Egg stage Temperature	0.130	0.057	0.023
	Egg stage Rainfall	0.032	0.020	0.106
	Egg stage wind speed	0.074	0.043	0.091
	Egg stage Temperature x Egg stage Rainfall	-0.002	0.001	0.060
Brood Survival	Chick stage Rain	0.085	0.030	0.004
	Chick stage Wind speed	0.209	0.125	0.095
	Chick stage Rain x Chick stage Wind speed	-0.007	0.003	0.012
Probability re-nesting	1st Breeding Attempt Temperature	-2.150	0.670	0.001
	1st Breeding Attempt Rainfall	-0.369	0.125	0.003
	1st Breeding Attempt Wind speed	-2.311	0.711	0.001
	1st Breeding Attempt Temperature x 1st Breeding Attempt Rainfall	0.012	0.005	0.009
	1st Breeding Attempt Rainfall x 1st Breeding Attempt Wind speed	0.019	0.007	0.005

#### a) Rainfall x Wind speed



b) Temperature x Rainfall



Figure 3.4: Fitted models (GEE-GLM) for the interactive effects of total rainfall and mean wind speed, and mean temperature and total rainfall during the first breeding attempt on the probability of a second brood being initiated in the Barn Swallow *Hirdundo rustica*. Black lines represent low values for wind speed (a) = 7.3 kph and temperature (b) =  $17.8^{\circ}$ C, grey lines high values wind speed (a) =  $12.1^{\circ}$ C. The mean value for temperature ( $14.7^{\circ}$ C) and wind speed (9.42 kph) were used for a and b respectively.

# **3.4.2** Results from stage 2: Sensitivity and combined effects of weather across breeding stages on seasonal fecundity

Below I present the results from the predictions generated under the 27 different weather scenarios, from the GEE-GLMS from stage 1, for: 1) the five individual components of seasonal fecundity separately, and 2) overall seasonal fecundity. The results are discussed in terms of the raw predictions, and via the use of sensitivity plots (Figures 3.5 and 3.6) to help visualise the impact of weather on the difference components and seasonal fecundity overall. This approach allows the values of terms retained in the final model to vary simultaneously, allowing a greater exploration of the effects of these on the response variable compared to exploring main-effects from the GEE-GLMs. As stated above sensitivity is expressed as the percentage difference between the predicted value under a given permutation and the value generated under "mean" permutation. These results also refer to the raw values which can be found in Table 3.5.

#### 1) Sensitivity to weather of individual components of seasonal fecundity

Clutch size showed little variation between breeding attempts (first and second clutch sizes; mean =  $4.22/4.19 \pm 0.74$ , range = 2.47 - 5.33, Figure 3.5). Overall, the sensitivity plot (Figure 3.5) shows that wind has a detrimental effect on clutch size, with negative sensitivity under all bar two of the nine high wind permutations (Figure 3.5) in both first and second attempts. Clutch size became more sensitive to high wind speeds with increasing temperature; conversely sensitivity was negative under just one low wind speed permutation. For both first and second attempts, larger clutch sizes were predicted under low temperature scenarios and smaller clutches under high temperature scenarios (Figure 3.5): 6/10 of the smallest clutches (2.48 - 3.97) were associated with high temperature scenarios.

As shown by the GEE-GLM, incubation duration was only sensitive to temperature. On average, first broods had a longer incubation period than second broods (overall means across 27 scenarios = 16.19 versus 15.66 days), but this difference declined with increasing

temperature: at lower temperatures, first attempts were up to 0.96 days longer, whereas this difference disappeared under high temperature scenarios (Table 3.5). Hatching success was virtually identical across all scenarios between first (mean across all scenarios = 0.89±0.12, range 0.51-1, Table 3.6) and second breeding attempts (0.88±0.14, 0.46-1, Table 3.6), and the pattern of sensitivity remained broadly similar over both breeding attempts. Within breeding attempts, hatching success was relatively in sensitive to weather (e.g., compare to clutch size) across most scenarios; hatching success was generally higher under high rainfall scenarios. The exception was under low temperature scenarios for first broods, where this relationship was reversed (Figure 3.5).

Chick survival was relatively sensitive to weather, particularly to wind with high wind speed permutations have lower hatching success over all – although this was more pronounced in first breeding attempts. Generally, hatching success was lowest in dry, windy conditions for both first (0.54) and second (0.66) broods: it nearly doubled under three mean rainfall-low wind speed scenarios and the six high rainfall scenarios (Table 3.6). Overall, more chicks were predicted to survive from second broods (0.66-1.00, Table 3.5), across all 27 conditions modelled, compared to first broods (0.54-1.00, Table 3.5). Second brood probability was typically highest (1.00) under low temperature scenarios and lowest under high temperature scenarios; only two of the nine low temperature scenarios had a probability of <1 (0.00-0.11), while only one high temperature scenario had a probability of 1, while a second had a probability of 0.98 (Figure 3.5 and Table 3.5).



Figure 3.5: Sensitivity of clutch size, incubation duration, hatching success, and brood survival under nine different weather scenarios expressed as percentage difference compared to the mean value for that particular scenario. The weather values for each scenario were based on the relative breeding attempt (first or second) and for the relevant phase. The panel is arranged by temperature and central value in each block of 27 is the prediction for the component derived under the mean values for the other weather variables. For example, the top left value of 4.22 is the clutch size predicted under a combination of low temperature, and mean rainfall and wind speed. Values for weather variables were:

First Attempts:

 $\label{eq:pre-laying} \mbox{(clutch size only); low = 9.27°C/0.8mm/6.4kph, mean = 13°C/21mm/9.26kph, high = 18°C/42mm/12.39kph. \end{tabular}$ 

Laying phase (clutch size only); low =  $12^{\circ}C/0mm/6.91kph$ , mean =  $20^{\circ}C/12.3mm/14.69kph$ , high =  $30^{\circ}C/24.6mm/23.94kph$ .

Egg phase (incubation duration and hatching success); low = 10.6°C/4.3mm/6.61kph, mean = 15°C/59mm/9.663333333kph, high = 21°C/116mm/12.72kph.

Chick phase (brood survival only); low =  $13.7^{\circ}$ C/0mm/7.28kph, mean =  $18^{\circ}$ C/62mm/9.86kph, high =  $24^{\circ}$ C/124mm/12.6kph.

Second Attempts:

Chick phase (brood survival only); low =  $15.5^{\circ}C/5.7$ mm/7.39kph, mean =  $18^{\circ}C/69$ mm/9.0kph, high =  $21^{\circ}C/134$ mm/10.66kph.



Figure 3.6: Sensitivity to weather of the number of fledglings produced in the first and second brood, the probability of a second brood being initiated, and seasonal fecundity overall. The values in the yellow cells are the prediction under mean temperature, mean rainfall, and mean wind speed – sensitivity is expressed as the percentage difference between this value and those predicted under the other scenarios. The number of fledglings per attempt was calculated based on Equation 2, based on the predictions generated for the different components of seasonal fecundity (see methods and Table 3.6), Seasonal fecundity was calculated as per Equation 3 (see Methods). Note that the reference values used for seasonal fecundity here and Table 3.5 are different; here it is the "mean" scenario, in Table 3. it is it the mean value overall.

#### 2) The sensitivity of fecundity to weather at the levels of attempt and season

Across the 27 weather permutations, seasonal fecundity was sensitive to weather and varied four-fold, from 2.05 to 8.13 fledglings (Table 3.5). Overall seasonal fecundity showed a negatively sensitivity to permutations with high wind speeds, except at low temperatures, high rainfall, and high temperatures (Figure 3.6). The negative sensitivity to high rainfall and wind speed produced at both the level of attempt and whole season was particularly evident for second broods (Figure 3.6).

Eight permutations resulted in seasonal fecundity above the mean (5.49 ±1.20), with aboveaverage fecundity achieved under mean or low temperatures (Table 3.5), with seasonal fecundity typically two to three times higher under "low" compared to "high" temperature scenarios. The three highest seasonal fecundity values (7.46-8.13 fledglings) were achieved under three low temperature scenarios, whilst the lowest (2.05-2.25 fledglings) were all achieved at high temperatures (Table 3.5). High values across all components of fecundity were not required to achieve a high value (or above the mean) for seasonal fecundity, although a high probability of a second brood appears important (Table 3.5). Seasonal fecundity was highest under the low temperature, mean rainfall, low wind speed scenario. Under this scenario, the probability of a second brood was 1.00, and a similar number of fledged chicks was produced from the first (4.04) and second (4.09) broods (Table 3.5).

The predicted number of fledglings per breeding attempt was similar for first (mean corrected for predictions from chick survival model =  $2.96 \pm 0.87$ , range = 1.15 - 4.35, Table 3.5) and second breeding attempts ( $3.04 \pm 0.72$ , range = 1.51 - 4.09, Table 3.5). In both cases, the fewest fledglings were produced under the high temperature, high rainfall, and high wind speed scenario. This was driven by a combination of a relatively small clutch size (2.68 in contrast to results above), and below average hatching success (0.68) and brood survival (0.66). However, the highest number of fledglings for first broods occurred under the low temperature, high rainfall, low wind speed scenario, and was driven by an above average clutch size (4.72 eggs), hatching success (0.97) and 100% chick survival (Table 3.6). For second broods the highest number of fledglings was produced under the low temperature, mean rainfall, and low wind speed scenario. Again, this was driven by an

above average (4.75) clutch size and high (1.00) brood survival, although hatching success under this scenario was close to average at 0.90 (mean 0.88, Table 3.6).

Seasonal fecundity was predicted to be lowest under the high temperature, low rainfall, and high wind speed scenario. Under this scenario, a first brood would produce 2.15 (minimum = 1.15) fledged chicks, while the probability of a second brood being initiated was essentially zero (Table 3.6). This can be compared to a seasonal fecundity of 2.66 chicks achieved when all weather variables were at their maxima: a condition where the probability of initiating a second brood was at its highest, but the numbers of fledged chicks in both broods were at their lowest (Table 3.6).

Table 3.5 Predicted values for clutch size (CS), incubation duration (ID), brood survival (BS), the number of fledglings produced (FL) for first (1.) and second (2) breeding attempts, and the probability of a second brood in the Barn Swallow under twenty seven weather permerutations FL was calculated based on equation 1 and seasonal fecundity (SF) was calculated based on based on equation 3 (see above) 2 (see methods). Red highlights for biotic factors denote values above the mean. Rank, order of seasonal fecundity from highest (1) to lowest (27); top ten highlighted in green. See also Figures 3.5 and 3.6.

Temperature	Rainfall	Wind Speed	CS1.	ID1.	HS1.	BS1.	FL1.	Prob 2nd	CS2.	ID2.	HS2.	BS2.	FL2.	SF	Rank
Low	Low	Low	4.79	17.23	0.78	0.54	1.92	1.00	4.79	16.26	0.94	0.61	2.64	4.56	13
Low	Low	Mean	4.81	17.23	0.85	0.72	2.82	1.00	4.81	16.26	0.96	0.71	3.13	5.96	7
Low	Low	High	4.85	17.23	0.91	0.90	3.81	1.00	4.85	16.26	0.98	0.81	3.67	7.46	3
Low	Mean	Low	4.75	17.23	0.89	1.00	4.04	1.00	4.75	16.26	0.90	1.00	4.09	8.13	1
Low	Mean	Mean	4.56	17.23	0.94	0.96	3.92	1.00	4.56	16.26	0.93	0.99	4.00	7.93	2
Low	Mean	High	4.32	17.23	0.97	0.80	3.20	1.00	4.32	16.26	0.96	0.93	3.71	6.90	5
Low	High	Low	4.72	17.23	0.97	1.00	4.35	0.00	4.72	16.27	0.85	1.00	3.83	4.36	16
Low	High	Mean	4.32	17.23	0.99	1.00	4.07	0.11	4.32	16.27	0.89	1.00	3.66	4.47	14
Low	High	High	3.85	17.23	0.99	0.66	2.43	1.00	3.85	16.27	0.93	0.99	3.41	5.84	8
Mean	Low	Low	4.53	16.44	0.90	0.54	2.10	1.00	4.53	15.83	0.97	0.61	2.58	4.68	12
Mean	Low	Mean	4.19	16.44	0.94	0.72	2.73	0.83	4.19	15.83	0.99	0.71	2.80	5.06	10
Mean	Low	High	3.79	16.44	0.97	0.90	3.19	0.05	3.79	15.83	0.99	0.81	2.90	3.34	20
Mean	Mean	Low	4.78	16.44	0.88	1.00	4.03	0.78	4.78	15.84	0.89	1.00	4.07	7.22	4
Mean	Mean	Mean	4.22	16.44	0.93	0.96	3.62	0.67	4.22	15.84	0.92	0.99	3.68	6.09	6
Mean	Mean	High	3.59	16.44	0.97	0.80	2.65	0.56	3.59	15.84	0.96	0.93	3.06	4.37	15
Mean	High	Low	5.05	16.45	0.86	1.00	4.18	0.01	5.05	15.84	0.74	1.00	3.56	4.20	18
Mean	High	Mean	4.26	16.45	0.92	1.00	3.74	0.44	4.26	15.84	0.79	1.00	3.20	5.15	9
Mean	High	High	3.40	16.45	0.96	0.66	2.07	1.00	3.40	15.84	0.85	0.99	2.75	4.82	11
High	Low	Low	3.97	14.89	0.99	0.54	2.03	0.25	3.97	14.89	1.00	0.61	2.32	2.60	24
High	Low	Mean	3.24	14.89	1.00	0.72	2.23	0.01	3.24	14.89	1.00	0.71	2.19	2.25	25
High	Low	High	2.48	14.89	1.00	0.90	2.15	0.00	2.48	14.89	1.00	0.81	1.91	2.15	26
High	Mean	Low	4.60	14.89	0.87	1.00	3.81	0.13	4.60	14.89	0.86	1.00	3.79	4.31	17
High	Mean	Mean	3.58	14.89	0.92	0.96	3.03	0.10	3.58	14.89	0.90	0.99	3.04	3.33	21
High	Mean	High	2.58	14.89	0.96	0.80	1.89	0.07	2.58	14.89	0.94	0.93	2.17	2.05	27
High	High	Low	5.33	14.90	0.51	1.00	2.62	0.05	5.33	14.90	0.46	1.00	2.36	2.74	22
High	High	Mean	3.96	14.90	0.59	1.00	2.25	0.98	3.96	14.90	0.51	1.00	1.95	4.16	19
High	High	High	2.68	14.90	0.68	0.66	1.15	1.00	2.68	14.90	0.59	0.99	1.51	2.66	23

#### 3) Case studies.

Table 3.5 presents the predicted values and the calculations for fecundity as if the weather remains constant across a breeding attempt/season. While some seasons can be characterised as, for example, "wetter" or "cooler" than "normal", given that a single breeding attempt in the Barn Swallow, including the pre-laying period, would cover approximately 50 days, it is reasonable to expect that the weather relevant to each parameter may vary substantially across this period.

In the following section I use a series of case studies to explore what effect of weather variation within an attempt can have on the number of fledglings produced (calculated via Equation2). I have concentrated on the level of attempt to simplify the narrative, but the process can easily be extended to the level of season with reference to Table 3.5 and Equation 3. I have concentrated too on exploring the effects of wind speed.

In each case study the greyed boxes represent the predicted values for each parameter (including the number of fledglings) if the weather remained constant throughout the breeding attempt (i.e., as presented in Table 3.5). Values in parentheses are the values of fecundity as found in Table 3.5 to provide a comparison between the calculated "FL1." in these case studies and those that would be predicted under a constant weather scenario.

#### Case Study 1:

Temperature	Rainfall	Wind Speed	CS1.	ID1.	HS1.	BS1.	FL1.	
Mean	Mean	Low	4.78	16.44	0.88	→ 1.00 —	→ 3.56	(4.03)
Mean	Mean	Mean	4.22	16.44	0.93	0.96 —	→ 3.62	
Mean	Mean	High	3.59	16.44	<b>→ 0.97</b>	→ 0.80	→ 3.12	(2.65)

A female laying a clutch under "typical" weather (mean rainfall, temperatures, and wind speeds). A reduction in speeds during incubation would result in a similar number of fledglings being produced compared to if the weather had remained constant (3.56 vs 3.62); with a lower hatching success (0.88 vs 0.97) under low wind speeds being compensated for by a higher brood survival (1 vs 0.80). But the smaller clutch size predicted under "mean" weather would result in fewer fledgling being produced compared to a female who had laid under low wind conditions (3.56 vs 4.03). From the same starting point

(i.e., "mean" weather), if wind speeds increase during incubation, fewer fledglings would result compared to "mean" conditions (3.12 vs 3.62), as a result of reduced brood survival, but more so that a female laying under high wind speeds (3.12 vs 2.65) due to a higher starting clutch size.

#### Case Study 2:

Temperature	Rainfall	Wind Speed	CS1.	ID1.	HS1.	BS1.	FL1.		
Mean	Low	Low	4.53	16.44	<b>0.90</b>	<mark>→ 0.54</mark> —		1.96	(2.10)
Mean	Low	Mean	4.19	16.44	0.94	0.72		2.73	
Mean	Low	High	3.79	16.44	0.97 -	→ 0.90		3.56	(3.19)
Mean	Mean	Low	4.78	16.44	0.88	1.00		4.03	
Mean	Mean	Mean	4.22	16.44	0.93	0.96		3.62	
Mean	Mean	High	3.59	16.44	0.97	0.80		2.65	
Mean	High	Low	5.05	16.45	0.86 -	→1.00 —		3.49	(4.18)
Mean	High	Mean	4.26	16.45	0.92	1.00		3.74	
Mean	High	High	3.40	16.45	0.96	0.66 —		2.57	(2.07)

A female lays a clutch under "typical" weather, with mean rainfall, temperatures, and wind speeds. If rainfall becomes low during incubation, remains so through chick rearing, a female would be predicted to benefit from high wind speeds producing nearly as many young as if the weather had remained average (3.56 vs 3.62) and slightly more than if she had laid during a period of low rainfall and high winds (3.56 vs 3.19). These similarities being driven by a similar degree of hatching success and brood survival; although which of these two parameters has the highest values varies between the different weather permutations. In contrast, low brood survival resulting from low rainfall and low wind speeds over the same period would result in a similarly low number of fledglings compared to laying in the same weather (1.96 vs 2.10).

If higher levels of rainfall occurred during incubation and chick rearing then a female would be more disadvantaged by low wind speeds, producing fewer chicks, due to a lower hatching success, compared to average weather (3.49 vs 3.62) and compared to if rainfall and wind speeds had been low during laying too (3.49 vs 4.18). A breeding attempt started in "average" weather would result in more young, if rainfall and wind speed were higher during incubation and chick rearing compared to an attempt starting under such conditions (2.07 vs 2.57); this would be driven by a larger clutch under "mean" conditions compared to "wet and windy" conditions (4.22 vs 3.40).

#### Case Study 3:

Temperature	Rainfall	Wind Speed	CS1.	ID1.	HS1.	BS1.	FL	1.
Low	Low	Low	4.79	17.23	0.78	0.54	1.9	2
Low	Low	Mean	4.81	17.23	0.85	0.72	2.8	2
Low	Low	High	4.85	12.23	0.91	→ 0.90 —	→ 3.7	6 (1.96)
Low	Mean	Low	4.75	XX	0.89	1.00	4.0	4
Low	Mean	Mean	4.56	1723	0.94	0.96	3.9	2
Low	Mean	High	4.32	17.2	0.97		→ 3.5	5 (3.2)
Low	High	Low	4.72	17.23	0.97	1.00	4.3	5
Low	High	Mean	4.32	17.23	0.99	1.00	4.0	7
Low	High	High	3.85	17.23	0.99	→ 0.66 —	→ 3.0	3 (2.34)

A female lays her clutch during a cool, dry, calm period. During incubation wind speeds and rainfall increase during incubation. In all cases the female would benefit by producing more young than if i) the weather had remained constant, or ii) they had experienced similar weather during incubation during egg laying. The largest gain is seen when wind speeds are high, but rainfall remains low, with almost two more chicks being fledged (3.76 vs 1.96). This is driven by a higher hatching success and brood survival rate predicted under these conditions. While the female would gain from both increased rainfall and wind speeds, compared to constant weather, the gains become less pronounced as both rainfall and wind speed increases.

## 3.5 Discussion

Bird species vary widely in their apparent sensitivity to weather, with different components of fecundity being affected differently, or not at all, by different weather variables, even in closely related species (Collister & Wilson 2007; Golawski 2008). In this six-year study of swallows, all components of seasonal fecundity (clutch size, incubation duration, hatching success, the proportion of the brood surviving to fledging and the likelihood of a second brood being initiated), showed varying degrees of sensitivity to local weather, highlighting the importance of disaggregating seasonal fecundity into its component parts. The results also highlight the importance of considering wind speed and interactive effects of weather in future studies. Wind speed was retained in all bar one of the component models (incubation duration), indicating the importance of this often-overlooked weather variable. Wind speed typically had a negative effect on seasonal fecundity and its components. However, as shown by the sensitivity plots (Figures 3.5 and 3.6) and the case studies, the effect of wind can be positive within certain contexts (for example case study 3).

#### Individual components of seasonal fecundity

In agreement with previous studies (e.g., Ward & Bryant 2006), I found that clutch size showed some sensitivity to both antecedent (i.e., pre-laying period) and current (laying period) weather. Low pre-laying rainfall had a negative effect on clutch size, whereas high rainfall had a positive effect. Larger clutches under high rainfall conditions may be linked to higher insect abundance, rather than the transient reductions in insect availability during the rainfall events themselves. For example, some rain may be needed to keep dung, and other habitats, moist enough to allow colonisation, emergence, or larval survival of prey species such as Scathophaga sp. (Gibbon 1987; Ward & Simmons 1990). Similarly, Chamberlain et al. (2008) found that the availability of earthworms to breeding Blackbirds was dependent on rainfall, suggesting that rainfall may be an important driver of invertebrate availability in the longer-term (compared to short-term, rainfall events) during the breeding season in other species. Likewise, warmer temperatures increase insect activity – and hence availability – once insects are flying. High wind speed was associated with reduced clutch size, in interaction with both temperature and rainfall. As described in Chapter 2, flying insects congregate near boundary features, and are found at higher abundance close to these features during high wind speeds, especially at low temperatures (Grüebler et al. 2008), but this "honey pot" of high food availability for swallows may be

80

diffused by higher temperatures (as invertebrates become more active and become more dispersed in the landscape) and higher rainfall (as invertebrate become less active/available). Pre-laying periods characterised by low temperatures and high wind speeds, or high temperatures during calmer conditions, when insects are more abundant in open spaces (Grüebler *et al.* 2008), are consistent with females being able to find sufficient food to lay more eggs (Figure 3.2 b). The decline in clutch size under high rainfall and high wind speed conditions is also consistent with this weather-induced change in insect distribution and availability.

Temperature during laying had a negative association with clutch size. Smaller clutches at higher temperatures could represent a parental decision to increase embryo survival; for example, Reid et al. (2000) found that smaller clutches cool more quickly than larger clutches. Laying smaller, faster cooling clutches would be of benefit to species that lay in environments that experience high ambient temperatures during incubation. Another, but not mutually exclusive, explanation is that simply represents a seasonal effect. In the current study, temperature and "day variables" were highly colinear (VIF>3) and therefore not included within the starting models but "attempt" provided some control for seasonal affects in terms of early (first attempts) and late (second attempts) broods. As warmer temperatures tend to occur later in the season (Figure 3.1), the decline in clutch size may simply represent a seasonal decline in clutch size. A seasonal decline in clutch size has been found in studies of seasonal fecundity in many multi brooding species (e.g., Eikenaar et al. 2003; Nooker et al. 2005; Young 1994). This likely represents a reduction in investment from females, as young from later broods may have a lower lifetime fitness; chicks from second broods often have a lower likelihood of recruitment into the breeding population (Raja-Aho et al. 2017). Or simply, in the case of second broods, that females have already invested in one brood already. A seasonal effect is also likely to explain why the probability of second brood was negatively associated with temperature during the first breeding attempt and was typically highest under low temperature scenarios; lower mean temperatures being more typical of the conditions experienced early in the season. This would be consistent with previous work on multi-brooded species (Carro *et al.* 2014; Hoffmann *et al.* 2015; Laet & Dhondt 1987; but see Nagy & Holmes 2005b) which showed that the earlier the first breeding attempt, the more likely a second brood was to be initiated.

Incubation duration was found to be affected by temperature, but not by rainfall or wind speed. The lack of effect of rainfall and wind speed suggests that females, at least in part, can compensate for the impacts of variation in daily weather during incubation, by altering the duration and number of absences from the nest to feed (Coe *et al.* 2015; see Chapter 4 for a more detailed account). Increasing temperature can result in early onset of incubation, before clutch completion, in order to preserve egg viability, especially where temperatures during egg laying may rise above the threshold (26°C) needed for embryo development (Ardia *et al.* 2006). This "ambient incubation", would also apply during incubation itself, facilitating a shorter incubation period, as the embryos continue to develop when the eggs are left unattended (Griffith *et al.* 2017). Additionally, Ardia *et al.* (2009) found that female Tree Swallows *Tachycineta bicolor* in experimentally heated nests spent more time incubating than controls and maintained higher nest temperatures, likely as a result of reduced energetic costs; both of which reduced incubation duration.

The interaction between temperature and rainfall during the egg stage was the only significant predictor of hatching success. Higher hatching success was predicted under

periods with no rainfall, but hatching success declined with temperature under high rainfall during the egg stage (laying/incubation). Higher temperatures during laying have been shown to have a positive effect on the hatching success (Siano et al. 2004); indeed, eggs laid during relatively warm weather tend to be of better quality, having a higher mass and higher innate immunity (Siano et al. 2004; Arida et al. 2006). Under cooler conditions, females may not be able to find enough prey of sufficient quality to invest more in egg quality; this may also account for the negative relationship between hatching success and temperature under high rainfall, despite the possible benefits of warmer temperatures. Alternatively, but not mutually exclusively, higher rainfall may cause incubating females to spend more time off their nests (Jones 1989; Coe et al. 2015) in order to forage, exposing their eggs to greater temperature fluctuations which can reduce viability (Olson et al. 2006) but see Chapter 3). Periods of heavy rain may reduce temperatures, temporarily, perhaps by wetting nest materials, or vegetation near nests (or in the case of swallows, concrete, or stable roofs), thus affecting the nest micro-climate, and in turn increasing egg cooing rates. Hatching success for both first and second broods was lowest under the high temperature /low wind scenarios, and highest under the high temperature/high wind scenarios. While wind speed was not a significant predictor of hatching success, the results from the fecundity model and case studies suggest that it may have an important role in certain circumstances. Continued exposure to high temperatures results in increased risk of developmental abnormality and embryo mortality (Conway & Martin 2000). Higher wind speeds are likely to cool eggs through increased air flow across the nest cup/eggs (Gray & Deeming 2017; Heenan & Seymour 2012), preventing or limiting the amount of time developing embryos are exposed to sub-lethal or even lethal temperatures. Wind speed may therefore only be biologically important under a narrow range of circumstances, which might account for the lack of any strong statistical association between hatching success and wind speed within the hatching success model (Table 3.4).

83

Temperature was not associated with chick survival. High temperatures would be expected to increase nestling mortality through dehydration, and this is particularly pertinent to species nesting in anthropogenic structures or other substrates that often become warmer than their surroundings (Andreasson et al. 2018; Ardia 2013; Imlay et al. 2019; Rodríguez & Barba 2016; Salaberria et al. 2014). High wind speeds would be expected to reduce this effect from the cooling effect of increased air movement around or over nests (Heenan & Seymour 2012). However, brood survival was positively associated with rainfall at low wind speeds and negatively at high wind speeds. Indeed, under the scenario testing, brood survival was lowest under the scenarios with low rainfall and low wind speed, in both first and second broods. The chicks in the current study died at various ages, and it may be that wind has a detrimental effect on younger chicks. Before they can properly thermo-regulate, young chicks require periodic brooding by their parents. High wind speeds may increase the rate that they chill during non-brooding periods, which may result in fatalities; however, there is insufficient data in the present study to explore this. Alternatively, but not mutually exclusively, the combination of high rainfall and high wind speeds reduces the availability/activity of insects, and hence the foraging success of provisioning parents (Grüebler et al. 2008; Schifferli et al. 2014), which may impact survival - for example by reducing the energy intake of chicks under already physiologically challenging conditions. Insufficient data were available to test for weather related mortality throughout the chick phase. Indeed, a combination of high wind speed and rainfall may only have negative effect aerial insectivores; high rainfall has been linked to higher nestling mass in terrestrial feeding species such as the blackbird (Chamberlain et al. 2008).

84

#### **Overall seasonal fecundity**

The seasonal fecundity modelling showed that the highest seasonal fecundity values (i.e., those above the mean of  $5.49 \pm 1.20$  fledglings per year) occurred under low temperature scenarios. These higher seasonal fecundities occurred under combinations of weather conditions that promoted large clutches and high brood survival, whereas the lowest were driven by small clutches followed by low brood survival.

An important result was that either at the breeding attempt or seasonal level, fecundity was not necessarily driven by weather conditions that promoted high values for each component. Instead, there is an element of "compensation", whereby a low value for one component can be mitigated to some degree, providing there are high values in the preceding or subsequent stages. For example, the highest fecundity was achieved when weather conditions promoted above-average clutch sizes, but these same conditions resulted in below average hatching success. This however was "compensated" for by all chicks being predicted to survive. This highlights the importance of disaggregating seasonal fecundity into its component parts, when examining the drivers of variation in overall fecundity.

Seasonal fecundity was predicted to be low under high temperatures, with the two lowest fecundity outcomes both occurring under weather scenarios involving high wind speeds. These conditions led to below-average clutch sizes and brood survival and had near- zero probability of a second brood being initiated (but see Figure 3.5). This suggests that, under future climatic predictions of increased summer temperatures and wind speeds (IPCC 2014), species such as the swallow may experience reduced seasonal fecundity. This may be particularly pertinent to human commensal species like the swallow species that nest

within or on buildings, where temperatures close to nests are likely to be higher compared to ambient temperatures outside in nearby fields (Imlay *et al.* 2019). Indeed, swallow daily nest failure at the chick stage has increased by 65% since 1966 (Woodward *et al.* 2019), coinciding with a period of rapid warming; although the habitat change during this time may also have played a more significant role (Evans & Robinson 2004; Robinson *et al.* 2003; and Chapter 2). Swallows may be able to mitigate some temperature increases, either at the individual level by nesting earlier in the year, to take advantage of cooler weather – in the UK, their mean first egg date has advanced by 12 days since 1966 (Woodward *et al.* 2019) – or at the population level through higher fecundity in cooler years.

Taken together, the results suggest that changes in local weather, driven by climate change, may have complex repercussions for seasonal fecundity in swallows. Earlier spring arrival may allow them to advance their breeding season, increasing seasonal fecundity through taking advantage of cooler early season temperatures, and through a greater probability of second broods. However, this may be offset by increasing summer temperatures, droughts, or excessive rainfall, and increasing wind speeds on individual components of fecundity.

## Chapter 4: The effects of weather on the incubation behaviour and within-nest temperature of Barn Swallows *Hirundo rustica*

### Summary

The within-egg environment experienced by developing bird embryos can affect their prehatching development as well as their post-hatching growth, survival, and future reproductive success. To maximise their lifetime fitness, incubating adult birds need to make strategic decisions to provide an appropriate developmental environment for the embryos, whilst simultaneously addressing their own self-maintenance. These decisions also need to consider environmental factors such as local weather. To investigate how birds alter their incubation behaviour in response to weather, I monitored diurnal and nocturnal incubation behaviour of female Barn Swallows Hirundo rustica at two temporal scales (hourly and daily) and related the frequency and duration of incubation bouts and incubation constancy (proportion of time spent incubating) to the prevailing temperature, rainfall, and wind speed. At the hourly level, bout duration was largely insensitive to weather variation, but was influenced by the time of day; around midday/early afternoon off-bouts were approximately one minute, or 25%, longer than those in the early morning or late evening. Incubation constancy was highest close to sunrise and sunset, lowest around mid-afternoon, and decreased with increasing ambient temperature, as females left the nest more frequently ("off-bouts") when temperatures were higher. Mean hourly nest temperature was positively associated with increased incubation constancy, and females maintained higher nest temperatures under higher ambient temperatures. At the daily timescale, females took fewer, longer breaks from incubation on rainy days, but these breaks became shorter and more frequent as incubation progressed. Mean daily nest temperature was affected by the interaction of daily rainfall and wind speed; nest temperature was relatively unaffected by wind speed on dry days but declined with increased wind speeds on wet days. There was evidence of diurnal incubation behaviour having carry-over effects on the nocturnal nest environment; nocturnal nest temperatures were higher following days with high nest temperatures, and on warmer and windier nights. Nocturnal nest temperatures were also higher following days of low incubation constancy, suggesting a compensatory response to low nest attendance during the day. The results show that, rather than incubation being a static process, females respond to – and

in part compensate for – changes in local weather conditions to maintain a favourable developmental environment for their embryos.

### 4.1 Introduction

Birds make behavioural decisions over a range of temporal scales, in order to maximise their short-term survival and reproductive success, and ultimately to maximise their lifetime fitness (Stearns 1992). Examples of such decisions include the regulation of body reserves (e.g., Ekman & Hake 1990), choice of prey type and size (e.g., Turner 1982; Marples et al. 2018), and habitat selection (e.g., Evans et al. 2010; Vafidis et al. 2014), as well as decisions about investment in reproduction (e.g., Fontaine & Martin 2006; Horváthová et al. 2012). These strategic decisions are based both on extrinsic factors such as environmental conditions, and on intrinsic factors such as an individual's current body condition (McNamara & Houston 1996; Marples et al. 2018). Some of the most important strategic decisions need to be made during the breeding season, when reproductive activities such as incubation or provisioning chicks, and self-maintenance activities such as foraging, are energetically costly and often mutually exclusive. Optimal life-history theory predicts that individuals should make strategic choices between alternative activities in order to maximise their lifetime fitness (Stearns 1992). This may be particularly important during incubation, as this is an energetically expensive activity, with implications for both long term parental and offspring fitness, the success of current and subsequent breeding attempts (Heaney and Monaghan 1996; Reid et al. 2000; Visser and Lessells 2001; Hanssen et al. 2005; de Heij et al. 2006; Nilsson et al. 2008), and in terms of both offspring quality and survival (Lindström 1999).

The thermal environment experienced by embryos within the eggs is important for their development, and can affect the success and synchrony of hatching, offspring quality and phenotype, and may even have carry-over effects on their own future reproductive success (Ambrosini *et al.* 2006; Ardia 2013; Ardia *et al.* 2010; Kim and Monaghan 2006; Nord and Nilsson 2011). The developing embryos of birds need to be kept within a relatively limited range of temperatures, 26.0-40.2°C, to facilitate proper development (Scanes 2015). Within this range, however, the relationship between temperature and development is non-linear, with optimal development generally considered to occur between 36.0 and 40.2°C (Conway and Martin 2000; Scanes 2015). Below 36.0°C, development slows, ceasing altogether below 26.0°C (known as "physiological zero temperature"), while prolonged exposure to temperatures above 40.2°C can lead to abnormal development and mortality (Conway & Martin 2000). The rate at which eggs cool after being left by an incubating female during an

off-bout will depend on factors that affect nest microclimate (e.g., ambient temperature, Jones 1989) and nest size, structure and insulation (Windsor *et al.* 2013; McClintock *et al.* 2014). While embryos can withstand periods of cooling, these are not without consequences, such as less efficient embryo development (Olson *et al.* 2006), increased incubation duration (Lydon & Montgomerie 2012), and reduced nestling immunity to infections (Ardia *et al.* 2010). Adult birds are therefore predicted to make strategic decisions during incubation, trading-off the challenge of maintaining thermally optimal conditions for their developing offspring against fulfilling their own energy requirements (Ardia *et al.* 2010; Nord & Nilsson 2011). This is particularly pertinent in species where just one parent (typically the female) incubates the eggs, especially among species with no provisioning of the incubating bird by its mate, as this necessitates frequent periods away from the nest with the eggs unattended.

The total time that parents are away from the nest is the product of the number of absences (hereafter referred to as 'off-bouts') and the duration of those bouts. Incubating parents can vary either or both of these parameters, in an attempt to obtain an optimal balance between their own needs and those of their eggs (Jones 1989; Conway & Martin 2000a & b; Haftorn 1988; McClintock *et al.* 2014). The decision to leave the nest is likely to vary over a range of time-scales, depending on factors known to influence these decisions, such as weather conditions, food abundance, clutch size and the perceived risk of nest predation (Ardia *et al.* 2010; Conway & Martin 2000a; Cooper and Voss 2013; Nagy & Holmes 2004; Zicus *et al.* 1995, Vafidis *et al.* 2018), with several studies suggesting that local weather conditions may have the largest effect (Ardia *et al.* 2010; Conway & Martin 2000a; Conway & Martin 2000a).

Ambient temperature is a significant driver of incubation behaviour (Conway and Martin 2000a). Higher ambient temperatures reduce the energetic costs associated with incubation, such as re-warming eggs (through reduced cooling rates) or by increasing foraging efficiency (Bryan & Bryant 1999; Griffith *et al.* 2016; Jones 1989; Reid *et al.* 1999). Thus, warmer ambient conditions have been linked with the maintenance of higher egg temperatures (Ardia *et al.* 2009), higher nest attendance (i.e., total time spent incubating, Bryan & Bryant 1999; Cresswell *et al.* 2004; Ardia *et al.* 2009; Camfield and Martin 2009) and longer off-bouts (Conway and Martin 2000a, 2000b). Conversely, at low ambient temperatures, females may employ an "all or nothing" strategy (Haftorn 1988). Under an "all" strategy females may continue to incubate but maintain a lower nest temperature

(Ardia *et al.* 2010), for example by taking more frequent but shorter off-bouts (Conway & Martin 2000a), or they may take "extreme" long-duration off-bouts when conditions prove severe. For example, McDonald *et al.* (2013) showed that female Horned larks *Eremophila alpestris* took off-bouts that were six to forty times longer than the typical 10 minute off-bouts when conditions, such as extremely low temperatures or storms, required prioritising self-maintenance over incubation. Alternatively, under a "nothing" strategy, females may cease incubation all together until conditions improve (Schulze-Hagen 1969; Ribault 1982).

In comparison to the influence of temperature, relatively few studies have considered the influence of precipitation upon incubation behaviour. Meadow Pipits *Anthus pratensis* have been shown to increase nest attendance and reduce off-bout duration in response to increased rainfall (Kovařík *et al.* 2009). Similarly incubating female Tree Swallows *Tachycineta bicolor* may reduce the lengh of off-bouts, especially in cold weather, during periods of high rainfall (Coe *et al.* 2015). However, the evidence for the impacts of rainfall is not unequivocal. For example, rainfall has been shown to have no effect on the number or duration of off-bouts, or incubation constancy in the Great Tit *Parus major* (Basso & Richner 2015; Schöll *et al.* 2019).

Despite the potential importance of rain and temperature on incubation behaviour, comparatively few studies have considered multiple weather variables and overlook the possibility of interactive effects. The potential importance of such interactions is illustrated by studies such as Coe et al. (2015), who showed that female Tree Swallows spent more time off the nest under cold and dry conditions, compared to when it was warm and dry, but this pattern was reversed under periods of rainfall; females took short off-bouts under wet and cold conditions compared to under warm and wet conditions. Furthermore, most studies only consider temperature or rainfall, ignoring the effects of other variables that might influence birds directly, or indirectly via effects on prey availability. There is, for example, increasing evidence that wind speed has important implications for several life history traits, such as breeding success and phenology, and adult survival (Møller 2013; Irons et al. 2017). Wind speed, via increased airflow, may have important implications for the nest microclimate (Gray & Deeming 2017), and can increase incubation effort (Hilde et al. 2016) and influence incubation behaviour (Capp et al. 2017). Wind may have an opposing effect on incubation behaviour compared with other variables; chestnut-crowned babblers Pomatostomus ruficeps increased on-bout length and attentiveness (incubation constancy) with ambient temperature but these traits were negatively related to wind speed (Capp et al. 2017). Yet the potential importance of wind effects on avian incubation has not been appraised to the extent of temperature and rainfall, especially in passerines (but see Capp *et al.* 2017).

A second gap in understanding the link between weather and incubation concerns nighttime. For diurnal species, nocturnal incubation represents a prolonged period of energy expenditure without the opportunity to replenish energy reserves. The lower ambient temperatures at night can significantly increase energy expenditure compared to daytime incubation (Nord et al. 2000; de Heji et al. 2007). As individuals use current or recent weather conditions as a predictor for conditions that may follow at night (Bednekoff et al. 1994; Thomas & Cuthill 2002), it would be expected that incubating females will make strategic decisions during the day to regulate dusk body reserves in proportion to the anticipated overnight conditions and the consequent nocturnal energy expenditure (Bednekoff et al. 1994; Thomas 2000; Thomas & Cuthill 2002). For example, birds are able to adjust their behaviour to compensate for both unpredictable weather conditions and less predictable food supplies (e.g., resulting from varying weather conditions), by adjusting their fat reserves at dusk (Cuthill et al. 2000; Ekman & Hake 1990). Precipitation and low ambient temperatures are both known to reduce insect abundance and activity density (Bryant 1975; Turner 1984; Nooker et al. 2005; Winkler et al. 2013; Vafidis et al. 2016), and female birds incubating under such conditions may need to prioritise foraging to obtain sufficient body reserves to undertake incubation at night. The energetic costs of nocturnal incubation may also have carry-over consequences for incubation behaviour the following day. Bryan and Bryant (1999), for example, found that experimental heating during nocturnal incubation led to lower energetic expenditure during the night and consequently more time spent incubating the following day. Studies that have examined nocturnal incubation in diurnal passerines have mainly concentrated on the metabolic costs of nocturnal incubation under natural (e.g., de Heij et al. 2006) or the effects of experimentally-warmed conditions (e.g., Nord et al. 2010), or the effects of reducing the cost of components of incubation (e.g., Vedder 2012). How nocturnal incubation relates to diurnal incubation – for example whether birds adjust nocturnal incubation to compensate for lower incubation constancy during the day – remains poorly understood.

The current study investigates how ambient temperature, rainfall and wind influence diurnal and nocturnal incubation behaviour of Barn Swallows *Hirundo rustica*; a species in which only females incubate, and males do not provision their incubating mates. Using

data-loggers to record nest temperatures and incubation activity through the day and night, overall incubation constancy (the proportion of time spent incubating) was quantified at hourly and daily scales, along with the frequency and duration of off-bouts. I tested the over-arching hypotheses that: i) incubation behaviour will differ under varying weather conditions; ii) sensitivity to weather will be greater over a short (hourly) time scale as birds respond rapidly to current conditions, whereas over a longer (daily) time scale birds will compensate for shorter-term variation in weather conditions, and iii) diurnal weather conditions and consequent incubation behaviour will have carryover effects into the nocturnal phase. I tested the prediction that female Barn Swallows will increase incubation constancy when ambient temperature is higher, as incubation is less costly under warm conditions. However, I predicted these relationships to be mediated by wind speed and rainfall, as both of these variables are likely to affect the energetics of incubation through mechanisms such as changes in food abundance and foraging efficiency (e.g., Jones 1989; Gray & Deeming 2017; Schifferli et al. 2014), or via more rapid cooling rates (e.g., Capp et al. 2017, Gray & Deeming 2017). I also tested the prediction that females will maintain higher nest temperatures on nights following days when incubation constancy and diurnal nest temperature were lower, as a compensatory behaviour for poor diurnal incubation conditions.

## 4.2 Methods

#### 4.2.1 Temperature probe deployment

The study took place at an equestrian centre adjacent to parkland within the city of Cardiff, Wales, UK (see Chapter 1 for details) in 2014, with all nests within horse stables. Fieldwork focused on the first brood of individual female swallows. Nests were visited every three to four days from late April, to look for signs that laying was imminent (i.e., the nest was lined with feathers) and to record clutch initiation date, clutch size, and hatching day. As the typical clutch size for swallows is 4-5 eggs (range 2-9, Robinson 2015), with one egg laid each day, this interval was sufficient to determine clutch initiation and completion dates.

Temperature probes (Gemini Talk Thermistor Probe PB-5005) connected to data loggers (Gemini TinyTalk TK-4023-PK) were used to record nest temperatures every 60 seconds

during incubation. Probes were fixed inside the nest cup once it had been lined and were repositioned after clutch completion so that the tip of the probe lay parallel with the nest lining in the centre of the clutch (no licence was required for this procedure, as it did not involve damage to the nest; Natural Resources Wales *pers. comm*). No nests or probes received direct sunlight. Probes were checked every two days to make sure that they were still in the correct position. It was obvious from the resulting temperature time series (hereafter referred to as 'traces') whether a probe had been dislodged from the nest cup (a sudden and prolonged drop towards the ambient temperature, followed by less variable temperature changes) -and any such data were removed from the analysis. Data loggers were connected to the probes, and placed out of sight of the incubating female, once a clutch was completed. Although swallows are typically synanthropic (commensal with humans) and generally tolerant of human disturbance near the nest, data loggers were programmed to record temperature from midnight at the end of the day they were put in place, to eliminate any effects of the initial disturbance on incubation behaviour.

Probes were initially deployed in 13 nests, but unusually high predation rates by Eurasian Magpie *Pica pica* and House Mouse *Mus domesticus*, at both the egg and nestling stages limited the number of breeding attempts available for study. Predation occurred during egg laying in four nests, whilst probes were dislodged in two nests, and access was not possible to re-adjust them before hatching occurred. Of the remaining seven study nests, two were predated at the chick stage and the remaining five were successful in fledging at least one chick. There was no evidence to suggest that the use of probes, or the visits to check and reposition them, affected nesting success, as there was no significant difference in success between nests with and without probes ( $X^2 = <0.001$ , df=1, n=35, p=>0.999) and this technique has been used safely with a wide range of species (e.g., Joyce *et al.* 2001; Eikenaar *et al.* 2003). Predation levels were sufficiently high in the 2015, 2016, and part of the 2017 breeding season to make repeat studies untenable. Predation levels reduced to virtually zero in the latter half of 2017, following the arrival of new Domestic Cats *Felis domesticus* at the equestrian centre. The final sample size was 29 days of continuous monitoring, distributed across seven nests.



Figure 4.1: Example temperature trace from the nest of a Barn Swallow showing periods of active incubation, or "on-bout" (blue), and when the female is absent from the nest, or "off-bout" (orange).

Incubation behaviour was split into two broad time periods: the diurnal, "active" period for swallows (sunrise to sunset), and the nocturnal "inactive" period. Female incubation behaviour was quantified for each diurnal period after full incubation had commenced (i.e., once females began to incubate consistently during the day and night after the clutch was completed). Off-bouts were defined as sustained, rapid drops in temperature of  $\geq 1.0^{\circ}$ C which continued for a minimum of two minutes (Figure 4.1). This definition was calibrated with observed presence/absence of incubating birds at the nest by filming three incubating females for a total of eight hours using a Raspberry Pi model a+ and NOIR camera module (Raspberry Pi Foundation, UK) illuminated with infra-red light-emitting diodes (LEDs) whilst temperature loggers were in place. On-bouts were considered any period in between defined off bouts, during which the eggs were actively incubated. For hourly-level analysis, each bout was assigned to the hour in which it was initiated. Only hours completely within the active period (i.e., those after the hour of sunrise and before that of sunset) were included in the analysis for hour-level models.

Incubation constancy was measured as the proportion of the time available at a given temporal scale that a female spent incubating. As the age of an embryo (i.e., degree of development) can affect nest attentiveness (Cooper & Voss 2013; Wang & Weathers 2009; Zicus *et al.* 1995), incubation day was expressed as a proportion of the total incubation period (interval between day of clutch completion and hatching, where date of final egg = day 1) for a given clutch and used as a proxy for stage of embryo development in the subsequent analyses (hereafter "stage of incubation"). Mean daily nest temperature (hereafter "daily nest temperature"), mean nocturnal nest temperature (hereafter "hourly nest temperature") were derived from all temperature observations over the relevant time periods.

#### 4.2.2 Weather data

Sunrise and sunset times, and weather data were obtained from the UK Meteorological Office. Hourly mean ambient temperature (°C) and total hourly rainfall (mm) were obtained from a UK Meteorological Office weather station (Bute Park; 51°29'16.7"N, 3°11'17.0"W, 9m above sea level, asl), 1.5 km south of the study site. These data were used to calculate daily mean ambient temperature and total rainfall. No wind data were available for this station and so these were obtained from another Meteorological Office weather station (St Athan; 51°24'18"N, -3°26'24" 49m asl) approximately 18.7km to the south-east.

## 4.3 Statistical analysis

All data analysis used R version 3.5.3 (R Development Core Team 2019). At the hourly scale, the effects of local weather on the swallows' off-bout frequency and duration, incubation constancy and both diurnal and nocturnal nest temperatures were investigated using generalised additive mixed-effects models (GAMMs), fitted using the mgcv package (Wood 2019). The default thin-plate regression spline was used to fit time of day (hour) as a smoothed independent variable in all models explaining off-bout duration and frequency (the number of off-bouts taken per hour or day), and nest temperatures. As nocturnal incubation was effectively one long "on-bout", the model for incubation constancy was

fitted using a cyclic regression spline to ensure that incubation constancy was modelled as starting and ending the night-time period at the same value, i.e., an incubation constancy of 1 (Wood 2006). At the daily scale, equivalent models were fitted using linear mixed-effect models (LMMs), with a 'Gaussian' error distribution and an 'identity' link function, fitted using the lme4 package (Bates *et al.* 2015).

All models included: i) female ID as a random effect, to account for multiple hours/days per nest; ii) the stage of incubation to account for any changes in incubation behaviour and nest attendance over time (Cooper & Voss 2013; Wang & Weathers 2009; Zicus *et al.* 1995); and iii) mean ambient temperature, total rainfall (mm) and mean wind speed (kph) at the appropriate temporal scales, as well as two way interactions between ambient temperature and rainfall, rainfall and wind speed, and temperature and rainfall. The nest environment models also included the two-way interaction between ambient and nest temperatures. The model for nest temperate also included incubation constancy. Although clutch size can influence nest temperature (Nord & Nilsson 2012), all clutches comprised five eggs except for one four egg clutch, so this was not considered in the analysis. Pair plots and variance inflation factor values (VIF) were used to assess co-linearity between variables; with variables being considered independent when showing a VIF of <3 (Zuur *et al.* 2010); none of the variables listed above showed a VIF >3.

In all cases the final models were selected using stepwise deletion, starting with interaction terms, until there was no further reduction in the AIC (Anderson & Burnham 2002). Model validation procedures followed Zuur *et al.* (2007) and Thomas *et al.* (2017). The overall explanatory power of the model was assessed using the marginal  $R^2$  value (Nakagawa & Schielzeth 2013), which is based solely on the fixed effects in the model (cf. the conditional  $R^2$  which is based on both random and fixed effects), or in the case of GAMMS, the adjusted  $R^2$ , both calculated using the 'MuMin' package (Bartón 2018).

## 4.4 Results

Summaries for variables relating to incubation behaviour, nest temperatures and weather are summarised in Table 4.1
Hourly Level	Day Level	
0.63 ±0.13 (0.22 – 1.0)	0.65 ±0.04 (0.56 – 0.74)	
4.30 ±1.85, (0 - 9)	63.31 ±15.16, (33 – 97	
5.94 ±3.74 (2-47)	5.38 ±1.20 (2.97 – 7.67)	
28.75 ±4.18 (18.53 – 38.03)	28.12±3.89 (18.69 - 37.31)	
N/A	27.44 ±4.33 (19.18 – 32.48)	
0.28mm ±0.9 (0 – 7.8)	4.9 ±5.9 (0 – 17.2)	
5.8 - 19.9	10.27 – 18.25	
1.85 – 55.56	8.18 - 38.96	
	Hourly Level 0.63 ±0.13 (0.22 – 1.0) 4.30 ±1.85, (0 - 9) 5.94 ±3.74 (2-47) 28.75 ±4.18 (18.53 – 38.03) N/A 0.28mm ±0.9 (0 – 7.8) 5.8 – 19.9 1.85 – 55.56	

Table 4.1: Mean values (± SD, range in parenthesis) for incubation behaviour, nest temperature, and weather variables at the level of hour and day. As temperature and wind speed values used in the analyses were means for the respective temporal scale, only the range is presented.

#### 4.4.1 Hourly effects of weather on incubation behaviour

At the hourly scale, there was evidence that swallows altered their incubation behaviour in response to weather, but this differed among the three measures of incubation behaviour (incubation constancy, number of off-bouts per hour, and off-bout duration; Table 4.2). Incubation constancy was primarily explained by time of day and was relatively insensitive to weather (Table 4.2, GAMM; adjusted  $R^2 = 0.38$ ). Constancy declined from c.0.8 (50 minutes of incubation) in the hour immediately after sunrise, to 0.6 (38 minutes) three hours after sunrise. It remained at approximately this level throughout the day, with a slight decline between midday and mid-afternoon, before increasing as sunset approached (Figure 4.2). Although temperature and rainfall were statistically significant, their effects were small, especially when set against the effect of time of day: incubation constancy decreased by 1 minute 48 seconds (3.69%) for every 5°C increase in temperature, whilst constancy increased by 36 seconds for every 5mm increase in rainfall. No relationship between wind speed and incubation constancy was found.

Amongst the two components of overall incubation constancy, there was no evidence that mean bout duration varied with weather or stage of incubation. The only significant predictor was time of day, with the duration of off-bouts taken around midday/early afternoon being approximately one minute, or 25%, longer than those in the early morning or late evening (Figure 4.2, GAMM; marginal  $R^2 = 0.013$ , Table 4.). The stage of incubation, temperature and time of day were all significant predictors of the number of off-bouts initiated per hour (GAMM; adjusted  $R^2$  = 0.13; Table 4.). The final model explaining the number of off-bouts taken per hour also contained the interaction between rainfall and wind speed, but this was not statistically significant. The number of off-bouts taken per hour by a female differed through the day, increasing rapidly in the hours immediately after sunrise and decreasing before sunset (Figure 4.2). Between these periods, the number of off-bouts per hour remained relatively constant, although it reduced (by approximately 1 bout per hour) in mid-afternoon (around 1500hrs). Within the framework of this overall hourly pattern, incubating females were predicted to take an additional off-bout per hour, a 16-17% increase, for every 5°C increase in temperature. The number of off-bouts per hour increased by approximately 5% (i.e., less than one bout per hour) for every 10% of incubation completed (Figure 4.2).

Diurnal nest temperature was affected by both incubation behaviour and weather, with the final model containing three significant predictors: ambient temperature, wind speed and incubation constancy (GAMM; adjusted  $R^2 = 0.62$ , Table 4.). A 10% increase in incubation constancy was associated with a small increase in nest temperature of 0.2°C. A 5°C increase in ambient temperature resulted in a 3°C increase in nest temperature (Figure 4.2). The model of diurnal nest temperature also contained two non-significant predictors: rain and a non-linear relationship with hour.



Figure 4.2: Modelled relationships (GAMMs) between time of day and a) off-bout duration, b) number of off-bout per hour and c) incubation constancy per hour, and d) nest temperature. Fitted lines show predicted mean +/- SE, when temperature = $13^{\circ}$ C (a, b, c), rainfall = 0.28mm (all), wind = 12.36km/h (all), stage of incubation = 0.5 (all), and incubation constancy =0.6 (c only)

Table 4.2: Effects of rainfall (total, mm), ambient temperature (mean, °C) and wind speed (mean, Kph) on aspects on the incubation behaviour of female Barn Swallows *Hirundo rustica* at the level of hour (left set, GAMMs) and day (right set, GLMMs).

Hour Level Models (GAMM)						Day leve	l models (GL	MM)				
Response	R <sup>2</sup>	Variable	Estimate	S.E	t value	p value	R <sup>2</sup>	Variable	Estimate	S.E	t value	p value
Incubation constancy	0.056	Temperature	-0.007	0.003	-2.267	0.024	0.23	Wind speed	0.002	0.001	2.798	0.010
		Rainfall	0.012	0.006	2.133	0.034		Rainfall	0.011	0.002	4.358	<0.001
								Rainfall x Wind speed	<0.001	<0.001	-3.473	0.002
Off-bout Duration	0.0129	Stage of incubation	-0.946	0.661	-1.431	0.153	0.30	Stage of incubation	-2.760	0.887	-3.113	0.004
		Temperature	-0.146	0.093	-1.572	0.117		Rainfall	0.132	0.027	4.824	<0.001
Off-bout Frequency	0.13	Stage of incubation	2.096	0.532	3.938	<0.001	0.33	Stage of incubation	31.064	10.249	3.031	0.006
		Temperature	0.141	0.050	2.815	0.005		Temperature	0.464	1.156	0.401	0.692
		Rainfall	0.189	0.293	0.645	0.520		Rainfall	-1.705	0.366	-4.662	<0.001
		Wind speed	-0.006	0.010	-0.581	0.562						
		Rainfall x Wind speed	-0.030	0.017	-1.733	0.084						

Effective degrees of freedom, F- and p-values for the non-linear (time of day) terms for the hour-level GAMMs

Response	edf	F value	p-value
Incubation constancy	7.222	21.590	<0.01
Off-bout Duration	1.923	0.648	0.047
Off-bout Frequency	7.426	10.170	<0.01

Table 4.3: Effects of rainfall (total, mm), temperature (mean, °C), and wind speed (mean, Kph) on the within-nest temperature of Barn Swallows *Hirundo rustica* at the level of hour (left set, GAMMs) and day (right set, GLMMs).

Hour Level Models (GAMM)									
<b>Response:</b> Mean hourly nest temperature, $R^2 = 0.06$									
Variable Estimate Std. Error t value p va									
Incubation constancy	2.079	0.923	2.252	0.025					
Temperature	0.623	0.059	10.636	<0.001					
Rainfall	-0.211	0.122	-1.726	0.085					
Wind speed	-0.049	0.024	-2.054	0.041					
Effective degrees of freedom	(edf), F- and p-value	es for the non-li	near term:						
edf F value p-value									

1.246

Hour

0.281

0.153

"Day" Level Models (GLMM)							
<b>Response:</b> Mean daily nest temperature, $R^2 = 0.16$							
Estimate	Std. Error	t value	p value				
-18.166	11.028	-1.647	0.116				
0.365	0.207	1.762	0.096				
0.459	0.174	2.644	0.016				
0.016	0.058	0.285	0.779				
-0.031	0.009	-3.316	0.004				
-3.289	1.773	-1.855	0.079				
	"Day" Level Mode operature, R <sup>2</sup> = 0.16 Estimate -18.166 0.365 0.459 0.016 -0.031 -3.289	Estimate Std. Error   -18.166 11.028   0.365 0.207   0.459 0.174   0.016 0.058   -0.031 0.009   -3.289 1.773	Bayer Level Models (GLMM)   Estimate Std. Error t value   -18.166 11.028 -1.647   0.365 0.207 1.762   0.459 0.174 2.644   0.016 0.058 0.285   -0.031 0.009 -3.316   -3.289 1.773 -1.855				

#### **Response:** Mean nocturnal nest temperature, $R^2 = 0.86$

Variable	Estimate	Std. Error	t value	p value
Stage of incubation	1.915	1.470	1.303	0.223
Incubation constancy	-29.616	8.833	-3.353	0.003
Diurnal nest temperature	0.750	0.120	6.280	<0.001
Nocturnal temperature	0.856	0.294	2.913	0.009
Nocturnal wind speed	0.151	0.041	3.655	0.002

#### 4.4.2 Day-level effects of weather on incubation behaviour

At the day level, rainfall had more of an influence, whilst temperature appeared to be less important. Incubation constancy showed had a weak relationship to weather at the daily level; the only significant predictor being the interaction between rain and wind. This, however, had a negligible effect on incubation constancy (Table 4.2). The number of offbouts taken per day had a significant, positive association with the stage of incubation (LMM; marginal  $R^2 = 0.33$ ; Table 4.2). Females took three more off-bouts per day for every 10% of incubation completed (Figure 4.3). Total daily rainfall was a significant, negative predictor of the number of off-bouts per day, with females taking nine fewer off-bouts per day for every 5mm increase in daily rainfall. The final model also contained one non-significant predictors of mean daily off-bout duration. Daily off-bout duration increased by 40 seconds for every 5mm increase in rainfall but decreased by 17 seconds for every 10% of incubation completed (Figure 4.3).

The final model to explain average daytime nest temperature contained two significant terms; rainfall and its interaction with wind speed, and three non-significant terms: incubation constancy, stage of incubation and temperature (LMM; marginal  $R^2 = 0.16$ ; Table 4.3). Nest temperature had a negative relationship with rainfall on windier days (mean wind speed 30km/hr), whereas under calm conditions (10km/hr) nest temperature had a slight, positive relationship with rainfall (Figure 4.3).

#### 4.4.3 Nocturnal nest temperature

Nocturnal nest temperature was sensitive to daily incubation behaviour (daytime incubation constancy), the diurnal nest temperature and nocturnal ambient weather (Table 4.3). An increase in daily daytime nest attendance of approximately 1.5 hour (an increase in incubation constancy from 0.6 to 0.7) was followed by a nocturnal nest environment that was approximately 3°C cooler (Figure 4.4Figure ). A 5°C increase in nocturnal ambient temperature or diurnal nest temperature was associated with an approximately 4°C increase in nocturnal nest temperature. Nocturnal wind speed also had a positive relationship with the nocturnal nest environment, with a 10kph increase in nocturnal wind

speed associated with an approximately 2°C increase in nocturnal nest temperature (Figure 4.4).



£

Figure 4.3: Modelled relationships (using GLMMs) for day level aspects of incubation behaviour; a) off-bout

Rainfall (b & d) = 3.697 mm, (a, b & d) stage of incubation = 0.6, and incubation Constancy (d) = 0.6. C and d: black lines = high wind speed (30kph), grey lines = low wind speed (10kph). Fitted lines show predicted

duration, b) number of off-bouts per day, c) Incubation Constancy, and d) diurnal nest temperature.

0

5

#### a) Off-bout duration

0.55 0.50

means +/- SE.

ð



10

Total daily rainfall (mm)

15

5

10

Total daily rainfall (mm)

15



Figure 4.4: Modelled relationships (using GLMMs) between a) mean nocturnal nest temperature and incubation constancy during the preceding daytime, b) ambient nocturnal temperature and nocturnal nest temperature c) nocturnal nest temperature and night nest temperature c) nocturnal nest temperature and night nest temperature. Fitted lines show predicted means +/- SE when incubation constancy (daytime) = 0.65, stage of incubation = 0.4, mean nocturnal wind speed = 19.37 kph, mean diurnal nest temperature = 28.04°C, and mean nocturnal ambient temperature = 11.10°C.

## 4.5 Discussion

Incubation is an energetically expensive activity (Scanes 2015; Williams 1996), during which incubating birds must balance their own energy requirements with providing an environment conducive to the development of their embryos. This study aimed to examine the effects of weather on female Barn Swallow incubation behaviour and the consequences for nest temperatures, examining the potential interactive effects of three weather variables and considering two temporal scales (hourly and daily). At both temporal scales, the frequency of off-bouts and nest temperature were sensitive to weather, whereas off-bout duration was only sensitive to weather at the daily (but not hourly) time scale. Incubation constancy was relatively insensitive to weather at both temporal scales. However, whereas temperature had the strongest relationships with incubation behaviour at the hourly level, rainfall was a better predictor of with incubation behaviour at the daily scale. This difference demonstrates that the observable impacts of weather on incubation behaviour may be dependent on the temporal scale over which behavioural end points and weather are determined. Wind speed had a small effect on nest temperature but little to no effect on the aspects of incubation behaviour examined here (Table 4.2 and Table 4.3). The results also demonstrate that the nocturnal nest environment is affected not only by current weather conditions but also by the nest environment and parental behaviour during the preceding diurnal period.

The sensitivity of incubating Barn Swallows to weather is consistent with studies for a range of other bird species (e.g., Ardia *et al.* 2009; Ardia *et al.* 2010; Capp *et al.* 2017; Coe *et al.* 2015; Jones 1987; Jones 1989; Møller 2013). Although there is increasing evidence of the importance of the interactive effects of weather variables on demographic parameters and processes (Coe *et al.* 2015; Mainwaring *et al.* 2016; and see Chapter 2, 3, and 5), I found only weak support for an interactive effect of weather variables on the incubation behaviour of Barn Swallows. Coe *et al.* (2015) showed that the interaction between rainfall and temperature influenced female incubation behaviour in the Tree Swallow, another aerial insectivore. The lack of agreement shown between that, and the current study may be the result of differences in the ecology of the two species, or the magnitude of weather variation between the two studies, or both of these. For example, the presence of livestock in buildings may confer a thermal advantage to female Barn Swallows, which is not available to nest box/tree cavity nesting Tree Swallows.

There were no significant weather predictors of off-bout length at the hourly level, which is governed by the interplay between a female's energetic need, foraging efficiency and egg cooling rate (Ardia et al. 2009; Bryan and Bryant 1999; Jones 1989; Turner 1981; Vleck 1981). The mean duration of off-bouts at the hour level was 5.69 minutes, which is consistent with those reported by other studies on Barn Swallows (Jones 1989; Tuner 1980). Jones (1989) demonstrated that off-bouts longer than this resulted in females entering an energy deficit, i.e., the cost of rewarming eggs that had cooled for longer than 5-6 minutes is larger than that gained from increased foraging. Some caution should, however, be applied here due to differences in the way off-bouts were determined between this and Jones' study (automated weighing of nest and female vs. nest temperature data logger). The slightly shorter but more frequent off-bouts observed earlier and later in the day is consistent this egg-temperature driving the duration of off-bouts; cooler ambient temperatures will increase cooling rates, such that leaving the nest more frequently but for less time would reduce the amount of time for which eggs were exposed to lower ambient temperatures. Slightly longer offbouts during the warmest part of the day may be facilitated by slower cooling rates and/or "ambient incubation" when ambient temperatures are high enough for embryo development within the egg (Griffith et al. 2016). Lower ambient temperatures may also reduce insect availability early and late in the day (e.g., Jones 1989; Winkler et al. 2013), compared to the middle of the day when temperatures are warmer, which could impact off-bout length. Grüebler et al. (2008) showed that aerial insect densities were frequently higher along hedgerows and trees, compared to adjacent fields, in cool conditions. As swallows forage more along boundary features under poor weather conditions (Evans et al. 2003), this "honey pot" effect of insect aggregations in cool conditions may compensate for reduced insect abundance overall. This adaptive foraging strategy may account for the low sensitivity of hour-level bout durations to local weather variation at this temporal scale, but there is nevertheless a significant effect of temperature on off-bout frequency, as females return to the nest more regularly to minimise the cost of re-warming eggs when the temperature gradient is higher. The interplay between egg cooling rates, female foraging efficiency and invertebrate prey activity and/or abundance is an area for future research.

At the hourly level, temperature appeared to have greater influence on incubation behaviour, appearing in all of the final models to explain off-bout duration, number of off-bouts and incubation constancy (although the effect was only significant in the latter two models). In contrast, rainfall appeared to play a more important role at the day level; again, appearing as an explanatory variable in all three models (albeit in interaction with wind in relation to incubation constancy). This suggests two possibilities i) that the amount of rain during the study was insufficient to have an effect on

incubation behaviour at the hourly scale, or that ii) it is the intensity -rather than the amount- of rainfall that drives a female's decisions regarding when to leave the nest, with females opting to "wait out" periods of rainfall. This would be consistent with the relatively small effect of rainfall on incubation constancy at the hourly level. With an average hourly rainfall of 0.28mm, a female would only have to "wait" an extra c.2 seconds per hour, and even the maximum of 7.8mm of rainfall would result in only c.56 seconds extra on the nest per hour (based on 36 seconds per 5mm increase in hourly rainfall); a female therefore could easily compensate for a "typically" wet hour with no meaningful increase in off-bout length. Even in a "wet" hour, taking one particularly long (i.e., c5 minutes vs. average of 4minute off bout), sharing out this additional time across the multiple offbouts within the hour, or not compensating at all, would not necessarily result in a large or discernible increase in bout length. This would also be consistent with the day level effect, i.e., perhaps often relatively minor changes to the length of individual off-bouts sum over the course of the day to create the observed day level effect of rainfall on off-bout duration. Similarly, it is likely that the greater variation in hour level temperatures (i.e., cold mornings vs. warm afternoons) that account for the importance of temperature on incubation at the hourly level compared to the day level. Female Barn Swallows have been shown to forage more intensively when insect availability is high, allowing a surplus intake of food to replenish body reserves (Schifferli et al. 2014). While this has been typically measured at the daily scale, it may be that there were insufficient "cool days" in the study year to detect changes at that (daily) temporal level. Incubation constancy was robust to weather variation on both time scales. This metric is a function of off-bout duration and frequency, and it is the plasticity in these behaviours that accounts for this. The antagonistic relationship between these two aspects of off-bouts is best illustrated by the daily scale; the significant predictors of both off-bout duration and frequency are the same but the relationship is reversed; for example, rainfall has a positive relationship with off-bout duration but a negative relationship with frequency of off-bouts. However, the hourly scale results hint at a much more complex interaction between these two variables, with females altering both the length and frequency of off-bouts with both weather and time of day. Indeed, as alluded to above, day level effects may well be the result of the summation of these comparatively minor hour-level adjustments to off-bout length and/or frequency.

I found no evidence of interactive effects between weather variables at the hour level, but there was support for a small interactive effect between rainfall and wind speed at the day level on incubation constancy and diurnal nest temperature. This relative lack of interactive effects contrasts with Coe *et al.* (2015), who found clear evidence for an interactive effect between rainfall and temperature on the incubation behaviour of female Tree Swallows. Whilst this may reflect a lack of interactive effects of weather on Barn Swallows, two aspects of the current study (cf. Coe *et al.* 2015) may have limited the scope for detecting such effects. First, the current study was limited to just 7 nests/29 days due to the high predation rate, restricting the statistical power compared to Coe *et al.* (n = 55 nests) Secondly, the weather variation observed in 2014 may have been insufficient to demonstrate clear interactive effects of different weather variables. Examining the responses to a greater variance in weather, for example by studying a population over multiple years or studying multiple populations over a climatic gradient (e.g., Morrison *et al.* 2010; Both *et al.* 2006; Burger *et al.* 2012) would allow a more powerful test of the role of weather variables and their interactive) effects of temperature and wind speed on the on- and off-bout durations in the Chestnut-crowned Babbler *Pomatostomus ruficeps*.

Subject to the caveats around statistical power potentially limiting the ability to detect subtle effects, this study has demonstrated that incubation behaviour as a whole is dynamic and highly responsive to weather variation. Swallows have evolved to cope with an unpredictable food supply by maintaining a relatively high body mass during incubation (Jones 1987; Jones 1989) and foraging more actively to maintain their body reserves when weather conditions result in abundant prey (Schifferli *et al.* 2014). Both factors should minimise negative energy balances during poor weather and high energetic demand, and thereby the impacts upon incubation. In addition, aerial invertebrate prey has been shown to vary in its availability and abundance in relation to weather; for example being higher along boundary features than adjacent fields in cooler, windier conditions (Grüebler *et al.* 2008). This, combined with the swallows' flexible feeding strategies, from choosing different sized prey (Turner 1982b), to favouring boundary features during poor weather (Evans *et al.* 2003), may allow them to compensate for adverse weather conditions. Future studies of this nature could be improved by contemporaneous data on insect availability and distribution, as well as tracking of female foraging locations within the landscape, in relation to weather and incubation behaviour.

The stage of incubation was linked to changing incubation behaviour in several of the models. Offbout frequency increased as incubation progressed at both temporal scales, whereas off-bout duration decreased as incubation progressed at the day level. These results both point to an overall pattern of females taking more frequent but shorter off-bouts as incubation progresses, perhaps in response to the changing physiology of the developing embryo. Cooper and Voss (2013) demonstrated that the rate of heat loss from the egg increases with embryo age in the Black-capped Chickadee *Poecile atricapillus*, with females responding by increasing the frequency but reducing the duration of absences from the nest as cooling rates increased. This is consistent with the results of the present study.

Before considering the results in relation to nest temperature, it is important to address a limitation of this study, namely the use of nest temperature as a proxy for egg temperature, rather than measuring the conditions experienced by developing embryos directly. Using a data logger probe within a sacrificed or artificial egg (e.g., Wang & Weathers 2009; Capp et al. 2017; Coe et al. 2015; Lord et al. 2011) would have allowed the environment experienced by the developing embryo and incubation behaviour of adult to be modelled more closely, and to explore whether females respond to cues based on egg temperature rather than just external abiotic factors. This method was not used in light of ethical considerations, as well as the practical difficulty of inserting a probe through the dried-mud matrix of a swallow's nest. However, given that an egg's position within the clutch is rotated during incubation, depending on its thermal requirements (Boulton & Cassey 2012), and that heat loss varies across an egg's surface, neither method (using fixed probes) is likely to provide a fully accurate picture of the conditions experienced by each embryo and potentially omits finer aspects of incubation behaviour. However, the nest temperatures recorded in the current study (mean daily average 27.91 ±3.65°C, range 20.72-33.06°C) were similar to those recorded by Coe et al. (2015) in Tree Swallows (mean daily average 33.67 ±0.11, range 17.97 – 39.16°C). Inserting data logger probes into nests does, however, provide a cheap, effective and non-invasive way of recording incubation behaviour in birds (Joyce et al. 2001) particularly where the focus of study, as is the case here, is on the behavioural decisions of incubating parents and their implications for the nest environment in general terms, rather than on embryo temperature per se.

Nest temperature was the only aspect of incubation behaviour over which wind speed had an effect; wind speed appeared as a significant term in all three nest temperature models. However, wind speed had a negative effect on diurnal nest temperatures at both temporal scales but had a positive effect on nocturnal nest temperatures. A negative relationship between wind speed and nest (egg) temperature is consistent with the results of Capp *et al.* (2017). Higher wind speeds are likely to increase cooling rates and decrease nest temperatures through increased air flow across the nest cup (Capp *et al.* 2017; Gray & Deeming 2017; Heenan & Seymour 2012). At the hourly level, the

effects of wind speed were independent of other weather variables, but at the daily level its effect was dependent on the effect of rainfall, with lower nest temperatures on windy, wet days compared to calm, wet days. Unlike the diurnal nest temperatures, nocturnal nest temperatures increased with increasing wind speed; this increase was relatively small, however, representing a 2°C increase for every 10kph increase in wind speed. The mechanism underlying this effect on nocturnal nest temperature is unclear; as incubating female passerines do not normally leave the nest at night (although they stand up in order to rotate eggs) (Austin *et al.* 2019; Slay *et al.* 2012), clutches are not exposed to air flow across the nest cup to the same extent as during the day when the female is absent. One possibility is that the female may sit more "tightly" during windier nights, perhaps by lowering her posture in the nest during incubation to reduce heat loss or increasing the heat she transfers to her clutch. Higher nocturnal nest temperature following days of lower incubation constancy may represent evidence of a compensatory mechanism to compensate for "neglect" during the preceding day; but the results of this study are unclear in this respect.

Nest temperature, at the hourly level, also had a positive and significant relationship with both incubation constancy and ambient temperature. This is consistent with other studies (Ardia et al. 2009; Coe et al. 2015). Increased ambient temperature, leading to increased nest temperatures, are likely linked to "ambient incubation" and/or a reduction in energetic expenditure (for example reduced cooling rates as discussed above), allowing females to divert more energy into rewarming their eggs. It is likely that similar mechanisms operate in relation to incubation constancy. While there is probably a mechanistic link between higher nest temperatures, ambient temperatures and incubation constancy, the relationship may not be straight forward. For example, Ardia et al. (2009) found that female Tree Swallows had two different types of responses to the artificial heating of nest boxes; early laying (i.e., higher quality) females maintained incubation constancy and increased nest temperatures, while later laying (i.e., lower quality) females only increased incubation constancy. The sample size of individual females available in the current study was too small to test the effects of laying date on incubation behaviour; thus, the results here may be influenced by variations in female quality too. The inclusion of both temperature and incubation constancy at the daily level is also indicative of females basing their decisions on fine scale (hourly-scale) changes in weather.

The results of the nocturnal model also showed free-over effects from the diurnal to the nocturnal incubation phase of incubation; lower incubation constancy in the preceding day resulted in higher

nest temperatures at night – as did higher diurnal nest temperatures. The former relationship may be a mechanism by which females mitigate for poor nest attendance during the day. It is worth noting that incubation constancy was retained in the diurnal model as a negative but non-significant term. This may hint at an overall mechanism used by Barn Swallows to compensate for low attendance, however the low sample size in the present study makes this difficult to resolve.

Overall, the results support the view that incubation is a dynamic process, with incubating females making strategic behavioural and physiological decisions in light of changing weather conditions and the changing demands of their developing embryos (Cooper and Voss 2013; Conway & Martin 2000). Such plasticity could provide a mechanism by which females can adapt to changing weather in the shorter term and a changing climate in the longer term. Future research, however, is needed to understand the limits of behavioural and physiological plasticity in relation to this important stage in the reproductive cycle, in light of climate change predictions.

# Chapter 5: Contrasting sensitivity of nestling and fledgling Barn Swallow *Hirundo rustica* body mass to local weather conditions

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## Summary

Local weather can influence the growth and development of young birds, either indirectly, by modifying prey availability, or directly, by affecting energetic trade-offs. Such effects can have lasting implications for life history traits, but the nature of these effects may vary with the developmental stage of the birds, and over timescales from days to weeks. I examined the interactive effects of temperature, rainfall, and wind speed on the mass of nestling and fledgling Barn Swallows Hirundo rustica, both on the day of capture and by averaging weather across the time since hatching. At the daily timescale, nestling mass was negatively correlated with temperature, but the strength of this association depended on the level of rainfall and wind speed; nestlings were typically heavier on dry or windy days, and the negative effect of temperature was strongest under calm or wet conditions. From hatching to post-fledging, nestling mass was negatively correlated with temperature at low wind speed. Fledgling body mass was less sensitive to weather; the only weather effect evident was a negative correlation with temperature at the daily scale under high rainfall that became slightly positive under low rainfall. These changes are consistent with weather effects on availability and distribution of insects within the landscape (e.g., causing high concentrations of flying insects), and with the effects of weather variation on nest microclimate. These results together demonstrate the impacts of weather on chick growth, over immediate (daily) and longer term (nestling/fledgling lifetime) timescales. This shows that sensitivity to local weather conditions varies across the early lifetime of young birds (nestling-fledgling stages) and illustrates possible mechanisms by which larger scale (climate) variations influence the body condition of individuals.

## 5.1 Introduction

The biotic and abiotic conditions experienced by an individual animal early in its development have consequences not only for short term growth, development and immediate survival, but also for long-term survival, reproductive success and social status (e.g.,; Richner *et al.* 1989; Magrath 1991; Naef-Daenzer *et al.* 2001; Saino *et al.* 2012). In birds, chick growth and survival is associated with factors linked to both the nesting attempt as a whole, such as hatching date, brood size, habitat quality and predator abundance (Podlesak & Blem 2001; Nilson & Gårdmark 2001; Mainwaring *et al.* 2009; Saino *et al.* 2012; Crombie & Arcese 2018), and factors that may vary within the nesting attempt, such as weather and food availability (Geiser *et al.* 2008; Salaberria *et al.* 2014; Crombie & Arcese 2018). A range of studies have linked these factors to post-fledging and over-winter survival, and fecundity in subsequent breeding seasons (e.g., Newton & Moss 1986; Greño *et al.* 2008; Öberg 2015), highlighting the importance of understanding the factors influencing early stages of development, and the role played by relatively short-term environmental factors during this period.

Weather is of particular interest in the context of understanding nestling development in wild birds, given predictions of both shifts in average weather conditions and increases in the frequency and magnitude of extreme weather events over the coming decades (IPCC 2014). Regional-scale climate conditions, manifested as local weather and nest microclimate, could impact chick growth via direct mechanisms (e.g., by altering energetic costs; Sikamäki 1996; Dawson *et al.* 2005) or indirectly (e.g., by altering prey availability; Ritz *et al.* 2005; Grüebler *et al.* 2008). The relative importance of these different mechanisms is likely to vary according to an individual's ability to thermoregulate, its food demands and, later, its ability to self-provision, all of which change from hatching to post-fledging (Elmen *et al.* 1991; Siikamäki 1996; McCarty & Winkler 1999; Ambrosini *et al.* 2006). Despite this, the majority of studies has focused on the effects of local weather variation on the nestling phase as a whole (e.g., Sikamäki 1996; Dawson *et al.* 2005; Ardia 2013; Mainwaring & Hartley 2016), and on future post-fledging survival or recruitment (e.g., Greño *et al.* 2008; Obërg *et al.* 2014; Rodríguez *et al.* 2016). The effects of local weather on body condition in the weeks immediately after fledging remain largely unexplored, despite survival being at its lowest during this critical period (Yackel Adams *et al.* 2006; Cox *et al.* 2014).

Temperature, rainfall and wind speed have been shown to affect nestling growth and development in a wide range of species. While warmer temperatures have been shown to increase nestling survival, feather development and body mass in many species (e.g., Podlesak & Blem 2001; Dawson *et al.* 2005; Ambrosini *et al.* 2006), extremely high or low temperatures have been linked to reduced growth rates, body condition and survival (e.g., Rodrigez & Barba 2016; Adreasoon *et al.* 2019; Imlay 2019). Rainfall has been shown to have a negative effect on nestling provisioning rates, survival, and fledging success (e.g., Arlettaz *et al.* 2010; Conrey *et al.* 2016; Crombie & Arcese 2018; but see Oppell *et al.* 2013). Negative effects of rainfall on nestling mass and growth have been shown in a number of species, for example, Cirl Bunting *Emberiza cirlus* (Evans *et al.* 1997), Pied Flycatcher *Ficedula hypoleuca* (Siikamäki 1996), Eurasian Bittern *Botaurus stellaris* (Kasprzykowski *et al.* 2014), Gambel's White-Crowned Sparrow *Zonotrichia leucophrys gambelii* and Lapland Longspur *Calcarius lapponicus* (Pérez *et al.* 2016). Although the effects of rainfall on chick mass seem to be typically negative, this is not universal. For example, Kruuk *et al.* (2015) found a positive association between chick mass and high levels of precipitation during the nestling phase in the Superb Fairy-wren *Malurus cyaneus.* 

Wind is an important meteorological variable that is likely to affect chick growth and development through changes in prey abundance and availability (Quinney *et al.* 1986; Dawson *et al.* 2000; Grüebler *et al.* 2008; Møller 2013), and by altering the nest microclimate and costs of thermoregulation (Salzman 1982; Bakken *et al.* 2002; Heenan & Seymour 2012; Gray & Deeming 2017). Only a few studies have linked higher wind speeds to reduced nestling growth; for example in nestling Blue Tits *Cyanistes caeruleus* (Mainwaring & Hartley 2016), Black-legged Kittiwakes *Rissa tridactyla* (Christensen-Dalsgaard *et al.* 2018) and Eurasian Bittern (Kasprzykowski *et al.* 2014). However, in contrast to rainfall and temperature, and despite growing evidence of its influence on reproductive traits (Møller 2013; Irons *et al.* 2017), the impact of wind speed on chick growth has received less attention and is less well known (Mainwaring & Hartley 2016; Irons *et al.* 2017). Similarly, the potential for interactive effects between different weather variables has rarely been considered (but see Dawson *et al.* 2000; Coe *et al.* 2015; Mainwaring & Hartley 2016; de Zwann *et al.* 2019 for examples), despite the potential for synergistic or antagonistic relationships; for example, de Zwann *et al.* (2019) found that the delay in nestling development in Horned Lark *Eremophila alpestris* chicks, induced by cold temperatures, was exacerbated by precipitation.

Major effects of weather on nestling growth and development are not universal. Several studies have found little or no effect of weather on chick growth (e.g., Bradbury *et al.* 2003; Gilroy *et al.* 2009). Parents may be able to ameliorate weather impacts, at least over short periods, by adjusting

the frequency, timing or nature of food delivered to the nestlings (Dawson *et al.* 2000; Paiva *et al.* 2006). Chicks too may be able to mitigate some of the negative effects on development, for example by slowing growth rates or by prioritising the development of certain tissues over others (Lepczyk & Karasov 2000; Metcalfe & Mongahan 2001; Schifferli *et al.* 2014; Honarmand *et al.* 2017). However, such nestling growth strategies are not without negative effects (Metcalfe & Mongahan 2001).

In the current study, I used a seven-year data set to investigate the combined and interactive effects of three key weather variables (temperature, rainfall and wind speed) on the mass and growth of nestlings in the Barn Swallow (hereafter 'Swallow'). The Swallow is expected to be particularly sensitive to short-term weather variation, as the young rely on their parents to brood and to provision them with food during both the nestling and immediate post-fledging stages. I examined the relationship between temperature, rainfall and wind, and individual Swallow mass during the nestling stage (8-12 days post-hatching) and fledgling stage (20-35 days post-hatching), representing the dependent and semi-/fully-independent stages of development. In both cases, separate analyses were carried out for short-term weather conditions (conditions on the day of weighing for nestlings or day before for fledglings) and average weather conditions over their elapsed lifetime (i.e., weather conditions from hatching until the time of weighing the nestling or fledgling, hereafter 'lifetime'), to assess their importance at different temporal scales. I tested the following predictions: i) Nestling body mass is positively related to temperature but negatively related to wind speed and rainfall, at both daily and lifetime scales; this could be due to impacts on, for example, aerial insect abundance and parental provisioning rates; ii) Fledgling mass is sensitive to weather in the shortterm (daily scale), probably due to weather-related variation in insect abundance and activity, but less sensitive in the long-term (lifetime scale), as fledglings are expected to be less susceptible to food-limitation once they have completed their growth. Furthermore, I predict that temperature, wind, and rain will interact to modulate their separate effects on body mass.

## 5.2 Method

#### 5.2.1 Nest monitoring

Nests were monitored from April to September (inclusive) between 2008 and 2014 at Cardiff Riding School (see Chapter1 for study site details). In each year, nest monitoring continued until no further clutches were initiated. Each nest was visited every three to four days, starting in late April, to record

first egg date, hatching date, brood size, and chick survival and fledging success. If hatching was not observed directly, nestling age was estimated based on feather development (Turner 2006) and by comparison with chicks of known age; it was possible to examine all chicks within four days of hatching in all years. All breeding attempts were monitored until the chicks had fledged or the attempt failed. Chicks were considered to have fledged when some or all of the brood was absent from the nest on at least one monitoring visit but observed to be alive on subsequent visits (at approximately 20 days after hatching, Robinson 2015). A second breeding attempt was considered to be any breeding attempt by the same female that followed a successful first breeding attempt. Breeding attempts that resulted from re-nesting after a failed attempt were not included in the study. To allow individual females to be assigned to each breeding attempt, they were caught and ringed with a British Trust for Ornithology (BTO) metal numbered ring and a combination of three plastic coloured leg rings to allow identification of individuals without the need to recapture them.

To determine the effects of local weather conditions on individual mass (as a proxy for growth) I used data from 248 nestlings (8–12 days old), and 75 fledglings: combined, these nestlings and fledglings represented 79 broods. Throughout the study period, I aimed to ring and weigh all chicks between eight and 12 days after hatching. At this age, tarsal development was sufficient to accommodate metal rings and plastic rings (the latter fitted as part of another study) but young enough to avoid premature fledging. All nestlings used in this study were those handled between 1700 and 2000hrs (British Summer Time, recorded to the nearest 30 minutes), when access to the study site and nests was most practical. This represents approximately 61% of the young ringed during the study; the remainder were either not weighed and/or were ringed under 5 days of age when young enough to accommodate only a metal ring.

Individuals ringed as chicks were also re-caught post fledging – either intentionally, as part of other studies, or unintentionally when targeting adult birds. Therefore, the sample of 75 fledglings comprised 34 individuals weighed at both the nestling and fledgling stages, and 41 individuals weighed as fledglings only. All fledglings were caught between 05:00 and 07:00 hrs. Fledglings were captured at dawn by placing a mist net across the entrance of the stable where they roosted. A minimum of 10 days elapsed between the ringing of nestlings and any subsequent re-capture as fledglings. All birds were caught and ringed under my BTO permit (A5411), following best practice guidelines (Jenni 1998, Redfern & Clark 2001) and weighed to the nearest 0.1 g using an electronic

balance (*Satrue SA-500 <u>http://www.satrue.com.tw/dp2.htm</u>*). Nestlings were ringed in all years, but fledglings were only caught from 2008 to 2011.

#### 5.2.2 Weather data

Daily mean ambient temperature (°C, mean of the daily maximum and minimum values), daily mean wind speed (km/h) and total daily rainfall (mm) were obtained from a UK Meteorological Office weather station (Bute Park;  $51^{\circ}29'16.7"N \ 3^{\circ}11'17.0"W$ ,  $9m \ asl$ ), 1.5 km south of the study site. Due to equipment failure, some data were missing from the Bute Park time series for parts of 2007, 2010 and 2011 for one or both of the rainfall and temperature variables and missing days were interpolated using data from a second Met Office weather station (St Athan;  $51^{\circ}24'18"N$ ,  $-3^{\circ}26'24"$ ,  $49m \ asl$ ) approximately 18.7 km to the south-east (see Chapter 3). Mean daily wind speed (km/h) data were also obtained from St Athan, as these data were not available from Bute Park. The three weather variables were only weakly correlated with each other (r = 0.005 to 0.026) and so their effects on chicks could be analysed in the same statistical models (see below).

Daily weather data were summarised over two timescales relating to the development of individual chicks: i) the day of handling in the case of nestlings, or in the case of fledglings (which were all caught around sunrise), the day prior to capture, and ii) the time elapsed between hatching and handling, either as a nestling (mean =  $9.9 \pm 2.0$  days) or as a fledgling (mean =  $26 \pm 3.4$  days). Mean values were calculated for temperature and wind, and the cumulative total across this period was calculated for rainfall.

## 5.3 Statistical analysis

The effects of local weather variation on the body masses of nestling and fledgling Swallows were investigated using linear mixed-effects models (LMMs), fitted using the R package "Ime4" (Bates *et al.* 2015). All analysis was undertaken using R statistical software, version 3.5.1 (R Development Core Team 2017).

I fitted four LMMs to test the effects of weather variation upon body mass: each model examined a different combination of the two life stages (nestling and fledgling) and two timescales (day of

handling and period since hatching). Collinearity between variables was assessed using pair plots and variance inflation factors (VIF), with a threshold of VIF <3 considered to represent sufficiently low levels of collinearity (Zuur et al. 2010). Each of the four starting models contained mean ambient temperature, mean wind speed and total rainfall, either for the day of handling or the period between hatching and handling, and all possible two-way interactions. In addition, age, date of handling (day 1 = 1st April), time of day, brood size and nesting attempt (first or second) were included in the starting models, to control for heterogeneity introduced by seasonal and diurnal changes, and changes between successive nesting attempts. With the exception of nesting attempt, all variables were standardised to have a mean of zero and a standard deviation of one, prior to model fitting. While nesting attempt and day of handling could both be considered proxies for seasonal effects, both were included in the starting models as parent birds can make different investment decisions in relation to first and second broods (Møller 1991; Grüebler & Naef-Daenzer 2010) and weather effects on first and second attempts reared in the same nest have been shown to vary seasonally (Salaberria et al. 2014), both of which may impact chick mass, for example through reduce provisioning rates. Adult female identity was used as a random factor in each model, to account for repeated observations (chicks and nesting attempts) from the same female; of the 48 females in the data set for the 'chick' models, ten were represented by more than one breeding attempt within the same year across the whole study period, but only three were represented in more than one season (one in three years and two in two years). None of the 27 adult females in the 'fledgling' models were represented in more than one year, and only two within the same year. Year was considered for inclusion in all models to account for other sources of temporal variation (e.g., food abundance), but was highly co-linear with other fixed effects (VIF >4, maximum VIF = 40), so was excluded from the models.

In all cases, the final models were selected using stepwise removal of explanatory variables until there was no further reduction in the AIC (Burnham & Anderson 2002). Model validation procedures followed Zuur *et al.* (2007) and Thomas *et al.* (2017). The explanatory power of the model was assessed using the marginal  $R^2$  (Nakagawa & Schielzeth 2013), which is based solely on the fixed effects in the model (cf. the conditional  $R^2$  which is based on the whole model fixed and random effects combined), calculated using the 'MuMin' package (Bartón 2019).

## 5.4 Results

Mean (± standard deviation) brood size across the study period was 4.33 g ± 0.92 (range 3 - 6), mean nestling mass (all ages combined) was 21.88 g ± 2.79 (11.3-28.7g), and mean fledgling mass 18.0 g ± 1.34 (15.4 – 22.0). Daily weather variation across the period can be seen in Table 5.1.

Table 5.1: The daily mean, and overall minimum and maximum values for temperature, rainfall and windspeed each year between the 1<sup>st</sup> May and 31<sup>st</sup> August. This represents the period between hatching and handling of > 95% of nestlings and fledglings.

		2008	2009	2010	2011	2012	2013	2014
Ire	Mean ± sd	15.84 ± 2.12	15.62 ± 2.70	15.73 ± 3.05	14.60 ± 2.13	14.75 ± 2.80	15.58 ± 3.65	15.73 ± 2.81
peratı	Minimum	9.90	8.25	6.80	9.80	8.10	7.63	9.91
Tem	Maximum	20.55	21.75	20.50	19.55	21.65	23.82	22.93
_	Mean ± sd	3.80 ± 5.97	3.68 ± 8.37	2.30 ± 5.60	2.80 ± 4.66	3.63 ± 5.64	1.83 ± 4.75	3.59 ± 6.91
infall	Minimum	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rã	Maximum	29.70	78.10	41.10	27.20	31.40	36.80	46.80
73	Mean ± sd	9.71 ± 3.65	9.00 ± 3.46	7.97 ± 2.50	9.33 ± 3.56	8.96 ± 3.60	8.86 ± 3.44	8.47 ± 3.56
Speed	Minimum	3.04	3.42	3.25	3.33	3.42	3.25	3.21
Wind	Maximum	24.00	19.38	16.42	18.88	25.79	17.88	21.04

#### 5.4.1 The effects of weather on nestling mass

Nestling mass was sensitive to local weather variation at both the daily and lifetime temporal scales. At both the daily timescale (LMM; marginal  $R^2$  = 0.339; Table 5.2) and lifetime scale (LMM; marginal  $R^2$  = 0.265; Table 5.3), chick body mass showed a negative relationship with temperature, although this was mediated by the interactive effects of wind speed (both time-scales) and rainfall (daily timescale only). At the daily time-scale, nestling body mass declined with ambient temperature, but the rate of decline was negatively related to both wind speed and rainfall; mass decreased with temperature at twice the rate under calm compared to windy conditions, and declined at three times the rate under wet compared to dry conditions (Figure 5.1). At the lifetime scale, nestling body mass was negatively related to temperature under calm conditions (at a rate of -0.89 g/ $^{\circ}$ C); however, as wind speed increased, the relationship between body mass and temperature was no longer evident (Figure 5.2). In the lifetime model, there was a small positive, seasonal effect; there was a 0.01 g difference between different individuals of the same age, and from the same sized brood, but weighed on consecutive days. Breeding attempt was not retained in any of the chick models. Both the daily and lifetime model showed effects of a similar magnitude for the increase in body mass with time of day (1.11 g and 1.18 g per hour, respectively) and a negative effect of brood size (-0.76 g and -0.89 g per additional chick in the brood). Predictably, chick mass was shown to increase with age, at a rate of approximately 1g per day of age (1.1 g/day and 0.8 g/day, daily and lifetime respectively). Chick mass declined with brood size at a rate of approximately 0.8-0.9 g per chick increase in brood size.

Table 5.2: Model outputs for daily effects of local weather on nestling and fledgling mass. All main effects for each of the weather variables were included in the global models, but only the interaction terms are shown here. Significant weather-related terms are shown in bold ( $P \le 0.05$ ); non-significant terms retained in the final model are shown for completeness.

Life Stage	Response variable	parameter estimate	se	t value	p value
	Age <sup>1</sup>	1.332	0.208	6.409	<0.001
Nestling	Brood size	-0.699	0.192	-3.641	<0.001
	Time of day <sup>2</sup>	0.877	0.194	4.532	<0.001
	Temperature x Rainfall	-1.858	0.808	-2.299	0.023
	Temperature x Wind speed	0.552	0.227	2.429	0.016
	Age <sup>1</sup>	-0.419	0.152	-2.748	0.008
Fledgling	Day handled <sup>3</sup>	0.392	0.177	2.222	0.033
	Temperature x Rainfall	-1.022	0.311	-3.285	0.002
	Temperature x Wind speed	0.596	0.310	1.922	0.063

<sup>1</sup>Days after hatching where day of hatching = day 0

<sup>2</sup> 17:00-20:00hrs

<sup>3</sup> Day 1 = 1 April



Figure 5.1. Fitted relationships and 95% confidence interval for the short-term (within-day) negative effects on chick mass on the from the two-way interactions between a) mean ambient temperature and wind speed, and b) mean ambient temperature and total rainfall. Modelled for a 10 day old chick, from a brood of 4, weighed at 1830hrs. Dashed lines represent low values of wind (3km/h) and rain (0mm), whereas solid black lines represent high values (wind = 12km/h, rain = 10mm).

#### 5.4.2 The effects of weather on fledgling mass

In contrast to the nestling stage, fledgling mass was only sensitive to weather at the daily scale (LMM; marginal  $R^2 = 0.293$ ; Table 5.3). At this timescale, fledgling mass was negatively related to temperature under wet conditions, but the relationship between mass and temperature was reversed under dry conditions (Figure 5.3). The two-way interaction between temperature and wind was included in the final model but the relationship with fledgling mass was non-significant (P = 0.063, Table 5.3)

Table 5.3. Model outputs for long-term (lifetime) effects of local weather on nestling and fledgling mass. Significant weather-related terms are shown in bold ( $p \le 0.05$ ); non-significant terms retained in the final model are shown for completeness.

	Response variable	parameter				
Life Stage		estimate	se	t value	p value	
	Age <sup>1</sup>	0.906	0.204	4.443	<0.001	
	Day handled <sup>3</sup>	0.663	0.236	2.810	0.006	
Nestlings	Brood size	-0.803	0.200	-4.012	<0.001	
	Time of day <sup>2</sup>	0.785	0.195	4.025	<0.001	
	Temperature	-0.835	0.269	-3.103	0.002	
	Rainfall	-0.138	0.246	-0.562	0.575	
	Wind speed	0.584	0.264	2.211	0.029	
	Temperature x Wind speed	-1.135	0.234	-4.857	<0.001	
	Rainfall x Wind Speed	-0.253	0.187	-1.355	0.177	
	Age <sup>1</sup>	-0.465	0.174	-2.677	0.013	
	Day handled	0.325	0.179	1.811	0.107	
Fledglings	Brood size	-0.354	0.185	-1.917	0.072	
	Nesting attempt	-0.637	0.432	-1.471	0.153	
	Temperature	0.154	0.210	0.733	0.468	
	Wind speed	0.154	0.214	0.718	0.488	
	Temperature x Wind speed	0.5316	0.2638	2.015	0.072	

 $^{1}$  Days after hatching where day of hatching = day 0

<sup>2</sup> 17:00-20:00hrs

<sup>3</sup> Day 1 = 1 April



Figure 5.2. Fitted relationship and 95% confidence intervals for the long-term (hatching to day of handling) effects of the two-way interaction between mean ambient temperature and wind speed on the mass of 10-day old swallow nestlings. Nestling mass was negatively related to temperature under calm life-time conditions (black line; wind speed = 7km/h cf. dashed line = 14km/h, brood size = 4, day weighed = 126 (1<sup>st</sup> April = day 1), time weighed = 1830hrs).



Figure 5.3. Fitted models and 95% confidence intervals for the relationship between daily ambient temperature and total daily rainfall the day before handling on the mass of fledgling swallows (dashed line = 0.0mm daily rainfall, black line = 8mm daily rainfall).

## 5.5 Discussion

I examined the effects of temperature, rainfall, and wind-speed on the mass of nestling and fledgling Swallows over two temporal scales: the daily scale (short-term) and at the scale of the individual chick's lifetime (long-term). Mass variations during both the nestling and post-fledging stages were associated with short-term (daily) variation in ambient temperature, rainfall, and wind speed, but only nestling mass was found to be affected by weather conditions at the lifetime scale. The current study provides evidence of the complex effects of multiple weather variables on an individual's development, and specifically that these effects vary with the stage of development.

I found a complex relationship between nestling mass, and temperature, rainfall, and wind speed, with evidence of interactive effects between temperature and rainfall, and temperature and wind speed. In the short-term, increased rainfall and wind speed both had a negative effect on nestling mass. While this study was unable to evaluate invertebrate prey abundance concurrently with the growth of nestlings, these interactive relationships are consistent with how weather changes the distribution and density of invertebrate prey in the landscape (Grüebler *et al.* 2008). For example,

aerial insect densities are higher along hedgerows and trees, compared to adjacent fields, at low temperatures coupled with high wind speeds (Grüebler *et al.* 2008). This is probably the reason that Swallows show a preference for foraging near boundary features in poor weather (Evans *et al.* 2010); by exploiting this 'honey pot' effect of concentrated food availability, parent Swallows may be able to provision their chicks effectively, even under cold and windy conditions (Pérez *et al.* 2008). The boundary effect is reduced by higher temperatures, lower wind speeds and higher rainfall, as insects become more active and more evenly distributed across the landscape (Grüebler *et al.* 2008).

Parent Swallows do not appear to increase their energy expenditure (foraging effort) sufficiently to maintain provisioning rates to compensate for low insect availability (Turner 2006, Schifferli *et al.* 2014). This could explain the negative relationships between nestling mass and temperature, which is especially strong under calm conditions; the combination of low wind speed and higher temperatures reduces the 'honey pot' of concentrated food abundance, while potentially increasing the difficulty of catching invertebrates due to increased insect activity at higher temperatures. The effect of rainfall only at the shorter temporal scale is suggestive that it is the duration, rather than the quantity, of rain that is most disruptive to foraging Swallows. At the timescale of the chick's lifetime, Swallows appear to be able to organise their foraging bouts to take advantage of good foraging opportunities when weather conditions allow.

Contrary to hypothesis 1, and to previous studies (e.g., Fernaz *et al.* 2012), I found that nestling mass had a negative relationship with ambient temperature. Temperature may influence nestling mass indirectly, by affecting insect activity/availability - and thus parental provisioning rates - over a daily timescale, or over the lifetime of a nestling, as discussed above. Overall, invertebrate activity and abundance tends to be reduced under cooler conditions (Bryant 1973; Turner 1983; Jenni-Eiermann *et al.* 2008); a higher body mass under cool conditions is consistent with the use of strategic deposition of fat reserves as a buffer against starvation under conditions with low or unpredictable food availability (Witter *et al.* 1994; Witter *et al.* 1995; Ratikainen & Wright 2013; Vafidis *et al.* 2014).

A second, but not mutually exclusive, possibility is that weather affects chick mass via the nestmicroclimate. Warmer nest environments can reduce the cost of self-maintenance activities, allowing individual nestlings to invest more in growth (Podlesak & Blem 2001; Dawson *et al.* 2005; Ambrosini et al. 2006). For example, Dawson et al. (2005) found that by experimentally warming Tree Swallow Tachycineta bicolor nests to reduce chicks' energetic demands, chicks had greater survival rates during the nestling stage, faster feather development and were heavier, compared to chicks in control nests. The body heat from livestock in the buildings in which Swallows breed, or the buildings themselves, can provide a thermal advantage to the nest environment in cold weather (Grüebler et al. 2010; Imlay et al. 2018). Conversely, very high nest temperatures may reduce nestling mass through evaporative heat loss and dehydration (Ardia 2013; Rodríguez & Barba 2016; Andreasson et al. 2018; Imlay et al. 2019). This may be particularly pertinent for species nesting in anthropogenic structures, such as hirundines. For example, Imlay et al. (2019) found that Cliff Swallow Petrochelidon pyrrhonota nests under barn roofs were subject to higher peak ambient temperatures, with chicks reared during periods of high temperatures having lower mass. This effect was greater under metal than under wooden roofs. The population studied here nests in a similar context – nesting within stables 10-15cm immediately below corrugated bitumen sheet roofing which reaches high temperatures under direct sunlight - and while temperature data were not collected from within the stables throughout the entire study period, the temperature within the stables was substantially warmer than ambient temperature outside (6<sup>th</sup> to 18<sup>th</sup> May 2014, mean ambient temperature inside stable =  $23.92 \pm 5.98$  °C, outside =  $12.74 \pm 1.64$  °C). Increased ventilation of the buildings and nests as a result of higher wind speeds (Gray & Deeming 2017; Heenan & Seymour 2012) would be expected to prevent or at least reduce thermal stress in nestlings.

My results are consistent with the negative effect of temperature being the result of increased evaporative heat loss, especially as nestling mass only had a negative relationship with temperature at low wind speeds. However, the results are in keeping with Schifferli *et al.* (2014), who found the body mass of nestling Swallows to be higher on colder days, probably as a buffer against lower adult provisioning under colder conditions. Further work is therefore recommended to investigate weather-mediated effects on the nest-microclimate, and the implications of nest microclimate for chick growth.

Consistent with hypothesis two, fledgling mass was less sensitive to weather in the long term. Fledgling mass was only significantly correlated with weather at a daily timescale, specifically by the interactive effects of daily temperature and rainfall. In contrast, weather over the lifetime of fledged Swallows had no effect on fledgling mass, suggesting that body mass is more likely to be driven by a need to maintain a wing-loading appropriate for an active, aerial insectivore (Møller 2016; Ricklefs 1967; Ricklefs 1968). Consistent with previous studies, brood size was a significant predictor of nestling mass (Lotem 1998; Saino *et al.* 2001; Saino *et al.* 2003) at both time scales, but was not a predictor of fledgling mass. This is suggestive of mechanisms that allow smaller siblings to compete with larger nest-mates, and thus facilitate similar mass at fledging (Lepczyk & Karasov 2000; Schifferli *et al.* 2014; Stier *et al.* 2015; Honarmand *et al.* 2017). Synchronised fledging can result in a higher level of adult provisioning for all juveniles, compared to those nestlings that remain in the nest after their siblings have fledged (Nilsson & Svensson 1996; Nilsson & Gårdmark 2001). As skeletal development cannot be compensated for later in life, due to early bone ossification (Schew & Ricklefs 1998), it is more advantageous for smaller (i.e., later-hatched) siblings to prioritise increasing body mass and skeletal development over wing-feather development (Mainwaring *et al.* 2009) which can be compensated for during the post-fledging stage.

The results presented here demonstrate the importance of considering the interactive effects of multiple weather variables over multiple timescales when examining the impacts of weather on chick growth. In this study, I have interpreted these effects on nestling and fledgling body mass in relation to likely changes in nest micro-climate, and food availability and distribution. Further studies could examine the effects of weather during the nestling and fledgling stages on subsequent survival and recruitment into the breeding population. Determining the relative importance of these effects in relation to population size and persistence may be an important and fruitful avenue of future research, given current climatic trends.

# **Chapter 6: General Discussion**

## 6.1 Overview

A rapidly changing climate will manifest itself through daily and seasonal, local and regional scale changes in weather conditions (Kendon *et al.*, 2014; Xoplaki *et al.*, 2005), with consequences for bird populations at these spatial and temporal scales (Balmer *et al.*, 2013; Morrision *et al.*, 2013; Risely *et al.*, 2012). Seasonal fecundity (the number of chicks fledged during a breeding season) is an important driver of population dynamics (Etterson *et al.*, 2011; Nagy & Holmes 2004; Nagy & Holmes 2005; Sillett *et al.*, 2000; Temple & Cary 1988; Bennett & Owens 1997), and while there is a growing body of evidence that the component parameters of seasonal fecundity show differing responses to local variation in weather (see Chapter 1 and Chapter 2), there remained important gaps in our understanding of the behavioural and demographic mechanisms by which weather affects each component of seasonal fecundity.

The aim of this thesis was to examine three areas where a gap, or a relative paucity, exists in our knowledge of the impacts of weather on seasonal fecundity: 1) the effects of wind on the component stages of seasonal fecundity; 2) the interactive effects of weather variables on the components of fecundity, and 3) simultaneously considering the potential for weather effects on a component parameter of seasonal fecundity and that on the component preceding it (carry-over and cascading effects). These aims (1) and (2) were considered across Chapters 2-4, whereas aim (3) was relevant largely to Chapter 3.

# 6.2 The effects of wind on the component stages of seasonal fecundity

The effect of wind varied across all components, ranging from no apparent effect (e.g., incubation duration) to significant directional effects (e.g., nest temperature and nestling mass). At the level of the individual component, the effect of wind seems to influence the impacts of temperature and rainfall, rather than having direct effects in its own right. Overall, increasing wind speeds in combination with other weather variables had a negative effect; clutch size, hatching success, and

brood survival, for example, were all reduced under high wind speeds. The only exceptions were nocturnal nest temperature (Chapter 4) and nestling mass (Chapter 5); in the former case, high nocturnal wind speeds were associated with high nocturnal nest temperatures. In the latter case, high wind speeds reduced the negative effect of temperature at the day level on nestling mass, and high winds suppressed any negative effect of temperature on nestling mass over its lifetime (Figure 5.2 & Figure 5.3 respectively).

While some previous work has examined direct effects of wind on some components of – or behaviours related to – seasonal fecundity (Capp *et al.*, 2017; Hartley & Mainwaring 2016; Heenan & Seymour 2012; Irons *et al.*, 2017; Møller 2013), this is the first time that the effects of wind have been assessed across multiple components, and interactively combined with other elements, to examine its combined effects on seasonal fecundity (see Chapter 3 especially); it is among the first to examine the effects of wind on incubation behaviour. Indeed, in a review of studies examining the role of local weather and climate variation on nestling growth, Sauve *et al.*, (2021) identified only two studies that considered the impacts of wind on nestling condition in passerine species; one of which was Facey *et al.*, (2020) which presented the results of Chapter 5.

Wind speeds are predicted to increase as a result of climate change (IPCC 2014, Vautard et al., 2010, Young et al., 2011s), and the results presented above suggest that overall, this increase in "windiness" is likely to be detrimental to seasonal fecundity in passerines. However, in the same way that temperature or rainfall have been shown not to affect clutch size or hatching success in some bird species (Golaswki 2008), it is likely that impact of wind on seasonal fecundity, and its components, may depend on life-history traits in other avian taxa. Therefore, it is reasonable to ask how widely applicable results based on an aerial insectivore may be, given that the foraging ecology of aerial insectivores may be more susceptible to wind than that of a terrestrial insectivore, such as a Common Blackbird Turdus merula. Studies that have examined some of the effects of wind (e.g., Wang & Beissinger 2009, Gray and Deeming 2017, Heenan & Seymour 2012) have often found the same directional effect in both aerial and non-aerial insectivorous passerines, suggesting that the effects of wind reported here are likely to be more universal. For example, Wang and Beissinger (2009), found that wind increases wind speed delayed the start of full incubation, which in turn led to lower hatching success, across five species including three non-aerial insectivores (Western Bluebird Sialia Mexicana, Oak Titmouse Baeolophus inornatus, Ash-Throated Flycatcher Myiarchus cinerascens) and two aerial forgers (Tree Swallow Tachycineta bicolor, and Violet-Green Swallow

*Tachycineta thalassina*). Overall, it is likely that wind does impact aspects of fecundity for a broad range of species, but where and how, and to what extent wind impacts exist is likely to vary with life history. For example, the difference in nesting ecology between the Barn Swallow (nest protected by a building) and the Chestnut-crowned Babbler *Pomatostomus ruficeps* (domed twig nest) is likely to play some role in why the former's incubation behaviour is not affected by wind, but the latter's is (Capp *et al.,* 2017). While this thesis has contributed to filling in the gaps regarding the potential for wind to impact on the components and behaviours related to fecundity of passerine birds, it also highlights why future research needs to consider this important meteorological variable.

The results from Chapter 2 showed that clutch size increased with the proportion of grassland, specifically in windier springs/areas. In a similar way that Vernasco *et al.* (2018) found that the extent of mature forest cover reduced the negative effects of drought on the survival of nestling Wood Thrush *Hylocichla mustelina*, this suggests that habitat quality and land use can play an important role in ameliorating negative impacts of increasing wind speeds on seasonal fecundity. Wind speeds have also been shown to be a driver of habitat selection in some species (Sunde *et al.*, 2014), suggesting that habitat heterogeneity, or at least the ability to exploit multiple habitats, may be an important factor determining or lessening the impacts of increased wind speed on population drivers such as seasonal fecundity. This may be a particular consideration for the conservation of declining species and highlights the importance of incorporating climate change predictions into policies related to land use and management (Oliver & Morecroft 2014).

### 6.3 The interactive effects of weather on seasonal fecundity

The unifying aim across all chapters within this thesis was to examine the interactive effects of weather variables on seasonal fecundity and its components. The interactive effects of weather on seasonal fecundity and its parameters have been less well documented than main effects (but see e.g., Capp *et al.*, 2018; Coe *et al.*, 2015; Mainwaring & Hartley, 2016). As climate change is likely to bring about, and has brought, changes in the temperature, rainfall, and wind patterns (IPCC 2014), this comparative lack of study represents a gap in how the changes across multiple weather variables will together impact on species and ecosystems as a whole.

This thesis helps to fill these gaps in our understanding by providing evidence of interactive effects across a number of components and behaviours associated with seasonal fecundity. Fifteen weather interactions were significant across all models, with an approximately equal distribution of these interactions across the three weather variables. The number of significant interaction terms per model varied from 0 to 3, suggesting that interactive effects of weather are not universal but are still an important consideration and can be complex. For example, in Chapter 3, clutch size was affected by weather interactions during the pre-laying period but not during laying.

The effect and composition, and indeed the number, of the interaction terms acting on a component varied depending on the temporal scale over which it was measured; Chapter 5 provides an example of this. Nestling mass was negatively affected by temperature at the level of day but more so under low wind speeds. At the lifetime scale, however, mass was only negatively affected by temperature at low wind speeds. Interactive effects may only be important and/or detectable when weather is considered at a temporal scale that is biologically relevant at the level of individual behavioural decisions. Or it may simply be context dependent. Considering multiple temporal scales simultaneously can, however, uncover potential mechanisms that would not otherwise be possible or missed by focusing on one temporal scale only. Related to this, the temporal and spatial nature of weather events, and how we describe weather may be important in determining interactive effects. Saken and Yakel Adams (2012) for example found nest survival and productivity in the Lark Bunting Calamospiza melanocorys were both positively correlated with breeding season rainfall, but nest survival was supressed by intense rainfall events. As alluded to above, one or more weather variables may only interact or have different directional impacts in different contexts; this is in part shown by the sensitivity plots (Chapter 3, Figures 3.5 and 3.6) and suggests that greater exploration of how we interpret, or model, weather impacts is needed to fully assess the interactive effects of weather.

## 6.4 Consideration of carry-over and cascading effects.

Chapter 3 and, to a lesser extent, Chapter 4 considered carry-over and cascading effects from one breeding stage to the next. While the approach taken in Chapter 3 builds on the work of previous studies (e.g., Crick *et al.* 2003, Freeman & Crick 2003, Paradis *et al.* 2000) it is one of the first studies to integrate weather affects directly into a productivity model at each stage (i.e., clutch size,
incubation duration etc.), thus allowing the effects of weather to be explored directly on a stage of fecundity, and allowing cascading effects from one stage to the next to be quantified. This allows outcomes from different changes in weather patterns to be examined, as explored through the example case studies. While Chapter 4 was primarily concerned with incubation behaviour, it presents evidence of diurnal incubation behaviour having carry-over effects on the nocturnal nest environment; nocturnal nest temperatures were higher following days with high nest temperatures, and on warmer and windier nights. This is the first study that I am aware of that has examined the relationship between day-time behaviour and the night-time nest environment.

Understanding the impacts of weather on productivity is an important part of research focused on understanding demographic process and change, particularly in vulnerable and declining species (e.g., Saken & Adams 2012; Oppell *et al.*, 2013). As was seen in Chapter 3, weather conditions that promote a high value of one breeding component (e.g., clutch size) do not necessarily promote a high value of the next. Focusing on the impacts of weather on a single breeding parameter, without considering carry-over effects or how they interact, might not be sufficient to determine the effects of current and future weather variability on seasonal fecundity (Mattsson & Cooper 2007, Etterson *et al.* 2011). This in turn could hinder our ability to accurately forecast climate impacts. The approach used in Chapter 3, provides a framework to overcome this.

The approach taken in Chapter 3 also has broader application. As demonstrated by the case studies it is possible to use the matrix of results as a contingency or "look up" table to "mix and match" across the different stages, to test the effects of weather variation over a breeding attempt or season. This approach could be used in several different theoretical and practical applications, when populated with species-specific or population-specific predictions. For example, this approach could be used for the management of species of conservation concern such as the Eurasian Curlew *Numenius arquata*, which is a species that is undergoing severe declines in the UK (and across its European range) because of land use change and nest predation (Brown et al., 2015). Curlew frequently nest in silage fields and the need to cut these during the Curlew's breeding season often results in chick morality. The approaches used in Chapter 3 could be used to more accurately predict when such fields could be cut for silage without causing chick mortality, for example by using predicted weather to calculate incubation duration more accurately and to determine the likely number of chicks that will be present on different dates based on the clutch size that was laid and weather during the egg stage. Similarly, for highly vulnerable species it could be used to determine

when more drastic intervention is needed; supplementary feeding can be an important but costly way of increasing chick survival in critically endangered species (Ferrière *et al.*, 2020). Where weather is a predominate driver of chick survival, the approach used in Chapter 3 could be used to forecast when weather would result in low brood survival and provide an early warning to provide supplementary feeding if necessary.

### 6.5 Considerations in relation to the approaches used.

While this thesis presents robust findings based on original research, there were limitations which are important to acknowledge. Many of these have been discussed within the relevant chapters, but here I explore more unifying considerations of the approaches used.

Lack of temporal ("seasonal") variables, e.g., first egg date, in both Chapter 2 and Chapter 3, means that the analyses may have failed to pick up on seasonal-scale weather effects; for example are early first and second breeding attempts affected by weather in the same way? While it was not possible to confidently separate first and second breeding attempts in the dataset used in Chapter 2, this was possible in Chapter 3. While there was overlap in timing between the initiation of first and second broods (Figure 3.4), these do provide some proxy for seasonal effects (at least in double brooded individuals); indeed, given that both first and second broods raised in the same nest location can experience different effects from local weather variation (Salabarria *et al.* 2014) these may provide a natural "experiment" to test for the effects of local weather variation. The high collinearity of temperature with "day" variables meant it was not possible to include both variables together in the same model. This lack of a finer temporal scale seasonal effect (e.g., first egg date) meant that it was not possible to test specifically whether early and late first breeding attempts were affected by weather in the same way. I have attempted to overcome this shortfall by considering both seasonal and weather specific explanations for the relationships seen between the response variables and temperature, especially in Chapter 3.

An understanding of the behavioural mechanisms underlying the weather effects described in individual chapters could be enhanced through the collection of contemporaneous data relating to invertebrate activity and abundance; this would have allowed a greater exploration of the relative impacts of nest environment and food resources on the strategic decisions that female swallows made in relation to their behaviour. This was attempted in 2014, but practical issues meant the data were incomplete and did not overlap in time with the monitored nests. Similarly, while Chapter 5 was based on historical data, it had been planned to augment this with novel data to examine the interactive effects of weather and invertebrate abundance on provisioning and growth rates. As discussed in Chapter 4, predation levels were sufficiently high in 2015 and 2016, and the first half of the 2017 breeding season, to make these additional studies untenable.

The seasonal fecundity model (Chapter 3) could be developed further; as the number of whole nest losses during the egg and nestling phases was small (n = 5), I maintained a constant value for daily failure rates. However, where applicable, including weather-based effects on these values should improve the predictive ability of these models; especially as weather can influence the both the activity of nest-predators and the rate of nest predation (Cox *et al.*, 2013; Schmidt & Whelan, 1999; Smith *et al.*, 2002; Zanette *et al.*, 2006).

## 6.6 Novel contributions

Chapter 2 examined how three components of seasonal fecundity (clutch size, hatching success, and brood size) in complex interactions with weather and land use. This is, to my knowledge, the first time that the interactive effects of weather and land use on productivity in aerial insectivores generally have been examined (Evans & Robinson 2004). For example, while Kettel *et al.* (2020) examined the role of land use and weather on productivity in the House Martin *Delichon urbica*, these effects were analysed separately rather than interactively, and no interaction terms between variables were included in the models.

Chapter 3 used detailed data from a specific population of Barn Swallows. The approaches used in this chapter were novel in that they acknowledged that the effects of weather may act on all variables simultaneously, thus allowing for the effects of weather on previous components of fecundity to be considered, resulting in the final estimate of seasonal fecundity to include carry-over effects. An important finding of this chapter was that high values across all component metrics were not necessary to result in the highest values of seasonal fecundity; highlighting the importance of disaggregating the components of seasonal fecundity to understand the specific mechanisms by which individual components of weather at different breeding stages may influence overall seasonal fecundity.

Chapter 4 examined the effect of weather on the behaviour of incubating female swallows. This builds on previous work on interactive weather effects on incubation behaviour (Capp *et al.* 2017; Coe *et al.* 2015) but represents a novel contribution in that unlike previous work it: a) examines interactive effects between three weather variables (cf. Capp *et al.* 2017 who examined the temperature x wind interaction, and Coe *et al.* 2015, who examined the temperature x rain

interaction), b) provides a direct comparison of incubation behaviour studied over two temporal scales (hourly vs. daily), and c) examines carry over and interactive effects from the day into the night.

Chapter 5 examined the interactive effects of local weather on the body mass of nestling and fledgling swallows on the day of handling (or in the case of fledglings, the day before handling), and over the individual's lifetime (the day of hatching to the day of handling). While other studies have examined weather effects on swallow growth or mass, none have considered direct or interactive effects of wind speed; Fernaz *et al.* (2012) provided evidence of the effect of rainfall on nestlings while Saino *et al.* (2012) provided equivalent evidence for temperature. As mentioned previously above, a review by Sauve *et al.* (2021) identified only two studies that had included the impacts of wind on nestling condition in passerine species; one of which was Facey *et al.* (2020, see Chapter 5). This chapter also provides a contribution to this area in that the effects of weather on body condition in the weeks immediately after fledging remain largely unexplored (Yackel Adams *et al.* 2006; Cox *et al.* 2014).

## 6.7 Future directions

### 6.7.1 Application of the seasonal fecundity model

The approaches used in Chapter 2 and Chapter 3 could be combined to determine the effects of weather variation, either temporal or spatial, and past and future, on seasonal fecundity and broader spatial scales. Indeed, while Nest Record Scheme data have been used to calculate spatially broad fecundity estimates, these do not use as broad a range of parameters as used in Chapter 3, and therefore do not necessarily capture the potential sensitivity to weather described here. A further area of work should be to examine whether detailed models based around a single population (e.g., Chapter 3) can accurately describe and predict fecundity in other populations of the same species. This would be particularly useful for predicting fecundity for locations where detailed studies are lacking or absent, or where recorder effort is low.

#### 6.7.2 Exploring heterogeneity and limits of responses to weather effects.

Another limitation of the small sample size in Chapter 4 is that it was not sufficiently large to examine heterogeneity of behavioural responses; Coe et al., (2015) noted that there was individual variation in female incubation behaviour, with the range of off-bout durations being around 7 minutes to 180 minutes. In the current study, off-bout length ranged between 2 - 47 minutes. This suggests that there is a high degree of individual variation in incubation behaviour and potential for behavioural plasticity in incubatio strategies. Do females all alter their incubation behaviour respond in the same way to the same environmental change? This may be a significant avenue for future research to explore, as plasticity of response, at least at the population level, will likely be essential to adjust to future environmental changes, which may or may not entail evolutionary adaption (Grant & Grant 1993, Green & Pearce-Higgins 2014). Indeed, an important line of research would be to examine the limits of behavioural responses to maintaining a nest environment conducive to embryo development. There is some emerging evidence that females in some species are adjusting their incubation behaviours in response to increasing temperatures. For example, the Jacky Winter Micoeca fascinans, a species found in semi-arid Australia, has been show to double nest attendance when temperatures exceed 28 °C, but switch to shading (rather than incubating) eggs when temperatures exceed 30 °C (Sharpe et al., 2021). Indeed, egg morality declined over 35.5 °C yet females continued to incubate even when mortality had reached 100%, suggesting that this loss from heat stress is a relatively novel experience with no appropriate evolved response. This is an area that needs more research across species from a range of habitats and life histories.

### 6.7.3 Understanding the weather-related causes of hatching failure.

The results of this thesis, that hatching success showed a degree of sensitivity over the long-(months/season, Chapter 2) and short-term (days/weeks, Chapter 3). However, while the mechanisms of hatching failure – infertility and embryo morality (both within the egg and via predation) – are well documented, few studies attempt to discriminated between these two types of failures (Assersohn *et al.*, 2021). While increased exposure to high temperature leads to embryo mortality, climate change can also impact on fertility (Walsh *et al.*, 2019). Hatching failure can have complex genetic, parental, and environmental components (MacHebe & Briskie 2010, Wilcoxen et al., 2011), and a focus of furture research should be to determine the mechanisim of hatching failure (infertilty or within egg embryo mortality) in relation to local weather variation, through examination of unhatched eggs. This may be particularly important for studies focussing on fecundity in highly threatened bird species, where hatching failure has been shown to can excerbate population bottlenecks (Briskie & Mackintosh 2010; MacHebe & Briskie 2010).

# **6.8 General Conculsions**

Climate change will have, and is already having, a profound effect on biodiversity across the globe. Understanding the effects of changes in local weather can help us to predict impacts on species and populations. In this thesis I have developed a framework based on direct and interactive relationships between weather and the inter-related components of seasonal fecundity, allowing a better understanding of the impacts that a changing climate will have on this important demographic driver. In particular, it provides evidence that:

- Wind speed has important implications for seasonal fecundity by exacerbating, or in some cases mitigating, the effects of other weather related impacts.
- Only by considering the interactive effects of weather can we properly understand the impacts of weather variaiton on seasonal fecundity.
- 3) It is important to simultaneously consider the potential for weather effects on each component of seasonal fecundity, and that on the component preceding it, to understand how these effects sum to affect overall fecundity across the whole breeding season.
- The temporal scale over which weather effects are considered can affect the predicted nature of those effects.

It is hoped that the results of this thesis will promote consideration of wind, and the interactive effects of weather, on demographic process and life-history traits.

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144

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158

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