Breeding biology of the Common Swift *(Apus apus)* in Ireland – the most north-westerly edge of the nesting habitat

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January 2022

I hereby certify that this material, which I now submit for assessment on the programme of study leading to the award of M.Sc., is entirely my own work and has not been taken from the work of others save and to the extent that such work has been cited and acknowledged within the text of my work.

Signed:

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Date: 28.01.2022

Table of Contents

List of Figures

List of Tables

Abstract

Ireland is at the north-western edge of the Common Swifts' (*Apus apus*) range, and information on the basic breeding parameters of the species in this region is sparse. Therefore, the main objective of this research was to provide a detailed study of the breeding biology of the Common Swift in Ireland using information gathered at two artificial nest colonies located in Castlebar, County Mayo, and Maguiresbridge in County Fermanagh. Quantitative analysis was carried out on aspects of the breeding biology of the Common Swift such as a) important dates during the breeding season, including arrival, egg laying, hatching, fledging and departure; b) the colonies' productivity and chick mortality in the nest; c) the chicks' feeding frequencies; and d) egg loss during the incubation period. In addition, some aspects of the breeding biology were measured for their response to environmental factors such as rainfall, temperature and wind. The design of this research was based on the use of artificial nest boxes fitted with cameras connected to recording equipment, which resulted in the analysis of 28,500 hours of footage. During this investigation a total of 128 breeding attempts were studied which included observations of 300 laid eggs, 244 fledged chicks, 39 egg ejections and 17 chick mortalities. The phenological breeding cycle of the Common Swift is rigid, and there is a little variation in the values of mean arrival, egg-laying, hatching, fledging and departure dates each year. The average clutch size in Castlebar was 2.33 (se± 0.07) and 2.41 (se± 0.65) in Maguiresbridge. The average brood size in Castlebar was 1.53 (se± 0.16) and 2.28 (se± 0.08) in Maguiresbridge. The average number of fledglings in Castlebar was 1.38 (se± 0.15) and 2.13 (se± 0.09) in Maguiresbridge. A low average brood size and number of fledglings in Castlebar were the result of significant egg loss during incubation, a phenomenon apparently accentuated by the smaller size of the nest cavity along with small and shallow nest moulds. The total number of chick-feeding visits to the nest during the entire chick-rearing period was dependant on the size of the brood but the relationship was not linear. On average: broods of one were fed 501.28 (se± 20.15) times in the season; broods of two were fed 746.80 (se± 18.15) times; and broods of three were fed 872.5 (se± 20.15) times. Daily patterns of chick-feeding frequencies were related to the brood's size and age. For broods of one, the feeding remained constant throughout the period and reduced only in the last ten days before fledging. For broods of two and three, feeding increased linearly during the first eight to ten days following hatching and dropped during the last ten days before fledging. Weather factors influenced the daily number of feeds, with wind having the most positive impact, and to a lesser extent temperature (positive) and

rainfall (negative). Egg loss for the most part was accidental with the adult swift knocking out the incubated egg. At both nest box projects; the size of the nest mould and the nest box was crucial in either influencing (Castlebar) or limiting (Maguiresbridge) egg loss. The presence of artificial nest moulds at both colonies appeared to influence poor nest construction, and in some breeding attempts led to a disregard for nest material collection. Overall, the findings of this study indicate that the Common Swift is well adapted to breed in Ireland, and if given suitable nest opportunities, it can produce sustainable colonies.

Acknowledgements

This project was developed in co-operation with the Swift Conservation Mayo and Galway-Mayo Institute of Technology Mayo Campus. This project was funded by a Research and Innovation Strategic Endowment Scholarship from the Galway-Mayo Institute of Technology and Swift Conservation Mayo and a contribution from Mayo County Council.

I wish to acknowledge the assistance of all who helped me during the study. Sincere thanks to my supervisors Fergal O'Dowd, Dr Yvonne McDermott, Chris Huxley, Dr Ian O'Connor for mentorship, patience, and encouragement. Special thanks to Lynda Huxley for her motivation, encouragement, and enthusiasm, helping me at every stage of this research. Thanks to John and Georgina Young for supplying the footage from their swift colony, but also for being very welcoming and supportive. Thanks to Deaglan O'Riain for designing initial data collection methods for the swift project. Thanks to the staff at GMIT Mayo Campus, especially to the library, and the IT staff. Thanks to the Research Office staff for the help with administrative aspects of the research. In addition, I would like to thank various other academic staff of GMIT Mayo Campus for guiding me through my academic journey so far, especially Stephen Hannon, Kevin O'Callaghan, Pauline Jordan, Orla Prendergast, Pearse McDonnell, Margaret O'Riordan, Niamh Hearns, Janine McGinn and Sinéad Kilgannon. Thanks to my family and friends for their encouragement. Thanks to my friend Jocelyn Doyle for helping me with proofreading and improving my writing skills. A very special thanks to my partner Marina Hafidz de la Iglesia, for your patience, support and laughs. Lastly, I would like to thank Austin Smith, a friend who may not even remember but once motivated me to return to college.

Chapter 1: Introduction

The Common Swift, *Apus apus* (Linnaeus, 1758, p. 192; Scopoli, 1777, p. 483) is a migratory bird belonging to the family Apodidae. Its breeding range is widespread across North Africa, Europe and Central Asia, while it winters in Sub-Saharan Africa (Chantler & Driessens, 1995, p. 222; Appleton, 2012, p. 16) (Figure 1). On the African continent, the nesting range occurs exclusively in the Mediterranean coastal regions. In Europe, the breeding region is extensive and excludes only the far northern regions of Scandinavia, the north of Scotland and European Russia (Tigges, 2007, p. 130). The Common Swift breeds throughout Ireland with exception of the North-West territory of County Mayo and coastal islands (Balmer, et al., 2013, p. 462; BirdLife International, 2021) (Figure 2). In Asia, the breeding range stretches from Israel to northern China and the Korean Peninsula (Chantler & Driessens, 1995, p. 222). The Common Swift is adapted to a broad range of habitats and its population is often concentrated in areas of human occupation, where they take advantage of the built environment for nesting purpose. This transition most likely occurred as a result of the reduction in ancient forests, where swifts used to nest in tree cavities (Holmgren, 2004, p. 412). However, tree nesting swifts are still observed today in a small number in the Caledonian Forests in Scotland, the Harz Mountains in Germany (Günther, et al., 2004, p. 309) and the Białowieża Forest in Poland (Jaroszewicz, et al., 2019, p. 5). Outside of the nest, the Common Swift is rarely seen when not in flight. They are seldom observed perched (Holmgren, 2004, p. 407) and only occur at ground level if injured, have fallen from the nest, or too young to fly. They are commonly observed clinging to vertical surfaces during severe weather conditions.

Figure 1. Distribution map of the breeding range (in yellow) of the Common Swift, exclusive to the Palearctic Region(BirdLife International, 2021)

Figure 2. Distribution map of the breeding range (in yellow) of the Common Swift in Ireland and Northern Ireland. (Birdlife International, 2021) with marked research locations – Castlebar and Maguiresbridge.

The current taxonomy of the Common Swift places it in the *Apodiformes* order of birds (*Aves*), along with owlet-nightjars, treeswifts and hummingbirds. Within that order, swifts form the Apodidae family, consisting of 116 currently known species (Gill & Donsker, 2020) (Figure 3). Most species of swifts can be found in tropical areas, and only a limited number migrate to mainland Europe to nest. Only one species of swifts migrates to Ireland to nest, and that is the Common Swift (Chantler & Driessens, 1995, p. 222). Morphologically the Common Swift is very similar to the Pallid Swift even though both species been separated by 1.9 – 2.1 million of years of genetic modifications (Pellegrino, et al., 2017, p. 7).

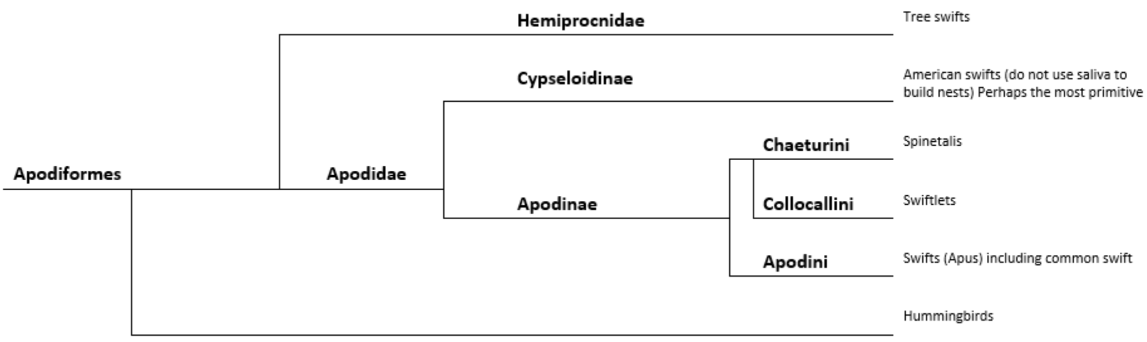
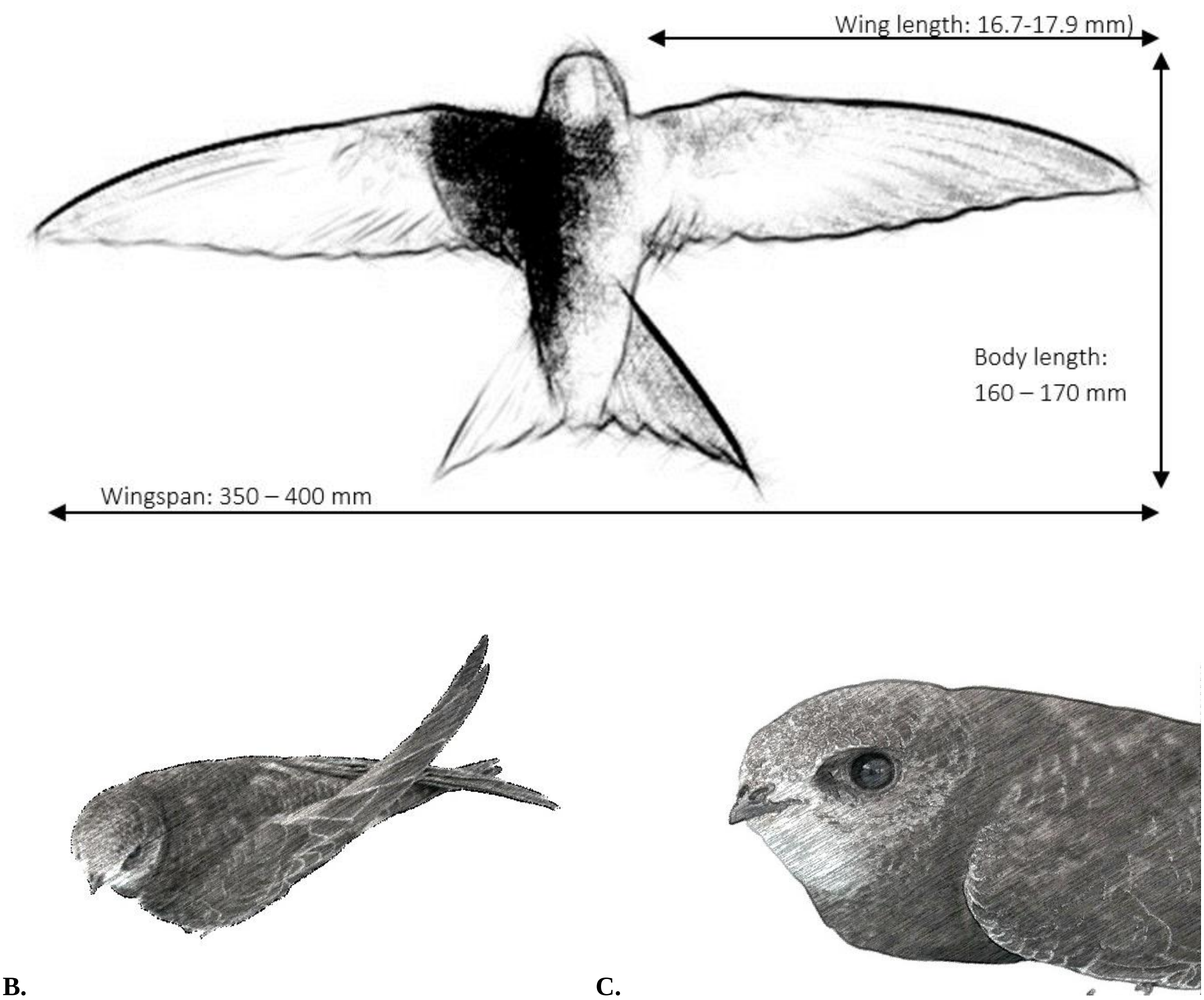


Figure 3. Family tree of the *Apodiformes* order (Lack, 1956, p. 215; Gill & Donsker, 2020)**.**

The Common Swift is a monomorphic species, and visual identification of the sexes is impossible (Chantler & Driessens, 1995, p. 223). An adult Common Swift is 16-17cm long (Figure 4A), and weight can vary between 31 and 46 grams depending on the period of the breeding season (Martins & Wright, 1993, p. 217). The head is small and rounded, with a white-grey patch around the beak and throat (Figure 4B). The beak is short and black with a sharp tip, pointing slightly downwards (Chantler & Driessens, 1995, p. 223). The plumage on the body, tail and wings is uniform black-brown, but the fringes of the feathers are often grey, especially when the plumage is fresh (Figure 4C). The wings are long and narrow, and they are proportionally large compared to the rest of the body. The size of the wing provides the swifts with an ability to glide, searching for upward currents and pockets of hot air (Lack, 1956, p. 110). To maintain speed and maximise distance, the wings are curved, narrow and rigid, and do not flex on the upstroke (Henningsson, et al., 2008, p. 729). The swift's forked tail can widen and restrict, depending on the speed of flight. During a high-speed glide, the tail stays narrow, allowing the swift to control the aerodynamic drag. At lower speeds, the tail can widen to allow for greater control. The immature Common Swift is similar in size and in plumage, but may appear darker, with more pronounced white-grey edges to the fringes of feathers (Chantler & Driessens, 1995, p. 223).

A.



B. C.

Figure 4. The Common Swift body morphometrics. Top picture (A) represents the shape and the measurements of the adult swift body (Martins & Wright, 1993, p. 217; APUSlife, 2021). Pictures below illustrate the shape and the plumage of the body (B) and head of the juvenile Common Swift (C).

The start of the breeding season varies depending on the geographical location of the nest (Tigges, 2007, p. 135). In Israel, the breeding season begins in March and finishes in June. Throughout most of Europe, the breeding season stretches from mid-May to early August (Lack, 1958, p. 496; Tigges, 2007, p. 131). In northerly regions, such as Scandinavia and the north of Russia, breeding begins in June and ends in mid-August. The nest cup is constructed with airborne material carried by the wind, such as dried pieces of vegetation or feathers, which are then put together with saliva (Cutcliffe, 1951, p. 47; Lack & Lack, 1951, p. 198). The Common Swift lays one clutch (not inclusive of replacement clutches laid due to egg loss) as it can raise only one brood per year (O'Connor, 1979, p. 136; Thomson, et al., 1996, p. 31). A completed clutch typically has one to three eggs (O'Connor, 1979, p. 135); however, clutches of four are also reported (Lack & Lack, 1951, p. 200). Both sexes share parental duties and display little difference in the level of parental care provided (Lack & Lack, 1951, p. 200;

Carere & Alleva, 1998, p. 1382). Eggs are laid at two- to three-day intervals (O'Connor, 1979, p. 135). Incubation of a single egg lasts between 19 and 21 days. Chicks fledge 36 to 49 days after hatching, and the adult swifts depart the nest within a few weeks after the last chick has fledged (Lack, 1958, p. 494).

The Common Swift is a long-lived bird, fully grown when fledging, and reaches its reproductive maturity at the age of one to four (Perrins, 1971, p. 64; Thomson, et al., 1996, p. 31). Breeding pairs form life-long bonds and return to the same nest each year (Lack, 1956, p. 38). The Common Swift can establish a wide range of colony sizes (Antonov & Atanasova, 2002, p. 231), but solitary breeders are frequent. Swifts defend their nests aggressively, fighting intruders using claws and beak (Tigges, 1999, p. 3). The diet of the Common Swift is composed exclusively of small, airborne organisms (Cucco, et al., 1993, p. 134). During a foraging trip the Common Swift may be able to catch a few hundred or even a few thousand individual insects and arachnids – most commonly Hemiptera (true bugs), Coleoptera (beetles), Hymenoptera (wasps, bees) Diptera (flies) and Araneidae (spiders) (Lack & Owen, 1955, p. 120). During periods of bad weather, birds may fly long distances to reach foraging grounds. If the difficult weather event is prolonged, the birds will reduce foraging activity, but compensate when conditions improve (Shaub, et al., 2020, p. 527).

Social behaviours specific to this species include “banging” and “screaming parties” (Lack & Lack, 1951, p. 192; Ološ, 2017, p. 47). “Banging” describes the practice of non-breeding swifts flying up to occupied or unoccupied swift nest cavities and holding onto or brushing against them. This display is practiced by groups of birds, meaning that an individual nest cavity can be targeted multiple times in succession. This behaviour can take place at any time of day but is most common during the evening. The swifts occupying a “banged” nest (adults but also chicks) may display signs of stress such as vocalisations and erratic displays of movement around the nest cavity (Ološ, 2017, p. 47). The reason for the “banging” behaviour is not yet explained but may be a form of intraspecific aggressiveness, colony control, or antipredator behaviour (Ološ, 2017, p. 50). A “screaming party” is the term used to describe a tightly packed formation of swifts that flies above and near the nests’ locations, emitting loud vocalisations by which the Common Swift is instantly recognisable (Lack & Lack, 1951, p. 192; Bretagnolle, 1993, p. 145). “Screaming” swifts fly very fast (111.6km/h – the highest recorded horizontal speed), perhaps displaying their aerial abilities (Henningsson, et al., 2010, p. 97), or “marking” their territory that is in proximity to the colony to reduce the competition for the nests (Tigges, 1999, p. 4; Bretagnolle, 1993, p. 145).

For the Common Swifts that breed in Ireland, the issue of conservation is multi-faceted and complex. The Common Swift is a migratory bird and spends most of the year outside of Ireland. The issues that swifts encounter during migration and at the wintering sites are likely to affect both survival rates and fitness (Newton, 2007, p. 454; Boano, et al., 2020, p. 7925) Nesting opportunities have decreased with the advent of modern modifications to the built environment, which, among other things, eliminate the gaps and crevices favoured by swifts (Huxley, 2017, p. 20). In addition, older buildings such as stone houses, churches or clock towers are frequently either renovated or demolished (Whelan, et al., 2019, p. 8). The food supply of the Common Swift has also been decreasing in recent decades. Studies across Europe indicate that insect populations are in sharp decline, and this is correlated with a decrease in numbers in many insectivore bird species (Møller, 2020, p. 5).

Under Article 12 of the EU Birds Directive 2009/147/EC (amended version of 79/409/EEC from 2nd April 1979), all European Union member states need to undertake an assessment of common bird populations every three years (European Parliment and Council, 2010, p. 3). According to the Red List for Europe for 2015, the Common Swift is categorised as a species of "Least Concern", meaning that the population in Europe was stable between 1980 and 2013 (BirdLife International, 2015, p. 41). A lower than 30% population decline in the species over this 30-year period, coupled with a relatively large population across the continent, were the key determinants for this status (BirdLife International, 2020, p. 1). However, the newly published in 2021 The Red List for Europe changed the conservation status of the Common Swift from "Least Concern" to "Near Threatened" considering recent changes in European population of the species (BirdLife International, 2021, p.19).

In the European Bird of Conservation Concern (EBCC) report published in 2017 by Birdlife International, trends in the European population of the Common Swift can be assessed by each country taking part in the Red List for Europe project. The overall status of the Common Swift on the continent is described as "Decreasing". This report estimates the total breeding pair population in Europe to be 19,100,000-32,500,000 (BirdLife International, 2017, p. 162). Most European countries reported a decline in the breeding population of the Common Swift. However, some states reported the population of the species as stable (e.g., Ukraine, Switzerland, Slovakia). Nevertheless, a small number of states recorded an increase in Common Swift numbers, with the highest increase found in Poland (est. 31-106%) (BirdLife International, 2017, p. 162).

The Birds of Conservation Concern in Ireland (BoCCI) provides a comprehensive assessment of population trends for the Republic of Ireland and Northern Ireland dating back to 1999. The conservation concerns of individual species are categorised by placing them on a coloured scale: Red (highest concern), Amber (moderate concern), and Green (least concern) (Lynas, et al., 2007, p. 150). According to the latest BoCCI assessment, the breeding population of Common Swift in Ireland is in decline. The current trend places the Common Swift on the Red List of Conservation Concern (Gilbert, et al., 2021, p. 8). This represents a change from the previous two BoCCI reports, which placed the Common Swift on the Amber List of Conservation Concern (Lynas, et al., 2007, p. 159; Colhoun & Cummins, 2013, p. 534). The decline in the Common Swift population in Ireland has led to the creation of a number of community-led projects such as the Northern Ireland Swift Group and Swift Conservation Ireland (Huxley, 2017; Swift Conservation Ireland, 2020). Both groups work to preserve the species by setting up swift nest box projects, education, rehabilitation, and surveying. BirdWatch Ireland is also involved in swift conservation efforts (Whelan, et al., 2019, p. 4).

The major challenge in preventing the decline of a threatened species is that of developing conservation strategies that are achievable and sustainable. Understanding the breeding biology of the Common Swift in Ireland is an important step in increasing our knowledge around the specific requirements of the species. Ireland is at the north-western edge of the swifts' range, and information on the basic breeding parameters of the species in this region is sparse. Therefore, the main objective of this study is to provide a detailed study of the breeding biology of the Common Swift in Ireland using information gathered at two artificial nest colonies located in Castlebar, County Mayo, and Maguiresbridge in County Fermanagh (Figure 2). The results of this research will support conservation efforts by supplying the most accurate data about species performance at both locations. This was achieved by a) recording important dates during the breeding season, such as arrival, egg laying, hatching, fledging and departure; b) measuring the colonies' productivity and chick mortality in the nest; c) monitoring chicks' feeding frequencies and other aspects of parental care; d) conducting an analysis of the issue of egg loss during the incubation period. The analysis of nest box camera recordings from both sites was central to this process. In addition, some aspects of the breeding biology were measured for their response to environmental factors such as rainfall, temperature and wind speeds (hourly, daily, and monthly averages) in order to further expand our knowledge of swifts' performance in this most north-westerly edge of their distribution range and nesting habitat.

The research plan was divided into four stages, each one assessing different aspects of the breeding biology of the Common Swift. These include: the breeding season calendar, patterns of parental care, productivity, and egg loss. The first stage was focused on analysing patterns of events such as arrival, egg-laying, hatching, fledging and departure dates. The second stage examined the clutch size, fledging success, and chick mortality in the nest. The third stage of the study was focused on the feeding frequency of the Common Swift as a measure of species response to environmental conditions in Ireland. The fourth aspect of the study examined the issue of egg loss during the incubation period, which appears to be prevalent for the Apodidae family of birds (Lack, 1956, p. 77; Pichorim, 2011, p. 189; Nguyên Quang, et al., 2006, p. 391; Rowley & Orr, 1965, p. 364).

The foregoing introduction has provided an overview of the Common Swift, their habitats and some of their key characteristics. It has addressed their conservation status in Europe and set out the aims of this research and established its justification. The following chapter will focus on the literature relevant to this research.

Chapter 2: Literature Review

2.1 Introduction

This chapter reviews relevant publications concerning the breeding biology of the Common Swift. Almost all of the published material on the subject concerns territories other than Ireland, thus demonstrating the need for this study. Moreover, Ireland's location on the map of the species' breeding habitat is unique due to it being on the north-westerly edge therefore exposing swifts to the North Atlantic coastal climate. The comparison between the results of this research and those of other studies conducted abroad will provide an insight into the birds' adaptations to breed successfully in this region. The following discussion will consider a range of literature in the areas of swift phenology, breeding success, parental care and egg loss.

Historically, the breeding biology of the Common Swift in Ireland has received little attention, and available reports on the species in the country are limited to a few publications on surveys (Whelan, et al., 2018, p. 100), and the phenological cycle (Carroll, et al., 2009, p. 121). In one historic resource, Ussher & Warren (1900, p. 102) reported that in the late nineteenth century the Common Swift was widespread in Ireland, breeding in every county, including coastal regions. They reported an abundance of nesting swifts in towns, in human-made structures, but also in the sea cliffs on Rathlin Island. In those days, swifts were observed to be commonly feeding over mountain ranges and on coastal islands. Ussher & Warren (1900, p. 103) noted the arrival of the swifts in late April and early May, and departure in August and early September, and even into October. They also noted the negative influence of cold weather on the swifts but did not elaborate further. Moreover, they reported the common occurrence of three egg clutches. Later, in the mid-twentieth century, Lack & Lack (1950, p. 502) mentioned that the Common Swift was scarce in the coastal regions of Ireland, due to the high rainfall and prevailing winds coming from the Atlantic Ocean, conditions that make feeding difficult. In many later publications, the presence of the Common Swift in Ireland is mentioned, but no specific details about the species breeding biology are provided (Chantler & Driessens, 1995, p. 221; Balmer, et al., 2013, p. 462). The presence of swifts in coastal regions of County Mayo and neighbouring County Galway were mentioned by Ruttledge (1989, p. 83) and Whilde (1990, p. 51) who reported arrivals in late April and in May and departures in August. On the whole, the subject of swifts in Ireland is inadequately researched; some of the information that has been published is contradictory and outdated, and it may not represent current knowledge of the species. Thus, the current study seeks to address this gap in the literature with reference to Ireland's swifts.

2.2 Phenology

2.2.1 Arrival, departures, and length of the breeding season

Lack (1958, p. 479) reported that in Oxford, UK, the return of breeding swifts to their nests takes place around the same time each year during the month of May and reported that variations in the mean arrival dates were not significant during the study. The arrivals of the swifts in their nests were noted by an overnight roosting of the swift in the nest. Lack (1958, p. 479) pointed out that the timing of arrivals stayed constant each year, regardless of the weather conditions at the colony location, or during the last stage of their migration north. However, he did note some irregularities in the timing of arrivals during periods of severe weather – anticyclones over France and Britain with cold northerly winds caused, in some years, a few days gap in arrivals. Lack (1958, p. 479) surmised that the cold weather experienced by the birds during this severe weather caused a shortage of airborne insects, halting the migration for a few days. Regardless of weather conditions, the colony was assembled during the third and fourth week of May each year. In contrast to arrival dates, Lack (1958, p. 491) reported the departure dates to be influenced by a number of factors. Firstly, the primary influence on the departure date was the arrival date in May – early arrival of a pair of breeding swifts caused an early onset of breeding behaviour, leading to early fledging of the chicks. This in turn allowed the adult swifts to begin migration early, usually in late June. Secondly, Lack (1958, p. 497) noted that, since weather conditions in June and July influence the length of the nesting period, this also has an effect on the departure dates of the adults. If there was an abundance of food, usually during warm summers, departures took place early. By contrast, during years with cold periods during June and July, when food sources were negatively affected, chicks took longer to fledge, and adults spent more time building the necessary fat stores before departure. The mean departure dates of the breeding adult swifts during the study in Oxford was 8 August, but the range of departures was stretched from mid-July to early September, depending on the chicks' fledging time and weather conditions. In most cases, the adult swifts depart the nest after the last fledgling leaves the nest. However, Lack (1958, p. 495) observed some irregularities in this behaviour; on occasion, one of the adult swifts would leave the nest before all the chicks had fledged, and others departed on the same day as their young.

The phenology of the Common Swift across the European continent was the focus of a study by Tigges (2006, p. 27; 2007, p. 127), who compiled records on the arrival and departure dates at 22 different locations. There was a clear influence of latitude on the timings of the arrival and departure dates of breeding swifts. The earliest arrival dates at the breeding grounds were recorded in February in the countries of the Middle East (Israel, Syria). Those regions are relatively close to the wintering grounds of the Common Swift in sub-Saharan Africa and in close proximity to an important migratory corridor of the species: the Sinai Peninsula, connecting north-east Africa with Asia (Chantler & Driessens, 1995, p. 222). Across western Europe (Spain, France, Netherlands), the earliest arrivals are in April, with the bulk of breeders arriving in early- to mid-May (Tigges, 2007, p. 133). A similar pattern was observed throughout central Europe (Germany, Czechia, Romania). The latest arrivals are recorded in late May and early June in the most northerly regions of the Common Swift's breeding grounds: the northern parts of Scandinavia (Finland, Sweden) and European Russia (Murmansk) (Tigges, 2007, p. 147). The timing of departures also varied across the continent, with the birds that breed earlier also being more likely to depart early. In Israel, swifts depart in early June. On the Iberian Peninsula swifts leave their nests before the end of July. Throughout the rest of the European continent, the mean departure date falls in early- to mid-August. The last to leave their nests, in late August, are those swifts breeding in Scandinavia and northern Russia (Tigges, 2007, p. 132). The same pattern of arrivals and departures across the European breeding habitat was later confirmed by Åkesson et al. (2020, p. 2381). Tigges (2007, p. 131) noted that the duration of a swift's stay in the nest also varies geographically. Swifts breeding in the north stay in their nests for 85-100 days, in central Europe for 90-100 days, and 100-120 days in the south. This pattern was explained by adaptations to climatic conditions in different geographical regions, influencing the timing of food abundance.

Åkesson et al. (2020, p. 2381) presented a detailed study of the Common Swift's phenology from various geographical locations to analyse the influence of latitude on the biology of the species. Confirming Tigges' observations (2007, p. 133), they provided evidence of late arrival dates in the northern breeding regions with mean arrivals falling in late April in Spain and late May in Sweden. They also studied the departure dates of the swifts occupying these northern breeding regions and found a difference of one month in the mean departure dates between Spain (14 July) and Sweden (15 August). The use of trackers, placed on the migrating birds provided evidence that the Common Swift exhibiting a chain migration pattern (Lundbegr & Alerstam, 1986, p. 408), whereby individuals occupying the southern breeding range depart early to the southernmost wintering grounds in southern Africa, while swifts breeding in the north spend their winter in the northernmost parts of the wintering grounds. This means that the swifts departing the breeding grounds early have a priority in choosing a suitable wintering range, while swifts arriving later may be limited to a lower-quality area, affecting their further development and performance (Åkesson, et al., 2020, p. 2381).

On a country scale, Gordo et al. (2007, p. 1072) analysed the arrival times of the Common Swift in Spain. Their findings confirmed the influence of geography and weather conditions on the pattern of returns to the breeding grounds in the country. The areas in close proximity to the Gibraltar Strait - one of the main pathways of migration of the species, were observed to be occupied first. The areas furthest away from the Gibraltar Strait saw the latest of the swifts. Gordo et al. (2007, p. 1074), also pointed out the importance of environmental factors on the phenological cycle of the species. The most influential factor was a summer climate in the Mediterranean region, where the summers are hot and dry. According to Gordo et al. (2007, p. 1074), this may favour an early start to the breeding season when conditions are more suitable, in order to have completed the breeding cycle by August, when conditions become difficult due to high temperatures and lack of rain.

Other long-term studies and publications reporting on the phenological cycle of the Common Swift support these observations confirming that the arrival and departure dates vary geographically, with the birds breeding early in the south and later in the north (Chantler & Driessens, 1995, p. 222; Khaleghizadeh, 2005, p. 80; Gordo, et al., 2007, p. 13). All research points to the hypothesis that the phenological cycle of the Common Swift is rigid within this framework, and there are almost no significant yearly variations in arrival times and departures at breeding grounds, regardless of geographical location (Lack, 1958, p. 479; Tigges, 2007, p. 128). Moreover, the increase in annual temperatures caused by climate change does not seem to have a major effect on the phenology of the Common Swift in England (Mason, 1995, p. 183), Scotland (Jenkins & Watson, 2000, p. 245) or in Ireland (Carroll, et al., 2009, p. 121). Gordo et al. (2007, p. 17) analysed long-term arrival trends in Spain for some of the most common migratory species (swifts, martins and swallows), and found that only the Common

Swift had not changed its arrival times since 1952. Additionally, a substantial amount of evidence suggests that many migrant birds breeding across the European continent are returning earlier to their summer habitats (Tryjanowski, et al., 2005, p. 202). Many speculate that climate change forces migratory birds to vacate their wintering areas sooner and arrive earlier at the nesting grounds (Menzel, et al., 2006, p. 1969). However, there is a limited amount of evidence confirming the influence of climate change on the phenological cycle of the Common Swift.

2.2.2 Timing of egg laying and incubation period

The timing of egg laying is one of the components of the birds phenological calendar. In Oxford, Lack & Lack (1950, p. 508) observed that the most common egg laying period for the Common Swift fell between the last week of May and the first week of June. Lack (1956, p. 89) observed that while the timing of egg laying does not change yearly to a large degree, bad weather can delay clutch initiation. Lack & Lack (1950, p. 508) observed that the interval between successive eggs was in most cases two days, but longer periods were also common (three to six days). The recorded hatching period ranged from 18 to 24 days, with 18- and 19-days hatching periods being most common. The variation in the length of hatching periods was explained by Lack & Lack (1951, p. 514) to be caused by the cold weather, when brooding may be interrupted. This was evident during one year of the study (1948), when what was described as “abnormally cold” conditions prevailed. May caused the incubation periods to be extended across the entire colony (22-24 days). Eggs laid in June of the same year, following this period of unfavourable weather, hatched in the range of 18 to 20 days.

In a later study, at the same location in Oxford, O’Connor (1979, p. 133), recorded an egg laying period which extended from 11 May to 10 June with the date of laying influenced by the weather of the three preceding weeks. A low temperature average during the period 1-20 May caused delays in the timing of egg laying, due to its influence on insect abundance. O’Connor (1979, p. 135), observed gaps of a few days during many of the studied years, when no birds at the colony laid eggs during what should be a busy egg laying period. These events were preceded by periods of low temperature, rain, and strong winds. This confirmed previous observations by Lack (1956, p. 89) who noted that swifts will delay a clutch in bad weather and require at least five days of favourable conditions to resume egg laying. O’Connor (1979, p. 135) recorded an interval of two to four days between consecutive eggs in the clutch, with intervals longer than two days being caused by adverse weather. In Berlin between 1993 and 2005, Tigges (2006, p. 29) recorded the median date of the first egg in the clutch to be 27 May (range: 18 May to 10 June). The interval between consecutive eggs laid by one pair was two to three days, and the incubation period was on average 19 days.

2.2.3 Chick-rearing period

According to Lack & Lack (1950, p. 518) the average chick-rearing time of the young Common Swift in Oxford was 42.5 days, with individual time ranging from 37 to 56 days. This discrepancy was explained by weather conditions during the chick-rearing period, with the shorter durations occurring in summers with favourable weather, and longer durations during cold seasons. At the same location, four decades later, Martins (1997, p. 100) reported the chick-rearing period for manually manipulated (by removing chicks from original nests and placing them in pre-determined nests and brood sizes to measure levels of parental care) in brood sizes as follows: 42.2-43.6 days for broods of one; 42.2–42.8 days for broods of two; 41.3–41.8 for broods of three. Similarly, in Berlin, Tigges (2007, p. 29), recorded the median stay of the first chick in the nest to be 41 days, with a range from 39 to 47 days.

2.3 Breeding success

2.3.1 Bergmann’s rule in relation to the Common Swift

According to Bergmann’s rule, in many of the species of birds occupying the northern hemisphere, individuals of larger size are more likely to occur at higher latitudes and in colder climates (Ashton, 2002, p. 518). Moreover, the geographical location of the nest can determine the size of the clutch (Lack, 1947, p. 26). In areas with high seasonal variability in food resources, the mean number of chicks in the clutch is expected to be higher (Rickliefs, 1980, p. 46). The Common Swift’s adaptation for breeding across different geographical locations and often in different climates results in a variance in the phenological cycle, coinciding with the timing of food abundance at the location of the nest. This may have implications on the fitness of individual birds and the productive output of breeding pairs.

Bergmann’s rule is less likely to be observed in migratory species of birds than in birds that overwinter in their breeding grounds (Meiri & Dayan, 2003, p. 343). For the Common Swift, knowledge around the influence of the latitudinal location of the nest is currently limited. Many studies focus on the influence of weather impact on breeding performance. Åkesson et al. (2020, p. 2385) reported a significant negative relationship between the size of individual breeding swifts and an increase in latitude, contrary to Bergmann's rule. Moreover, swifts breeding in northern regions produced significantly fewer chicks per breeding attempt than those breeding in the lower latitudes of central and southern Europe. Geographical variation in timing and clutch size was also found in the Alpine Swift *Apus melba*, where birds at higher latitudes laid eggs later and produced fewer eggs (Antonov & Atanasova, 2002, p. 7). Swifts breeding in the southern breeding range are also more likely to lay four eggs in a clutch (Sicurella, et al., 2015, p. 70). Across the rest of Europe, reports of four-egg clutches or four hatchlings in one breeding attempt are scarce (Chantler & Driessens, 1995, p. 224; Lack, 1956, p. 187), or come from studies that manipulated the size of brood to determine levels of parental care (Martins & Wright, 1993, p. 62).

2.3.2 Clutch size

Lack & Lack (1950, p. 508) found that the most common clutch size in Oxford was two eggs. Three-egg clutches were also common, but one-egg clutches were rare. They also compared these with results from other locations in central England and three other sites in Switzerland, Sweden, and Finland. The results showed that there was a significant relationship between the location of the breeding ground and the size of the clutch, with Sweden, Finland, and central England having a low percentage of more than two-egg clutches (range: 19-26%), while this figure is high in Switzerland (70%). Lack & Lack (1950, p. 510) noted that the size of the clutch was also related to the timing of egg laying within the season, meaning that larger clutches were more common during the early egg laying window (before 8 June). There was also a significant yearly variance in the proportion of three-egg clutches (excluded were clutches laid after 8 June; range: 3-64%). This was explained by a variance in maximum daily temperature during the second half of May, with high temperatures correlating with a high ratio of large clutches.

In a later study in Oxford, O'Connor (1979, p. 135) confirmed that if an individual pair lays their clutch early (mid-May) the probability of three eggs is more likely (75%) than in the later stages (5% in early June). O'Connor (1979, p. 143) studied the size and weight of eggs of the Common Swift and stated that weather conditions influenced individual egg parameters. If food was limited during the period of egg formation, clutches would consist of fewer eggs of normal weight, rather than a large clutch number and lighter eggs. Eggs laid during periods of cold and wet conditions were lighter if laid after two days, but of normal weight if laid after three days. In general, the third egg in the clutch was lighter than the first and second. As heavier eggs correlated to larger chicks and a higher chance of survival to fledging, the third chick hatched had a higher chance of mortality. O'Connor (1979, p. 144) concluded that the Common Swift regulates the size of the clutch and the egg based on environmental conditions and fluctuations in insect abundance. Therefore, parent swifts setting up for a possible brood reduction when food is scarce, make sure that the last chick hatched is likely to be less able to compete for meals with its older and stronger siblings. When food availability is at a good level, all chicks are fed and eventually fledge. If the opposite is true, the youngest chick is selected not to be fed and is instead starved, raising the chance of survival for the rest of the brood (O'Connor, 1978, p. 79). This observation confirms Lack's (1950, p. 516) theory that clutch size in birds developed through natural selection and is optimised for the highest possible number of offspring in a season. A similar pattern was observed in the Pallid Swift, where the first two eggs in the clutch are of similar size and the third egg being smaller potentially produces a weaker chick, thus in times of food scarcity cannot compete with older siblings (Cucco & Malacarne, 1996, p. 318)

2.3.3 Brood size and successful fledging

Lack & Lack (1950, p. 516) reported that brood size and chicks' survivability are both strongly correlated with weather conditions during the chick-rearing period, using average hours of sunshine per day throughout June and July in Oxford as an indicator of the quality of weather conditions. Because of low rates of both predation and accidental death, nearly all chick mortalities during the study were reported to be caused by starvation (Lack & Lack, 1950, p. 515). In years with below average daily hours of sunshine, the rate of survival of chicks from hatching to fledging was low (range: 35-44%). In contrast, during seasons with above average daily sunshine hours, the rate of survival among chicks was high (survival range: 91-100%). Moreover, the weather had a varied influence on the survivability of chicks from different brood sizes. For broods of one, the chick's chances of survival were not changed during years with favourable or unfavourable weather condition (range: 83-86%), meaning that even with low food availability, adult swifts were able to provide enough for one chick. However, the weather had much more effect on the fledging rates of larger broods. For a brood of two, the difference was reported at 50% in seasons with below average daily hours of sunshine, and

95% during those with above average hours. The survivability of chicks in broods of three was even lower in below average seasons, at 31%, but was relatively high in above average seasons, with 80% of total chicks fledging. Moreover, during years of bad weather, the broods of three experienced so much mortality that they produced fewer chicks on average (0.91 fledged per brood) than broods of two (1.00 fledged per brood), and almost the same number as broods of one (0.87 fledged per brood). In contrast, in good weather years, the average number of fledged chicks in different brood sizes was recorded as follows: 0.83 for broods of one; 1.90 for broods of two; 2.40 for broods of three. Overall, during the period studied (1945-1950), the average number of chicks fledged per breeding attempt in Oxford was 1.4, regardless of brood size (Lack & Lack, 1950, p. 517).

According to Lack & Lack (1950, p. 518), the weather was also a determining influencer of the length of the chick-rearing period. During the 1948 season, that with the lowest average daily hours of sunshine, the range of the fledging period was between 44 and 56 days. In 1949, when the hours of sunshine were very high, the chicks fledged between 37 and 47 days.

In a later study in Oxford, Martins (1997, p. 100) recorded chick-rearing periods and conditions of Common Swift chicks in manipulated broods (by removing/adding chicks to predetermine brood size) over two seasons (1988 and 1989) with contrasting weather conditions. Regardless of weather conditions, the age at fledging increases with an increase in brood size, but weight and wing length both decrease. This meant that the chicks from manipulated broods of three, in general, reached maturity later and were of poorer condition when they left the nest. Martins (1997, p. 100) found that this impact was even more pronounced in the season with cold, wet and windy conditions, when chicks from broods of three fledged on average two days older, weighing 20% less and having 6% shorter wings, than those fledging in a season that was warm and dry.

In Scotland, Thomson et al. (1996, p. 32) studied the effects of weather on the breeding success of the Common Swift between 1954 and 1993. On average, 1.63 (±SE 0.069) chicks were produced per breeding attempt. Thompson et al. (1996, p. 32) argued that yearly breeding success was regulated by the mean daily maximum temperature in June, coinciding with the early stages of the chick-rearing period. Temperatures in May and July had no significant effect on the numbers of chicks reared, and neither did daily rainfall during any stage of the breeding season, contrary to some previous observations (Lack & Lack, 1950, p. 518).

In one long-term study (1980-97), Richard et al. (2006, p. 66) studied the effects of the weather on the annual breeding success of the Common Swift in Czechia. Of all breeding attempts, the most common number of fledglings were three (38.9%) and two (33.7%). Less commonly seen was one fledgling per nest (11.9%), and the least common was four (0.87%). The remaining 14.5% of the breeding attempts were reported as failed (no chicks fledged). According to Richard et al. (2006, p. 68), temperatures in June had a significant effect on the breeding success of the Common Swift. Still, contrary to Thompson et al. (1996, p. 32), increasing temperature was seen to lead to lower fledging success. Moreover, the rainfall in May was also negatively correlated with breeding success, an observation earlier reported by Lack & Lack (1950, p. 518).

In one season-long study in Italy, Sicurella et al. (2015, p. 70) reported the average size of the clutch as 2.38 (±SE 0.08). They found that the chicks in broods that hatched later in the season experienced faster growth but were smaller on average. Moreover, fledglings from larger broods were also smaller than those from broods with fewer chicks. Therefore, the hatching date and brood size were consistent indicators of the fledglings' condition during their growth period. Sicurella et al. (2015, p. 74) also stated that chicks grew faster when temperatures oscillated around the seasonal norm for the location, but growth was slower when the weather was hotter or colder. Additionally, there was a positive correlation between daily growth and rainfall or wind. This finding was contradictory with previous studies of the Common Swift that claimed a negative effect of rainfall and wind on breeding performance (Lack & Lack, 1950, p. 516; Rajchard, et al., 2006, p. 70). However, Sicurella et al. (2015, p. 75) pointed out that the climate associated with the geographical location of the colony was typically hot and arid. In such conditions, rainfall may cause an increase in insect abundance rather than a reduction, leading to a positive impact on breeding success.

In the most recent study of the Common Swift breeding phenology at various geographical locations across the European continent, Åkesson et al. (2020, p. 2382) published the mean maximum young per nest at 14 different locations. They found a significant negative relationship between reproductive output and an increase in the latitude of the breeding site. Swifts breeding in Sweden and Finland produce fewer young (range: 1.81–2.16 per nest) than in regions such as the UK, Spain, Germany or Italy (range: 2.02–2.35).

2.3.4 Brood reduction and chicks' mortality

The hypothesis of brood reduction states that, in some species of birds, the clutch is set up for asynchronous hatching as a mechanism for possible brood reduction when there is a disruption in the food supply. In such events, the chicks that hatched last are smaller, and therefore can be selectively starved to preserve the food for the older and stronger siblings. This theory was proposed by Lack (1947, p. 328), and was later the focus of numerous studies (Ricklefs, 1965, p. 509; O'Connor, 1978; Slagsvold, 1986, p. 1131). Ricklefs (1965, p. 509) argued that brood reduction should be suspected in any bird species that may suffer from fluctuations in food supply during the chick feeding period. The evidence of this theory in relation to the Common Swift was presented by Perrins (1964, p. 1147), O'Connor (1979, p. 143), and Martins & Wright (1993, p. 63).

Many publications state that nestling mortality in the Common Swift is predominately a result of starvation, which is most commonly seen in large broods, especially in years with difficult weather conditions. Lack and Lack (1950, p. 93) stated that, in years with a high average number of daily sunshine hours, the survival rate in large broods was high and in general, broods of three fledged more chicks than broods of two. However, in years with lower average number of daily sunshine hours, nestling mortality in large broods was so high that the broods of two fledged on average more chicks (1.0) than broods of three (0.9). Increased mortality in larger broods was later confirmed in manipulated broods by Perrins (1964, p. 1148) and Martins & Wright (1993, p. 63). O'Connor (1979, p. 144) argued that high chick mortality in large broods might be a result of the fact that the last laid egg in the clutch is, in general, smaller and lighter than other eggs. Therefore, hatchlings from the last egg laid tend to be smaller and are more likely to be sacrificed when food is in short supply. The high mortality rate among large broods of Common Swift chicks was also confirmed by Sicurella et al. (2015, p. 70).

Koskimies (1948, p. 274) reported on swift chicks' ability to survive without parental care for many days. Under manipulated conditions, by removing swift chicks' from the nest, starving them and placing them alone in a controlled environment of 24°C, Koskimies (1948, p. 275) observed chicks' losing their ability to maintain their metabolic temperature after two days of fasting and regulate their body temperature close to the temperature of the environment, seemingly losing consciousness and minimising movement. Lack (1956, p. 82) also reported that swift chicks have the ability to withstand prolonged periods of malnourishment and cold by entering a state of torpor (Ruf & Geiser , 2015, p. 891) but fully recover once the conditions and food supply returns to normal. In Koskiemies's (1948, p. 275) experiment 4-6 week old chicks were able to survive on average up to nine days of starvation. According to Lack (1956, p. 82) this ability to enter a state of torpidity allows the young swift to survive when the temperatures drop and food becomes scarce as a result. Torpor was also observed in the White-throated swift (*Aeronautes saxatalis*) and the White-throated needletail (*Hirundapus caudacutus*) in the Apodidae family and it is common in the Trochilidae family (Hummingbirds).

The swift lousefly *Crataerina pallida,* is a known parasite of the Common Swift (Lack, 1956, p. 199; Walker & Rotherham, 2010, p. 451). *C.pallida* can occur in abundance on swifts bodies and supports itself by cyclically drawing out a substantial amount of blood from the host (Lack, 1956, p. 198). However, studies suggest that the parasitic load does not have a significant negative effect on the breeding success of the Common Swift (Walker & Rotherham, 2011b, p. 219; Tompkins, 1996, p. 738).Parasite abundance was found to have no effect on the survival and fitness of the chicks (Walker & Rotherham, 2011a, p. 507; Tompkins, 1996, p. 736).

2.4 Patterns of feed frequencies

The Common Swift feeds on air-borne insects. During the chick-rearing period, the adult swifts deliver food to their chicks in the form of a bolus – a pellet of saliva-bound insects stored at the back of the throat, which is then regurgitated and passed on to the young. The first published evidence of the patterns in feed frequencies was presented by Lack & Owen (1955, p. 123) in Oxford. The study was conducted during 21 days of observations between the hours of 8 a.m. to 5 p.m. Feeding was less frequent in poor weather (average range per hour: 4.7–11.0) than in fine weather (range: 12.3–19.5). The peak of feeding was 4 p.m. to 5 p.m. in poor weather and 11 a.m. to 12 p.m. in good weather. However, Lack & Owen (1955, p. 127) did not provide the number of total daily feeds or take into account the size and age of the brood.

Much more advanced data on the Common Swift' feeding frequencies was provided by Martins & Wright (1993, p. 153). In their research, false-floor electronic scales were to gather data rather than visual observations of the nest. The daily adult visits to the nest was monitored by detecting minimal changes in weight with each visit, permitting detection of bolus deliveries. According to Martins & Wright (1993, p. 215), adult swifts increase feeding rates in broods with an increased number of chicks, but this relationship is not linear. Feeding rates increase significantly between broods of one and two but do not increase further in larger broods. This means that larger broods may be at risk of not receiving the same amount of nutrients as chicks from small broods. However, during seasons with good weather conditions, adults raising larger broods were able to increase the load mass of their food deliveries in response to the abundance of food, rather than increasing the number of trips, improving their chances of raising more chicks per breeding attempt (Martins & Wright, 1993, p. 153). This contrasts to the chick feeding behaviour of the Pallid Swift (*Apus pallidus*), where the bolus size does not significantly differ with the increased brood size. Still, the number of food deliveries increases significantly and linearly from one to four chicks in the brood (Cucco & Malacarne, 1995, p. 1385).

In Rome, Italy, Carrere & Alleva (1998, p. 1383) monitored nest visits by the use of video recordings from the nest boxes. However, they did not record all nests continuously, but rather in three-hour periods per day, rotating between different nests until day 25 after hatching. Carrere & Alleva (1998, p. 1385) reported an increase in the feeding rates of larger broods, but also a linear increase with the age of the brood. This approach also provides useful insight for the methodology used in the current study (**3.5**).

In Germany, Schaub et al. (2020, p. 520) were able to measure seasonal and daily frequencies of nest visits of adult swifts using light-level geolocators during three consecutive breeding seasons. The aim of the research was to improve nest monitoring methods of the Common Swift. In total they were able to record 3862 nest visits for 10 individual breeding swifts giving a mean of 5.63 (median 5, range 0-20) nest visits per day. Shaub et al. (2020, p. 523) provided evidence for periods of high and low daily activity among the swifts, with a high number of visits in the morning, followed by a period of low activity from late morning until afternoon, and a peak again in the evening. Shaub et al. (2020, p. 523) also measured seasonal changes to the nest visits, with the peak of activity recorded during the first 30 days of the chick-rearing period. The average maximum daily visits reaching its peak on 3 July. The weather was observed to have affected the swift activity during the study, but the results were complex. In general, ambient air temperature had a positive effect on the number of visits to the nest, while wind and rain had a negative effect. However, Shaub et al. (2020, p. 523) noted that rainfall had a higher negative effect when combined with low temperatures, when it coincided with high temperatures the effect of rainfall on swift activity was reduced. In contrast wind had a negative effect on the number of nest visits during high temperatures and less so in low temperatures. Therefore, the most optimal conditions for the Common Swift may be high temperatures, combined with low rain and wind. However, Shaub et al. (2020, p. 521) only measured activity relating to the nest entries and exits and noted that 8-16% of those events may have been missed due to the inconsistencies in the measuring method. Such methods may provide some indication of the number of daily and seasonal numbers of chick food deliveries but cannot be used to measure that characteristic without a large margin of error.

During the chick-rearing period in Oxford, adult swifts did not feed their chicks with every visit to the nest. Martins & Wright (1993, p. 216) recorded that in 25% of all nest visits, there was no food delivery to chicks, and this was explained by the adult swifts' requirement for self-feeding. For small broods, no-feed visits to the nest were more frequent in the early stages of the chick-rearing period, while for the broods of three, they occurred more often in the late stages. No-feed visits were also observed in Rome by Carerre & Alleva (1998, p. 1384), but the frequency was lower than in Oxford, at 8% of total recorded nest visits.

2.5 Egg loss

Previous observations of the Common Swift's breeding biology have reported the issue of egg loss during the incubation period (Lack & Lack, 1951, p. 200; Lack, 1956, p. 76; Cutcliffe, 1951, p. 53; O'Connor, 1979, p. 136). Egg ejection may happen at any stage of incubation and the whole clutch can be lost in that fashion. Once ejected, eggs are ignored, and adult swifts do not make a concerted effort to return the egg back into the nest cup. Many studies have reported that ejected eggs were cracked or chipped, but some remained fertile, and when manually returned to the nest, they eventually hatched (Lack & Lack, 1951, p. 201; O'Connor, 1979, p. 136). Often, the whole clutch was ejected, and a replacement clutch was laid if there was sufficient time remaining in the season. Cutclife (1951, p. 53) claimed that the ejection of eggs was caused by spells of bad weather. Lack & Lack (1951, p. 201) did not provide an explanation for this behaviour but found no evidence of the weather causing egg ejection. Later studies were also inconclusive with explanations of egg loss. O'Connor (1979, p. 136) again suggested that eggs are ejected in bad weather. Later, Newell (2019, p. 26) stated that egg ejection might be deliberate when incubation is disturbed, but it also may be accidental when the swifts observed, occupy nest boxes with artificial concave-shaped nest moulds.

Observations of egg loss are common in other swift species (Lack, 1956, p. 77; Pichorim, 2011, p. 189; Nguyên Quang, et al., 2006, p. 391; Rowley & Orr, 1965, p. 364). The White-Rumped Swift *(Apus caffer)* was observed carrying eggs in its beak to eject from the nest entrance (Lack, 1956, p. 77). Egg loss is common for the Biscutate Swift *(Steptoprocne biscutata),* due to a range of reasons: unexplained egg disappearance (most common), damage, ejection (eggshells found outside of the nest), adult death, or damage to the nest (Pichorim, 2011, p. 189). Egg loss is also common for the House Swift *(Apus nipalensis)* and is most often observed in the first clutch and in larger clutches (Nguyên Quang, et al., 2006, p. 391). Egg loss was also reported for the White-Naped Swift *(Streptoprocne semicollaris)* (Rowley & Orr, 1965, p. 364).

The issue of egg loss in the *Apodiae* family appears to be common, but the nature and possible causes of this behaviour are still not well understood. However, the loss of eggs during the incubation period has a negative effect on species' productivity and would impact upon the survival of the species. If the issue is prevalent for the Common Swift, expanding our knowledge around the nature of this behaviour is important for conservation efforts.

2.6 Conclusion

The majority of research material regarding the breeding biology of the Common Swift came from a few decades-long studies of the species in Oxford (Lack & Lack, 1951, p. 501; Perrins, 1964, p. 1147; O'Connor, 1979, p. 133; Martins & Wright, 1993, p. 61). Early work by David Lack and various collaborators provided ground-breaking information on many aspects of the species' behaviour and adaptations, including breeding (Lack & Lack, 1950, p. 501; Lack, 1956, p. 12), feeding (Lack & Owen, 1955, p. 120), and phenology (Lack, 1958, p. 477). In later studies at the same colony, Perrins (Perrins, 1964, p. 1147), O'Connor (1979, p. 133), and Martins & Wright (1993, p. 213) detailed the significance of the clutch and brood size, brood reduction, and the effect of weather conditions on the breeding performance of the Common Swift. Outside of Oxford, important studies of the swifts' phenology and migration were completed by Tigges (2007, p. 127), Gordo et al. (2007, p. 1065), and Åkesson et al. (2020, p. 2377). The effect of weather conditions on the breeding performance of the Common Swift was studied by Thompson et al. (1996, p. 29), Rajchard et al. (2006, p. 66), and Sicurella et al. (2015, p. 64). Therefore, many aspects of the breeding biology of the species are well researched and known.

Conclusions drawn from the published research consistently suggest that the geographical location of the breeding grounds plays a major role in the breeding performance of the Common Swift (Lack & Lack, 1951, p. 509; Tigges, 2007, p. 133; Åkesson, et al., 2020, p. 2381). The analysis of the phenological cycle suggests that birds breeding in the south arrive, lay eggs, and depart earlier than their counterparts breeding in the north (Tigges, 2007, p. 138; Åkesson, et al., 2020, p. 2385). However, the breeding cycle of the swifts in a selected region is rigid and is timed to coincide with the peak of food availability (Lack, 1958, p. 479; Tigges, 2007, p. 128). Moreover, so far climatic changes appear not to have a significant effect on the breeding cycle of the species (Mason, 1995, p. 183; Jenkins & Watson, 2000, p. 254; Carroll, et al., 2009, p. 121). Productive output is also varied geographically, with breeding pairs producing more chicks per breeding attempt in the southern regions, contrary to Bergmann's Rule (Åkesson, et al., 2020, p. 2385).

Different publications from studies at various geographical locations present different results regarding the impact of weather on the reproductive success of the Common Swift, with many inconsistencies. Thompson et al. (1996, p. 32) reported that the high mean maximum daily temperatures in June were a major positive factor influencing swifts breeding in Scotland, while Rajchard et al. (2006, p. 67) reported a contrasting negative effect of high temperatures in June in Czechia. Additionally, Sicurella et al. (2015, p. 73) found no negative impact of temperature, rainfall or wind on the fledging success of the Common Swift in northern Italy. The inconsistencies in reporting the impact of weather conditions on the breeding biology of the species may, in many cases, come from differences in the reporting of those weather conditions. Lack & Lack (1951, p. 505), used the daily average of sunshine hours as a proxy for defining "good" and "bad" weather years. Thompson et al. (1996, p. 30) used the monthly mean of daily maximum temperature and the number of days of rainfall in excess of 1mm. Rajchard et al. (2006, p. 67) used average monthly temperature and rainfall in May, June and July. Therefore, while the impact of weather conditions in different geographical locations forces swifts to adapt their breeding behaviour to the local environment, the difference in the reporting of this impact may be in part caused by the inconsistencies of methods.

Indeed, regardless of the extensive nature of the current literature, there are still knowledge gaps in the breeding biology of the Common Swift, especially with regard to Ireland. Currently, there are no published studies detailing chick feeding frequencies throughout the entirety of the chick-rearing period for different types of broods. Some attempts were made to detail the daily activity of the parent swifts during the chick-rearing period, but the information published was either incomplete (Lack & Owen, 1955, p. 123), presented results from a small sample size (Carere & Alleva, 1998, p. 1385), or was not specific and lacked accuracy in results (Schaub, et al., 2016, p. 527). Additionally, there is currently little literature available on the phenomena of egg loss and consequently replacement clutches.

The current study recognised some of the significant gaps in knowledge in relation to the Common Swift and has thus presented comprehensive data on the breeding phenology of the species in Ireland, emphasising the arrival, egg-laying, hatching, fledging and departure dates. Moreover, the data on aspects of the breeding success, such as clutch size, brood size, productivity and fledging success, were also studied, informing how the climate in Ireland affects the breeding performance of the species. Additionally, it advances the methodology for studies of the chick feeding frequencies using a video recording analysis approach. The development of a novel equation that allows the study of the influence of weather conditions on the parental care for the entire colony, rather than an individual breeding pair was also employed. Therefore, for the first time, it was possible to study every feeding event during the breeding season at the Common Swift colony, detailing the hourly, daily and seasonal patterns and totals of feeds. This enabled a comprehensive study of the effects of weather characteristics on the levels of parental care of the species. This includes a study of how extreme weather events such as storms and heatwaves affect chick feeding behaviour. Additionally, the methodology of this study allowed for the first comprehensive study of the phenomena that is egg-loss – a behaviour that received little attention in previous studies. For the first time, the results of this study will provide evidence on the nature of egg loss for the Common Swift. This study intends to improve the understanding of the breeding cycle of the species and help better inform the conservation efforts of the species in Ireland and around the world.

This chapter has demonstrated that, while many aspects of the breeding biology of the Common Swift are well studied, there are still considerable gaps in the knowledge of the species, especially when it comes to swifts breeding in Ireland. The following chapter focuses on detailing the methodology that this research used, while attempting to fill some of the knowledge gaps mentioned.

Chapter 3: Methodology

3.1 Introduction

This chapter outlines the range of methods used in the course of this research to capture the data that will be analysed and discussed in the following chapter. It provides information on the two artificial colonies of the Common Swift selected for this study, lists the materials, hardware, and software used to gather data. This chapter outlines the methods that were used to study various aspects of the breeding biology of the study subject. Lastly, this chapter outlines the statistical techniques used to analyse the data gathered during this research.

3.2 Background

The design of this research is based on the use of artificial nest boxes fitted with cameras connected to recording equipment. In the past, studies of the breeding biology of the Common Swift were largely completed with the use of artificial nest boxes not fitted with cameras (Lack & Lack, 1951, p. 187; Perrins, 1971, p. 61; Shaub, et al., 2020, p. 164; Newell, 2019, p. 24; Wilson, 2011, p. 10). While studying the species is, in many aspects, difficult, the majority of Common Swifts nest in urban areas in man-made structures. Therefore, they are often quick to inhabit purpose-built nest boxes (Shaub, et al., 2020, p. 174). Moreover, in recent years, the installation of swift boxes has become somewhat popular due to quick nest uptake and relatively low maintenance, providing at the same time a suitable replacement for the loss of nest sites due to rapid modernisation of buildings (Luniak & Grzeniewski, 2011, p. 3). Furthermore, developments in camera technology now allow us to monitor nest boxes that may be hard to access and thus minimise the potential impact of human interaction that may be a cause for nest abandonment and subsequent breeding failure. Artificial nest boxes and cameras can be used to study many aspects of the breeding biology of birds, such as parental care, nest productivity, nest mortality causation and brood reduction (Zarybnicka, et al., 2016, p. 483). There is also the potential that the use of novel methods of nest monitoring, such as online streaming and video sharing, can contribute to research through citizen science. Both of these are characteristics of the current research.

3.3 Study area

The study was conducted at two locations in Ireland (Figure 5). The first location was on the site of the Galway-Mayo Institute of Technology (GMIT) Mayo Campus, in Castlebar, Co. Mayo (53° 52’ 14.976’’ N, 9° 18’ 6.264’’W, elevation 49m). The second location was at a private residence in Maguiresbridge, County Fermanagh (54° 18’ 32.33’’ N, 7° 25’ 34.33’’ W, elevation 10m). At both locations, Common Swifts nest in artificial nest box projects that began independently in 2012, led by the efforts of local swift conservation groups. The colony in Castlebar is located in an urban setting, with known natural and artificial swift nest colonies (Figure 6). By contrast, Maguiresbridge is located in a rural setting with a low swift population. (Figure 7). The nearest swift colony to Maguiresbridge is 10 kilometres away in Enniskillen The wider hinterland of both colonies is comprised mainly of farmland, predominantly livestock with low crop production. Both locations are close to large waterbodies, Lough Lannagh in the case of Castlebar and Lough Erne in Co. Fermanagh.

Figure 5. The geographical location of studied colonies in Castlebar and Maguiresbridge (Scribblemaps, 2021).

Figure 6. Location of the Castlebar colony within its immediate and extended surrounding areas. A) Satellite image showing Castlebar urban area and surrounds; B) Satellite image showing the Galway-Mayo Institute of Technology, Mayo Campus grounds. (Scribblemaps, 2021)**.**

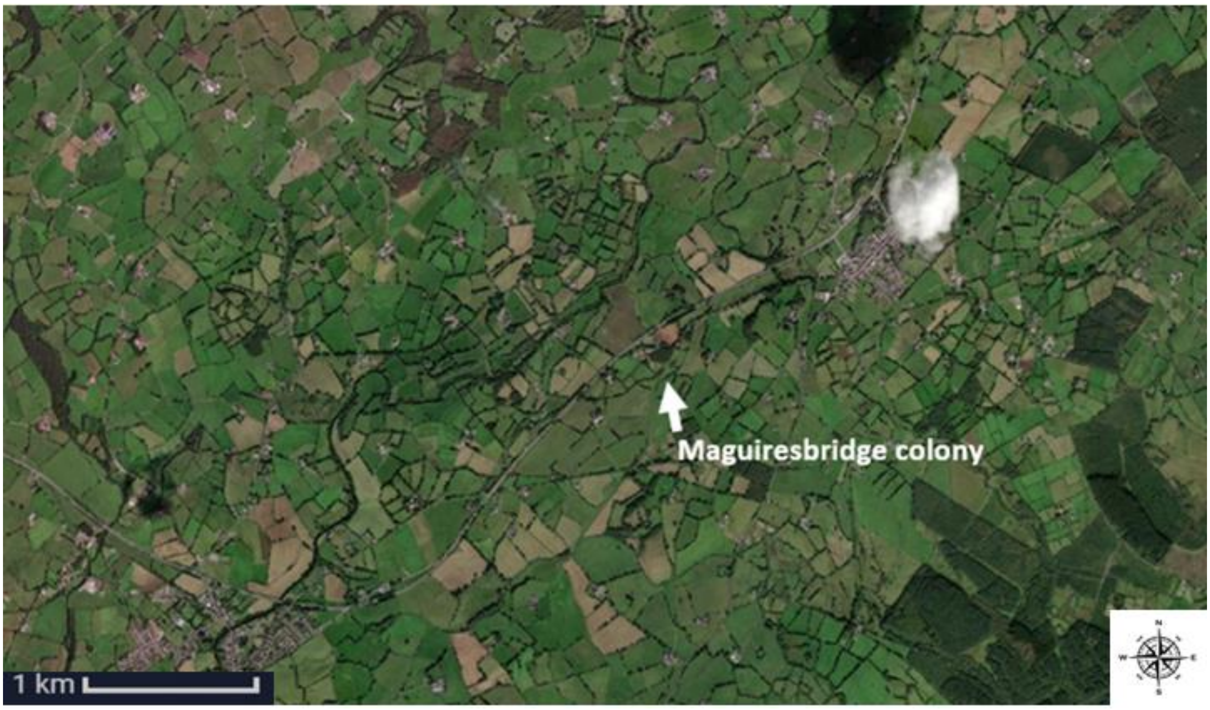


Figure 7. Location of the Maguiresbridge colony within its immediate and extended surrounding areas. A) Satellite image of the surrounding area of the Maguiresbridge colony; B) Satellite image of the immediate surrounding area of the Maguiresbridge colony.

In Castlebar, all 18 swift boxes are installed on one of the campus's northwest facing walls, under the eaves of the roof, at a height of 10 metres. The nest box project at Maguiresbridge comprised of 33 swift boxes and is located at a private residence – a two-storey family home, with 16 boxes facing west, 11 boxes facing south, and six facing east. All boxes in Maguiresbridge are installed at various heights ranging from four to six meters (Figure 8).

3.4 Materials, hardware, and software

The Castlebar colony uses a single style of nest box – the triple-entry 17A Schwegler swift nest box made out of woodcrete material. Between 2012 and 2018, the project used four triple-entry boxes, providing 12 nest cavities (Table 1). In 2019 two additional boxes were installed, bringing the total number of nests to 18. All nest cavities in Castlebar are uniform, although earlier installed boxes have a small and shallow nest cup (7cm diameter, 1.5cm deep). The newly installed boxes (2019) were not fitted with a nest cup to provide a future opportunity to compare the swifts' adaptation to boxes with and without artificial nest moulds.

The nest boxes in Maguiresbridge are of various sizes and dimensions and were fitted with three styles of nest cups (all of them deeper than those in Castlebar) (Figure 9). Since 2012, the property owner has increased the number of boxes each season in line, with the increase in swift occupancy. There are currently 33 nest cavities. Most of them (26) are the Model 16 Schwegler swift box, but seven were custom-built to fit the house's specification (Table 1).

At both colonies all of the swift boxes are equipped with infra-red cameras (Table 2). This enabled the continuous recording and storage of footage from inside the cavity, in addition to online streaming (Castlebar only). Cameras were installed at the entrance to the nest box with lenses pointed at the nest area, thus allowing the monitoring of changes in the nest with to-the-second precision. In the first phase of the project in Castlebar, the recording of the footage was carried out using four stationary (PC) computers and an Adobe Flash Media encoder (2015-2019). However, due to travel and access restrictions associated with the Covid-19 pandemic, the recording equipment was upgraded to two multi-channel digital video recorders (DVRs). This upgrade of the recording system required less daily maintenance and required less digital storage space. These changes had no adverse effect on the continuity of the research or the quality of the data. The cameras in Maguiresbridge were connected to two multi-channel DVRs provided by GMIT, but only for the 2020 season, as footage from previous years at the colony was not saved. The Castlebar colony as a result provided the most extensive set of recordings – approximately 120,960 hours which spanned the breeding seasons 2015 to 2020. As mentioned, the Maguiresbridge colony recorded and stored data from the 2020 season only, providing approximately 92,160 hours of footage.

The footage recorded at both colonies was viewed and analysed using a VLC Media Player and VSplayer (Table 2). Both applications allowed for precise and efficient analysis of footage using a 'skip by five seconds' command, backwards and forwards. Data from observations were compiled and stored in MS Excel sheets and partially analysed using PowerPivot, Power Query, and Data Analysis Expressions functionality. Subsequent statistical analysis of the data was completed with the XLSTAT 2021.3.1 package.

Table 1. Specifications of the nest boxes installed at both studied locations.

Specifications	Castlebar	Maguiresbridge
Number of nest cavities	18	33
Box type	6x 17A Schwegler swift nest box (Triple Cavity)	26x Model 16 Schwegler single cavity swift box, 7x boxes custom-made single cavities (dimensions unknown)
Dimensions	All: Internal: 14x14x30cm External: 15x15x98cm	26x Schwegler: Internal: 17x16x36 cm External: 24x22x43cm 7 x custom-made, various sizes
Nest mould	Boxes installed in 2012 (12 cavities) Size: 13.5x12 cm Nest cup: 1.5cm deep, diameter: 7cm Boxes installed in 2019 (6 cavities) No nest cups.	3 different nest cups: Old type: Size 12.5x12.5cm Nest cup: 2cm deep, diameter 8cm New type: Size: 12.5x12.5cm Nest cup: 2.5-3cm deep, diameter 9cm Custom-made: Nest cup: 2cm deep with steep sides.

Table 2. List of hardware and software used to stream, capture, and store the video footage from the nest boxes at the Castlebar and Maguiresbridge colonies. Not all equipment was used in both locations, and some changes were made during the 2020 season due to Covid-19 restrictions on travel and access to public institutions.

Cameras:	Green Feathers analogue (PAL/NTSC) 2.8mm wide-angle lens
Video digitising hardware:	SpyCamera USB Digitiser
Recording hardware:	2 Hikvision Turbo HD DVR 7200 Series, 16 and 8 channel, 6TB (2020) 4 Windows desktop PCs (2018-2019)
Recording software:	Adobe Flash Media Encoder (2018-2019)
Video encoding software:	VLC (2018-2019) VSplayer (2020)
Recording format:	640x480 MP4
External HDD:	WD Elements, Seagate, Maxtor M3 Portable (1TB, 2TB, 4TB).

Figure 8. Visual representation of the swift boxes at both studied locations. Top left: All nest cavities at GMIT Mayo Campus in Castlebar facing north-west; Top right: Maguiresbridge swift boxes facing west; Bottom left: Maguiresbridge swift boxes facing east; Bottom right: Maguiresbridge swift boxes (some custom-made) facing south.

Figure 9. Visual representation of the different nest moulds installed in the nests. Top left: nest moulds in Castlebar (12 out of 18 boxes); Top right: nest moulds installed in most of the nest boxes at Maguiresbridge; Bottom left: nest mould installed at Maguiresbridge in six custom-made boxes; Bottom right: nest moulds that were in use in the nest boxes at Maguiresbridge in the early years of the project and are still in place in several boxes.

3.5 Observations

This research project began in 2019, but many aspects of the data collection process utilised recordings and data gathered since 2014. A significant part of this investigation into the breeding biology of the Common Swift in Ireland is based on observations and notes from people who managed the two colonies studied. Lynda and Chris Huxley provided notes, footage and partial analysis for the Castlebar colony between 2014 and 2018. John Young provided notes from the years 2014 to 2020 and managed video recording in 2020 in Maguiresbridge.

The recording equipment used at the nest boxes permitted streaming and recording of in-nest behaviours throughout the entirety of the breeding season. The footage was recorded from all nests during the research period in Castlebar, and in the 2020 season in Maguiresbridge. Each year, recording commenced in mid-April in anticipation of early arrivals and continued until the last swift left the nest; in most years, this was early to mid-September. Initially, it was planned for this study to focus on providing results only from observing the colony in Castlebar, and the work of collecting the data was already in progress when the opportunity arose to add a data set from Maguiresbridge. Therefore, not all aspects of breeding biology were studied to the same degree at both colonies. However, the colony in Maguiresbridge provided enough meaningful data to be included, in particular the key dates, productivity, and egg loss footage, thus providing a useful comparison with the site in Castlebar. Each year, several nests at both colonies were occupied by swifts that did not lay a clutch. Recordings from those nests were not analysed.

All aspects of the breeding biology of the Common Swift were studied as part of the video analysis. Approximately 28,800 hours of recorded footage was viewed and analysed (approx. 22,500 hours of breeding attempts in Castlebar, plus an additional 5,500 hours of additional footage from Castlebar and Maguiresbridge). Footage recorded between 2015 and 2017 in Castlebar was partially analysed by students of GMIT and Lynda Huxley. However, most of the footage analysed for this research was recorded between 2018 and 2020 in Castlebar, 2020 in Maguiresbridge, and analysed by the author. To summarise, 19 breeding seasons were studied, giving a total of 1480 days (24 hour periods) of footage analysis. As 24 hours of footage took approximately 90 minutes of real-time to analyse, the author spent approximately

2220 hours studying the videos (or about 277.5 8-hour working days). Additionally, approximately 200 hours were spent maintaining the recording equipment and transferring the video files from the recording equipment to external hard drives.

3.5.1 Breeding calendar

The first major aspect of the study was to provide a detailed breeding calendar of the Common Swift in Ireland and measure egg productivity at both colonies. This was achieved by detailing the following parameters:

a) Arrival dates of the breeding swifts – defined by the observation of the first night roosting in the nest. The arrival dates of both adults were recorded to determine the breeding pair assembly date.

b) Nest material collection period – defined as the interval between the arrival of the second swift in the nest and the laying date of the first egg.

c) Egg-laying dates – recorded after visual evidence of the first and following eggs in the clutch.

d) Hatching dates – the first observation of chicks in the nest. In some cases, when day- or two-day-old hatchlings were not visible due to a deep nest cup, the hatching date and age of the brood were determined by the observation of the onset of feeding behaviour.

e) Fledging dates – noted by the chicks' absence from the nest.

f) Departure dates – recorded when one or two adult swifts were not present in the nest at night.

3.5.2 Breeding success

The second aspect of this study was recording the size of the clutch, and consequential number of hatchlings and fledglings in each of the studied nests. Egg productivity was calculated as a ratio of eggs laid to successful fledglings per breeding pair. Productivity was used to determine the overall breeding performance of the colonies. (Ricklefs, 1973, p. 87).

Egg productivity equation:

$$Productivity = \frac{Number\ of\ eggs\ laid}{Number\ of\ fledglings} \qquad (1)$$

3.5.3 Patterns of feed frequencies

The third aspect of the study was monitoring the timing, frequency and pattern of the swifts daily feeding. To achieve this, footage from the 19 breeding attempts in the colony in Castlebar was selected based on the following criteria: (a) that the breeding attempt was successful, with at least one chick hatched and fledged from the nest; (b) that footage from the entirety of the breeding season was intact, with no gaps in recordings; (c) the nest cup was clearly visible throughout the whole season, meaning that any footage where the camera lens was moved or became dirty was eliminated.

Seasonal and daily patterns of food provision to chicks are critical in understanding birds' foraging strategies and adaptations (Royama, 1966, p. 313). Those strategies may be affected by external factors such as adverse weather conditions, leading to decreased feeding frequency and chicks' mortality due to a lack of nutritional support. Weather can affect the adult birds' ability to forage in two ways: directly, by changing energy requirements in low or high temperatures, and the effort needed to catch insects in calm weather or strong winds; or indirectly, by reduction or increase of food availability, and possibly forcing a change in prey preference and/or influencing a change in the choice of the feeding area (Finney, et al., 1999, p. 29). Analysis of the feeding frequencies does not account for the quality or size of the bolus delivered to the chicks, therefore providing an imperfect model for measuring parental care levels in birds (Royama, 1966, p. 313). However, while the variation in the size of the bolus and its nutritional value must be acknowledged, the number of visits to the nests is often used as a measurement of food provision to chicks of cavity-nesting birds such as tree swallows (McCarthy, 2002, p. 13).

The study of seasonal and daily patterns of feeding and other aspects of parental care during the chick-rearing period were measured through analysis of the following parameters:

a) Monitoring the age of the brood – since, in most cases, the hatching date was hard to determine just with the use of video footage, the age of the brood was calculated from the date of the first observed feed.

b) Detailing the presence of the adult swifts in the nest. Each change in presence was time-coded and this allowed the measurement of total daily brooding time.

c) Analysis of the adult swifts' visits to the nest – each visit was marked as either 'feed,' where there was clear evidence of food exchange between adult and chick, or 'no-feed' when feeding did not take place.

An analysis of adult visits to the nest was completed for all 19 selected breeding attempts throughout the entire chick-rearing period. This allowed the determination of patterns in feed frequencies with regards to the age and the size of the brood. Studies suggest that a chicks' feeding patterns can be influenced by the weather (Lack & Owen, 1955, p. 123; Winkler & Luo, 2013, p. 130). To determine if this assertion is true for the Common Swift, the number of daily feeds can be used to measure a response to changing weather variables such as rainfall, wind, and temperature. The influence of this external force on swifts' behaviour is yet to be understood, especially when it comes to measuring the colony's response as a whole, as opposed to that of an individual nest. All nesting swifts at the colony are experiencing the same weather; therefore, this study concentrates on presenting the influence of weather on the total number of feeds in the colony, rather than analysing each of the breeding pairs' responses individually. While it is known that the Common Swift may fly a very long distance to forage, perhaps to avoid some unfavourable weather at the nest location, this research is focused on their response only to local conditions.

The total number of feeds in the colony on a given day can be calculated as the sum of all observed feeds in all nests. However, daily feeds alone cannot be used to measure the influence of external factors such as weather, because this number does not indicate whether feeds on a particular day are high or low. The total daily number of feeds at the colony is dependent on the number of nests with chicks and sizes of individual broods. Additionally, as noted in the previous section, the number of daily feeds depends on the age of the brood (calculated from the first observed feed). Therefore, by knowing how many nests are occupied and the sizes and ages of the broods, it is possible to calculate the expected number of feeds at the colony on a particular day during the breeding season, based on the average daily feeds data collected during the three-year research period. As a result, two numbers were generated:

- EXP_{feeds} = Expected Number of Daily Feeds at the colony; based on the average number of feeds per day considering the size and age of the brood.
- ACT_{feeds} = Actual Number of Daily Feeds at the colony; based on the total number of feeds recorded each day.

The percentage difference between ACT_{feeds} number and EXP_{feeds}, provided a measure of the change in the chicks' feeding behaviour at the colony – delta of actual to expected feeds at the colony (DAX):

DAX equation:

$$\Delta\left(\frac{ACTfeeds}{EXPfeeds}\right) = (1 - (EXP_{feeds} - ACT_{feeds})/EXP_{feeds}) - 1 \tag{2}$$

This equation allowed for the calculation of the ratio between the actual recorded number of feeds at the colony on all relevant dates during the study period and the predicted number of feeds that should occur at the same colony with the same number of chicks at the same age (measured from the first observed feed). The author developed the proprietary delta equation for the purpose of this research and it will be from this point referred to as DAX.

3.5.4 Egg loss

The fourth aspect of the study was to analyse the issue of egg loss, which was observed to a large degree at both sites. This issue was commonly noted in previous studies (Lack, 1956, p. 77; Pichorim, 2011, p. 189; Nguyên Quang, et al., 2006, p. 391; Rowley & Orr, 1965, p. 364). However, the reason for this phenomenon remains unclear. Therefore, this part of the research was designed to analyse every recorded egg loss event recorded in Castlebar and Maguiresbridge. This was achieved by undertaking a detailed analysis of each egg loss event, including a visual determination of its nature, indicating whether the behaviour was intentional or accidental. (Cutcliffe, 1951, p. 26; O'Connor, 1979, p. 136).

3.6 Statistical analysis

Statistical analysis was performed in MS Excel with the use of the XLSTAT 2021.3.1 package. In all tests, the significance level (α) was 0.05. The data from Castlebar and Maguiresbridge provided mean (or median) yearly data for each of the studied breeding parameters for both colonies and produced a total mean (or median) for each of the colonies across a period of seven seasons (2014-2020). As the colony occupation grew each year, the number of samples for all variables was different with each recorded season. Therefore, a one-way ANOVA Kruskal-Wallis *H* test was used to assess the variance level between breeding seasons (Sokal & Rohlf, 1969, p. 423). If any stochastic dominance of any sample was found at a significance level (α) of 0.05, a post hoc Dunn’s test was used to determine which year’s sample was different from any others. A General Linear Model II was used to analyse the relationship between two independent variables, such as the influence of weather on different breeding biology parameters (Sokal & Rohlf, 1969, p. 543). Spearman’s rank correlation was used to measure monotonic relationships between dependent variables, such as number of daily feeds with the age of chicks.

3.7 Conclusion

The goal of the preceding chapter was to outline the methods used in this research. This includes descriptions of the studied colonies, materials and hardware used during the study. Outlined here was a detailed description of the approach used to gather data on each aspect of the breeding biology of the Common Swift and the statistical approach to data analysis. Some elements of the methodology used during this research were proprietary and aimed to develop novel methods of research into birds’ breeding biology. These include applying the video analysis method and developing the DAX equation that allowed for the studying of the swifts colony response to weather conditions. The goal of Chapter 4 is to provide the results of this study and validate the use of the methodology outlined in this chapter.

Chapter 4: Results

4.1 Introduction

This chapter presents the results of data collection undertaken in Castlebar and Maguiresbridge using methods outlined in Chapter Three. Over the duration of this research (2014-2020), a total of 128 breeding attempts were studied at two colonies: 40 in Castlebar and 88 in Maguiresbridge. Data from all 128 breeding attempts were used to describe the phenological calendar of the Common Swift in Ireland. For the study of feed frequencies and other aspects of parental care, the video footage recorded from 19 breeding attempts in the Castlebar colony was analysed: six nests from 2018; six nests from 2019; and seven nests from 2020. This step required the analysis of approx. 28,500 hours of footage. For the study of egg loss, footage recorded during the incubation period of 47 breeding attempts was analysed: 24 nests from Castlebar (2018-2020) and 23 nests from Maguiresbridge (2020). Taking into account the overall, number of breeding attempts observed during the study, a total of 300 eggs were laid, 39 egg ejected, 244 chicks fledged, and 17 chick mortalities were recorded.

4.2 Population of studied colonies

In Castlebar, the first 12 boxes were installed in 2012. The nest box project included a speaker system that played swift vocalisations to enthise the swifts to explore the new nesting opportunities. The first breeding pairs were observed in 2014 (Table 3). The colony in Maguiresbridge began with three boxes in 2013, with an additional four boxes added in 2014. In the same year, the first breeding pairs were confirmed in Maguiresbridge (Table 4). At both sites, the number of breeding pairs grew each season between 2014 and 2020 (Table 5a). In Castlebar, the number of breeding pairs increased by one or two each year. In contrast, the colony in Maguiresbridge grew at a higher rate, increasing by two to five breeding pairs per season (Table 5b). At the end of the research period, when the number of breeding pairs to available nest cavities was compared, the level of occupancy at Maguiresbridge was higher than in Castlebar by 19.7%. Once a nest box hosted a breeding pair, there was a high probability that the same box saw a breeding attempt in the following years. This took place in seven out of eight nest boxes in Castlebar and 17 out of 19 boxes in Maguiresbridge (some boxes were occupied for the first time during the last year of the research and excluded from this observation). Two boxes in Castlebar and three in Maguiresbridge were occupied throughout the entirety of the studied period (seven years).

Table 3. The population of the colony in Castlebar during the study period. B.P – breeding pair, Non/B.P. – non-breeding pair. The greyed-out areas show nest boxes that were not yet installed.

Castlebar

	2014	2015	2016	2017	2018	2019	2020
Box 1	B.P.	B.P.	B.P.	B.P.	B.P.	B.P.	B.P.
Box 2						B.P.	B.P.
Box 3							Non/B.P.
Box 4							Non/B.P.
Box 5			B.P.	B.P.	B.P.	B.P.	B.P.
Box 6							Non/B.P.
Box 7					B.P.	Non/B.P.	B.P.
Box 8					Non/B.P.	B.P.	B.P.
Box 9				B.P.	B.P.	B.P.	B.P.
Box 10			B.P.	B.P.	B.P.	B.P.	B.P.
Box 11		B.P.	B.P.	B.P.	B.P.	B.P.	B.P.
Box 12	B.P.	B.P.	B.P.	B.P.	B.P.	B.P.	B.P.
Box 13							
Box 14							
Box 15							
Box 16							
Box 17							
Box 18							Non/B.P.

Table 4 The Population of the colony in Maguiresbridge during the study period. B.P – breeding pair, Non/B.P. – non-breeding pair. The greyed-out areas show nest boxes that were not yet installed.

Maguiresbridge

	2014	2015	2016	2017	2018	2019	2020
Gable 2	B.P.	B.P.	B.P.	B.P.	B.P.	B.P.	B.P.
Gable 3		B.P.	B.P.	B.P.	B.P.	B.P.	B.P.
Gable 4	B.P.	B.P.	B.P.	B.P.	B.P.	B.P.	B.P.
Gable 5			B.P.	B.P.	B.P.	B.P.	B.P.
Gable 6			B.P.	B.P.	B.P.	B.P.	B.P.
Gable 7	B.P.	B.P.	B.P.	B.P.	B.P.	B.P.	B.P.
Gable 8							
Gable 9							Non/B.P.
Gable 10						B.P.	B.P.
Gable 11						Non/B.P.	B.P.
Gable 12				B.P.	B.P.	B.P.	B.P.
Gable 13							
Gable 14							B.P.
Attic 15							
Attic 16				B.P.	B.P.	B.P.	B.P.
Eaves 1					B.P.	B.P.	B.P.
Eaves 2							
Eaves 3			B.P.	B.P.	B.P.	B.P.	B.P.
Eaves 4							Non/B.P.
Eaves 5			B.P.	B.P.	B.P.	B.P.	B.P.
Eaves 6					B.P.	B.P.	B.P.
Eaves 7				B.P.	B.P.	B.P.	B.P.
HI Eaves 1					B.P.	B.P.	B.P.
HI Eaves 2							
HI Eaves 3							
HI Eaves 4							
Back 8				B.P.			B.P.
Back 9							
Back 10					B.P.	B.P.	B.P.
Back 11				B.P.			B.P.
Back 12						B.P.	B.P.
G. Attic							B.P.

Table 5. A) Yearly population numbers of breeding pairs at the colony in Castlebar (2014-2020); B) Yearly population of breeding pairs at the colony in Maguiresbridge (2014-2020).

A. Castlebar, County Mayo

Year	Total number of nest cavities	Number of breeding pairs	% Occupancy	Yearly growth %
2014	12	2	16.7	
2015	12	3	25.0	50
2016	12	5	41.7	67
2017	12	6	50.0	20
2018	12	7	58.3	17
2019	18	8	44.4	14
2020	18	9	50.0	13

B. Maguiresbridge, County Fermanagh

Year	Total number of nest cavities	Number of breeding pairs	% Occupancy	Yearly growth %
2014	7	3	42.9	
2015	13	5	38.5	67
2016	14	9	64.3	80
2017	30	14	46.7	56
2018	30	16	53.3	14
2019	30	18	60.0	13
2020	33	23	69.7	28

4.3 Breeding Calendar

4.3.1 Arrivals

During the study period, 80 individual arrivals of breeding Common Swifts were recorded in Castlebar, and 176 in Maguiresbridge. The earliest arrival of a breeding swift was recorded in Castlebar on 25 April 2020, two days before the arrival of the second bird (Table 6A). In Maguiresbridge, the earliest arrival took place on 27 April 2020 (Table 6B). The mean time of arrivals for the whole of the study period was 13 May (se±1.04, n=80) in Castlebar, and 13 May (se±0.66, n=176) in Maguiresbridge.

Arrival dates in the last week of April are rare (Castlebar 2.5%; Maguiresbridge 2.27%), and the majority of swifts arrive back in their nests in May (Castlebar 92.5%; Maguiresbridge 91.48%). The remaining breeders returned in early June (Castlebar 5%; Maguiresbridge 6.25%) (Figure 10). The latest arrival of a swift that attempted to breed was on 4 June 2017 in Castlebar, but this attempt was unsuccessful. At Maguiresbridge, one swift that arrived on 11 June 2015 and was able to breed producing one hatchling that season.

Table 6. Arrival dates of breeding birds in Castlebar (A) and Maguiresbridge (B).

A. Castlebar

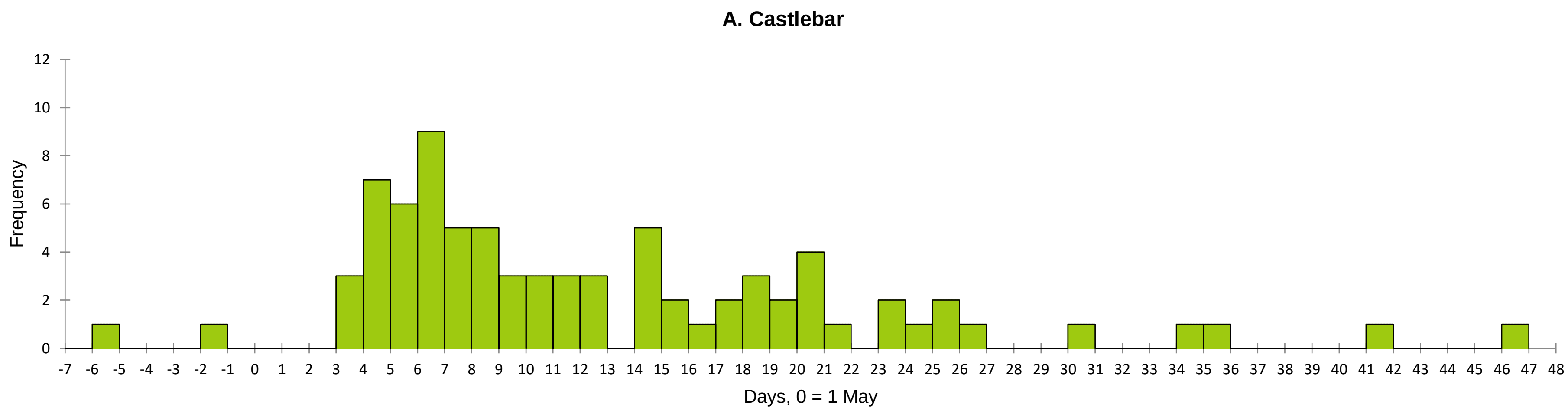
Year	n	Earliest breeding swift arrival	Latest breeding swift arrival	Mean date of arrival	SE±
2014	4	15 May	19 May	16 May	0.87
2015	6	06 May	13 June	18 May	5.60
2016	10	06 May	04 June	15 May	2.99
2017	12	05 May	05 June	13 May	3.35
2018	14	07 May	24 May	17 May	1.37
2019	16	07 May	31 May	12 May	2.99
2020	18	25 April	26 May	07 May	1.72

B. Maguiresbridge

Year	n	Earliest breeding swift arrival	Latest breeding swift arrival	Mean date of arrival	SE±
2014	6	08 May	13 May	10 May	0.80
2015	10	08 May	14 May	14 May	2.57
2016	18	04 May	11 June	14 May	1.95
2017	28	04 May	02 June	12 May	1.97
2018	32	08 May	04 June	15 May	1.42
2019	36	30 April	04 June	14 May	1.28
2020	46	27 April	01 June	11 May	1.36

The seven-day frequency breakdown of all arrivals during the observational period at both colonies showed that over half of swift returns (Castlebar 58.75%, Maguiresbridge 62.5%) took place in the first two weeks of May. By the end of the fourth week of the same month, the colonies were almost all assembled, with fewer than one-tenth of arrivals occurring after 29 May (Castlebar 6.25%; Maguiresbridge 7.39%).

The timing of most arrivals falls into the same period each breeding season, and is always between the last week of April and the first week of June. The mean arrival date fell into the second week of May for most years studied. Exceptions to this were recorded twice in Castlebar. During the 2015 season (μ=19 May, se± 5.60, n=3), the results were skewed by small population size. The second exception occurred in 2020 (μ=07 May, se± 1.72, n=18), when most swifts returned early compared with other years (Kruskal-Wallis test: x^2=21.89, p=0.0013, α=0.05). Statistical analysis of the Maguiresbridge recordings revealed that the mean dates of arrival did not differ in any year with the exception of 2020 (μ=11 May, se± 1.36, n=46), when the arrival of the swift occurred earlier than in any other year. (Kruskal-Wallis test: x^2 =14.75, p=0.022 0.0013, α=0.05).



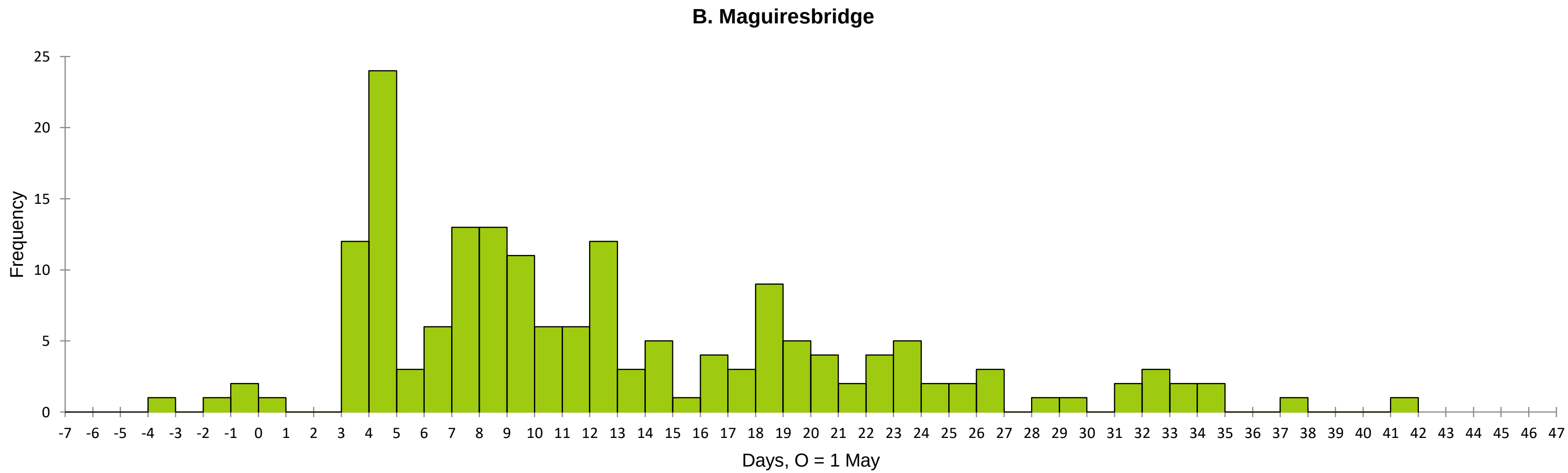


Figure 10. Frequency distribution of all arrival events (2014-2020

Arrivals of both swifts (in a breeding pair) on the same day occurred only in 7.5% (n=40) of observations in Castlebar and 10.2% (n=88) in Maguiresbridge. The earliest recorded pair in a nest was 4 May 2020 in Castlebar and 1 May 2019 in Maguiresbridge. In 4% (n=40) of arrivals in Castlebar and 7.95% (n=88) at Maguiresbridge, the second swift appeared in the first or second week of June. In some of those records, there was a two- to four-week gap between the arrival of the first and second birds. There was no significant difference in the mean of pair assembly dates at the colonies between 2014 and 2020 (Kruskal-Wallis test: Castlebar: x^2=7.25, p=0.298, α=0.05; Maguiresbridge: x^2=9.90, p=0.129, α=0.05).

4.3.2 Interval between the pair assembly and first egg.

The breeding pair would lay their first egg on average 11 days (se± 0.79) in Castlebar and 10 days (se± 0.41) in Maguiresbridge after the second bird arrived in the nest. In Castlebar, the shortest gap between the two events was four days, and the longest 28 days. In Maguiresbridge, the shortest recorded interval was three days, and the longest 29 days. There was no significant difference in the average length of a time between pair assembly and first egg in any of the surveyed seasons at the colonies (Kruskal-Wallis test: x^2=3.806, p=.703, α=0.05; Maguiresbridge: x^2=11.117, p=.085, α=0.05).

4.3.1 Egg laying dates

In the Castlebar colony, the average date of first egg in all breeding attempts during the study period (2014-2020) was 26 May (se±1.65, n=40) (Table 7A). The earliest laid egg in all studied years was on 10 May 2020. The latest clutch was laid on 24 June 2019 (exclusive of replacement clutches). In total, 95% (n=36) of first eggs were laid between 14 May and 12 June (Figure 11A). There was no significant difference in mean dates during the years studied (Kruskal-Wallis test: x^2=8.935, p=0.177, α=0.05). The late mean of first egg-laying in 2015 was skewed by the low population number. The remaining years saw the mean dates fixed in the last two weeks of May. A small number of pairs laid their clutch in June, but never later than the third week of that month. However, when we take replacement clutches into consideration, the last laid egg in any year in Castlebar was laid on 30 June (two nests in 2018). No instances of egg laying was recorded in July.

4.3.2 Egg laying dates

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Table 7. Yearly mean date of the first egg laid in Castlebar (A) and Maguiresbridge (B).

A. Castlebar

Year	n	First egg mean date	SE±
2014	2	25/05/2014	1.41
2015	3	9/06/2015	6.62
2016	5	26/05/2016	4.35
2017	6	20/05/2017	2.19
2018	7	19/05/2018	1.33
2019	8	29/05/2019	4.49
2020	9	30/05/2020	5.65

B. Maguiresbridge

Year	n	First egg mean date	SE±
2014	3	2/06/2014	3.27
2015	5	28/05/2015	3.79
2016	9	27/05/2016	2.25
2017	14	23/05/2017	2.94
2018	16	29/05/2018	1.84
2019	18	26/05/2019	1.87
2020	23	23/05/2020	2.02

At Maguiresbridge, the earliest laid egg in the studied season was on 11 May 2020 (Figure 11A). The latest clutch was laid the 25 June 2019 (excluding replacement clutches). In terms of recorded dates of the first eggs, 93% (n=82) were laid between the 14 May and the 15 June. The mean date of the first egg at Maguiresbridge in the years between 2014 and 2020 was the

27 May (SE± 1.01, n=88) (Table 7b). To compare the mean values of the first egg dates in the nest from all of the years studied, Kruskal-Wallis test was used. The results revealed that there was a difference in mean dates during the studied years (x^2=15.824, p=0.015, α=0.05). A post hoc Dunn's test revealed only significant difference was measured between the hatching data from 2017 and 2018.

The late mean of first egg-laying in 2014 was skewed by the low population number and is therefore not regarded as significant. Between 2015 and 2020, the mean laying date fell between 23 and 29 May. In June, 35.22% (n=31) of the swift pairs at Maguiresbridge began egg incubation, while only 27.5% (n=11) at Castlebar did so in this month. In 2017, one pair of swifts in Castlebar attempted to lay their first egg very late, on 25 June, but failed to incubate the clutch.

4.3.3 Hatching and fledging dates

The average timing of all hatchings for the colony in Castlebar in the years 2014-2020 was 22 June (se± 1.72, n=61) (Table 8). The earliest hatchling in a season was recorded on 2 June 2016, and the latest on 21 July 2018 (49 days difference). The earliest record of a swift chick leaving the nest was on 16 July, and the latest on 28 August, both of which occurred in 2018 (Figure 12). The mean date of fledging at the colony was 3 August (se± 1.79, n=56). There was no statistical difference between the seasonal means of fledging dates (x^2=7.92, p=0.244, α=0.05) or fledging numbers each season (x^2=2.059, p=0.914, α=0.05).

Table 8. The mean dates of hatching and fledging in each studied season (2014-2020)

Castlebar

	Hatching (all eggs)			Fledging (all chicks)		
	n	Mean Date	se±	n	Mean Date	se±
2014	4	16/06/2014	1.12	4	27/07/2014	0.41
2015	4	24/06/2015	3.75	2	14/08/2015	1.06
2016	6	16/06/2016	3.90	5	27/07/2016	2.96
2017	9	16/06/2017	1.97	6	28/07/2017	2.33
2018	13	02/07/2018	4.15	12	10/08/2018	4.18
2019	12	21/06/2019	3.78	12	01/08/2019	3.87
2020	14	23/06/2020	4.02	12	05/08/2020	4.04

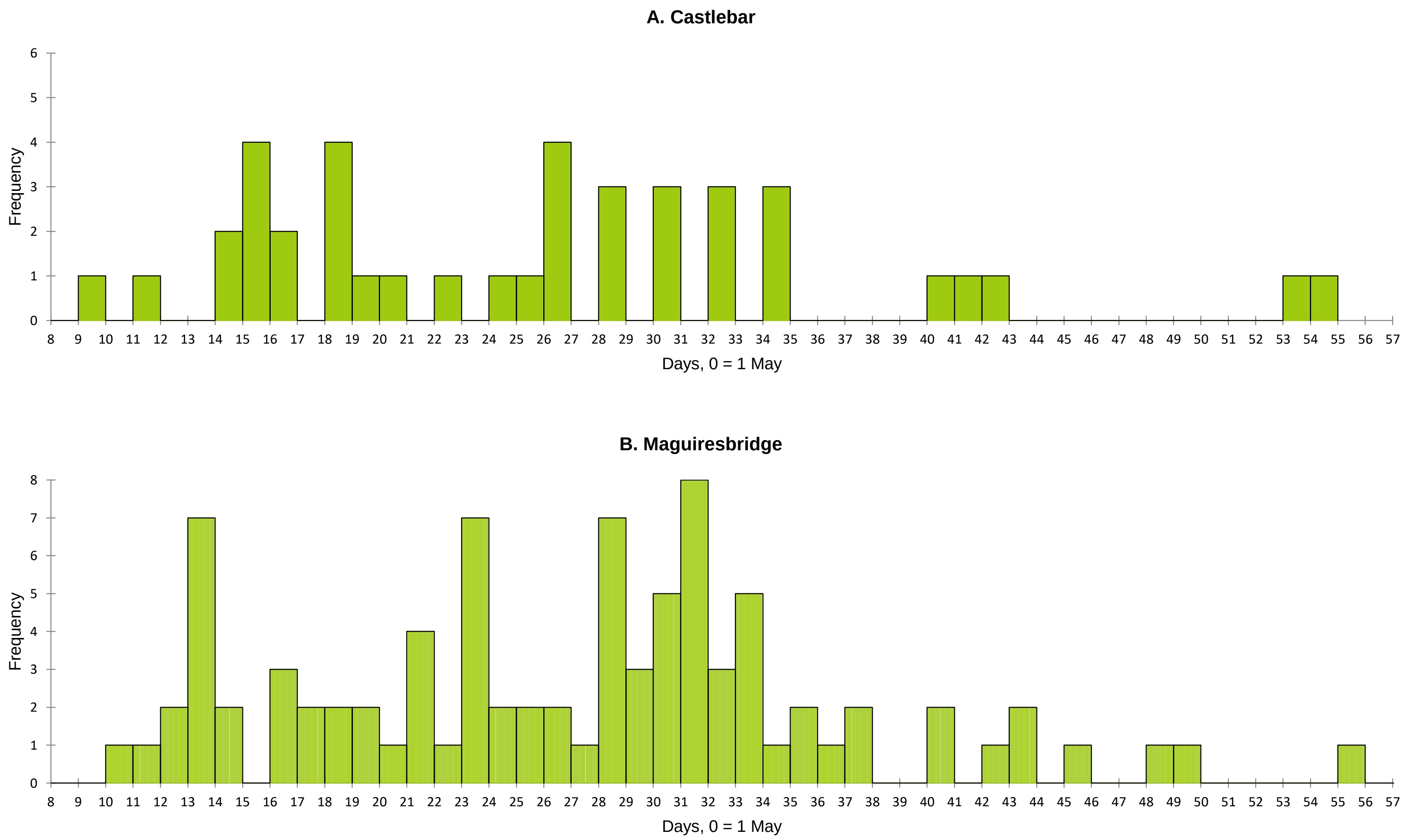


Figure 11. Timing frequency of the first egg in the clutch during the study period (2014-2020)

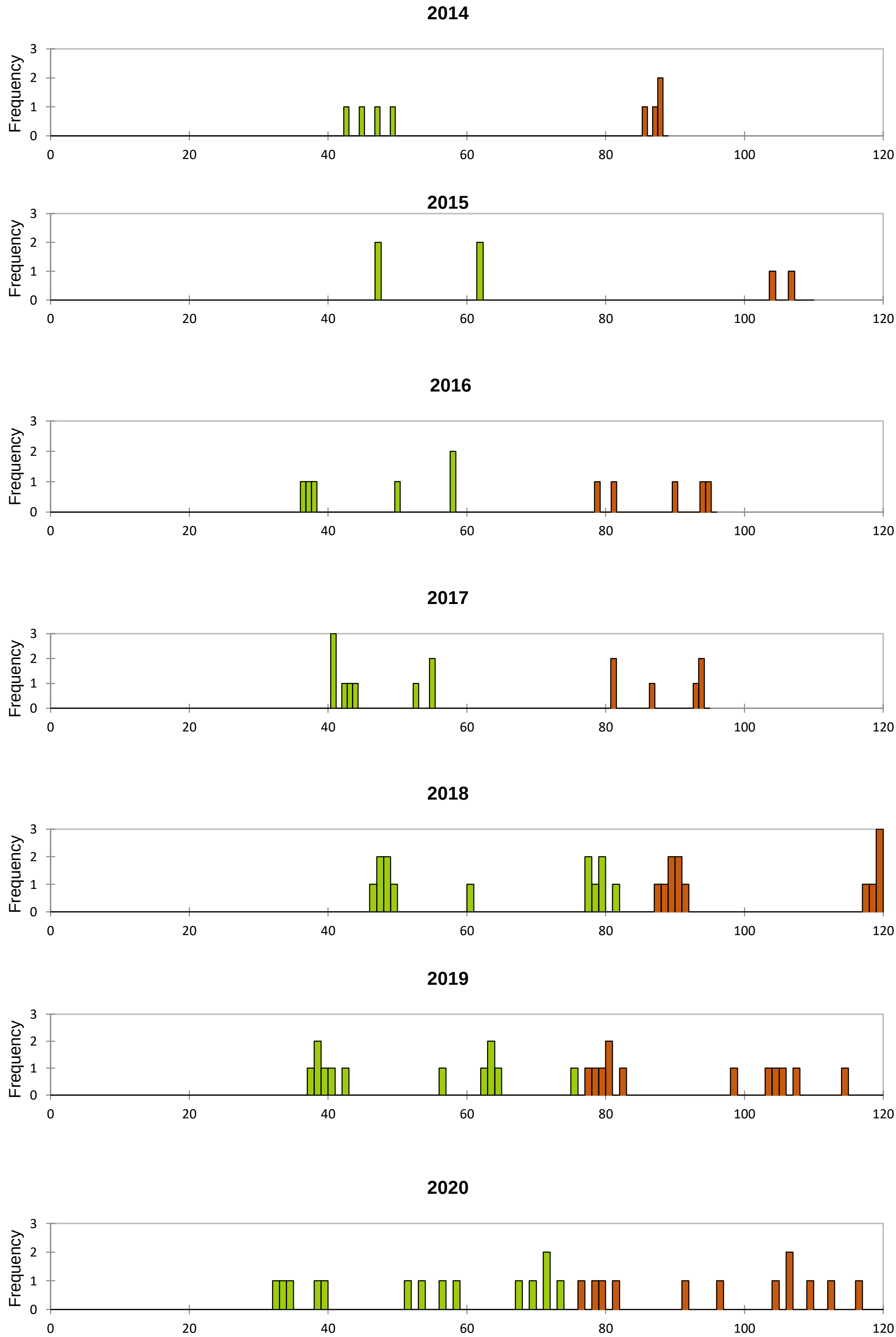


Figure 12. Frequencies of all hatching (green) and fledging (dark orange) events in Castlebar**.**

The earliest hatching at Maguiresbridge took place on 14 June 2020 and the latest on 7 July 2019. The mean hatching date for the whole population of the Maguiresbridge swift colony was 16 June (se± 0.58) (Table 9). The statistical test results concluded that the mean hatching dates in 2020 and 2017 were different from previous seasons (Kruskal-Wallis, x^2=19.310, p-value= 0.004, α=0.05).

The average timing of fledging in Maguiresbridge was 27 July (se± 0.64). The earliest fledging was recorded on 15 July in 2020 and the latest on 22 August 2019 (Figure 13). There was a slight variation in the mean of yearly hatching dates in 2017 and 2018 (Kruskal-Wallis, x^2=12.592, p-value= 0.002, α=0.05).

Table 9. The mean dates of hatching and fledging in each studied season (2014-2020)

Maguiresbridge

	Hatching (all eggs)			Fledging (all chicks)		
	n	Mean Date	se±	n	Mean Date	se±
2014	4	26/06/2014	3.38	4	04/08/2014	3.38
2015	11	19/06/2015	2.20	11	31/07/2015	2.73
2016	17	15/06/2016	1.56	16	27/07/2016	1.97
2017	32	13/06/2017	1.74	29	22/07/2017	1.39
2018	35	18/06/2018	1.18	35	30/07/2018	1.20
2019	41	16/06/2019	1.16	40	27/07/2019	1.22
2020	57	12/06/2020	1.18	51	24/07/2020	1.38

There was a significant difference between the two observed colonies when it came to the timing of hatching (Figure 14). In all of the studied years, the average timing of hatching and fledging took place earlier in the season in Maguiresbridge. The only exception during the study was recorded in 2014 when a small population number skewed the result. The average timing of all 61 hatching events throughout the whole study period in Castlebar (μ = 22 June, sd = 14.2) compared to the average timing of 197 hatching events in Maguiresbridge (μ = 15 July, sd = 8.6) took place much later (Independent T-test, t(256) = 4.8, p < 0.0001). Similarly, the average timing of all 53 fledging events in Castlebar (μ = 3 August, sd = 13.1) compared to the average timing of 186 fledging events in Maguiresbridge (μ = 26 July, sd = 8.8) was also recorded as occurring later in the season (Independent T-test, t(237) = 4.8, p < 0.0001).

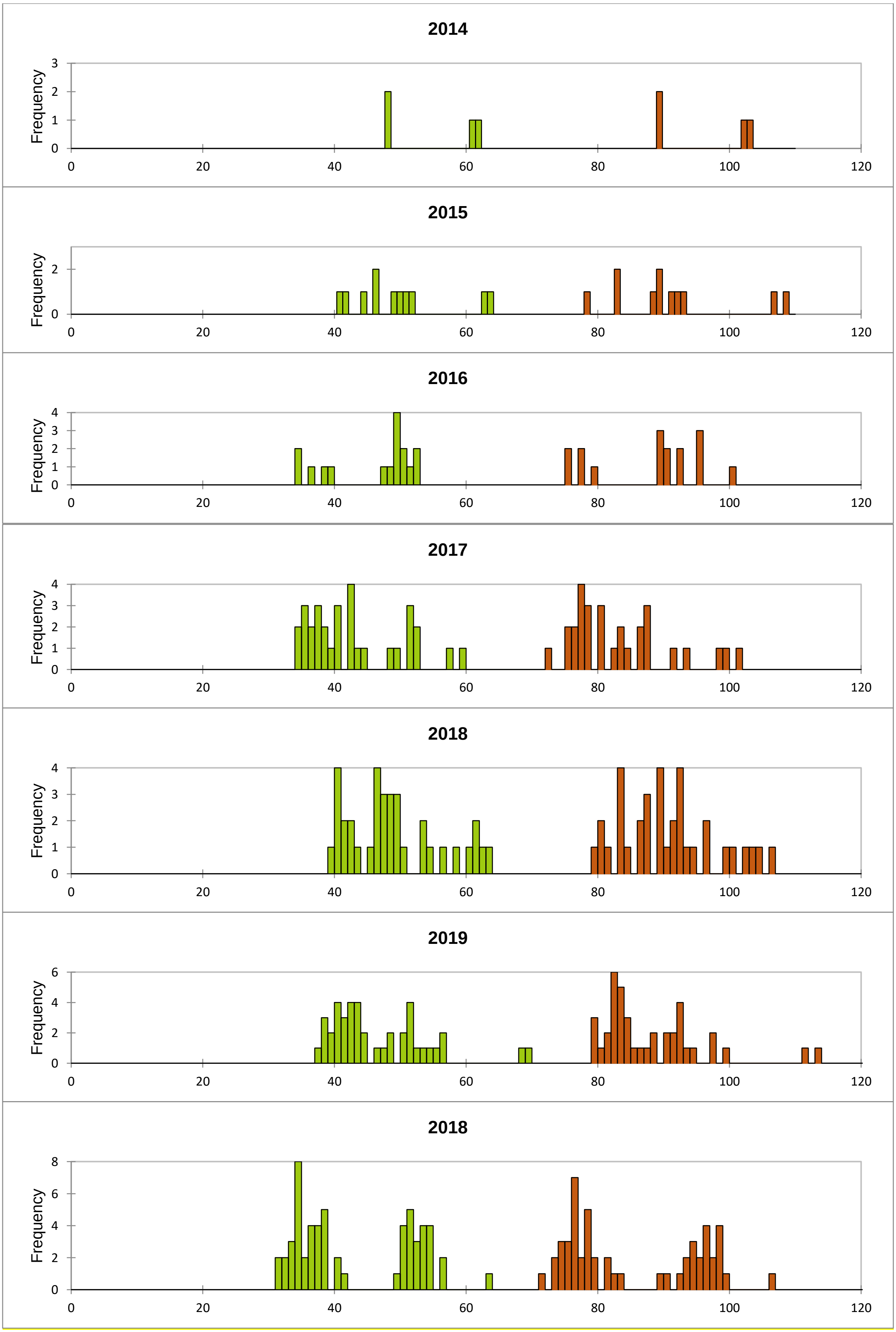


Figure 13. Frequencies of all hatching (green) and fledging (dark orange) events in Maguiresbridge.

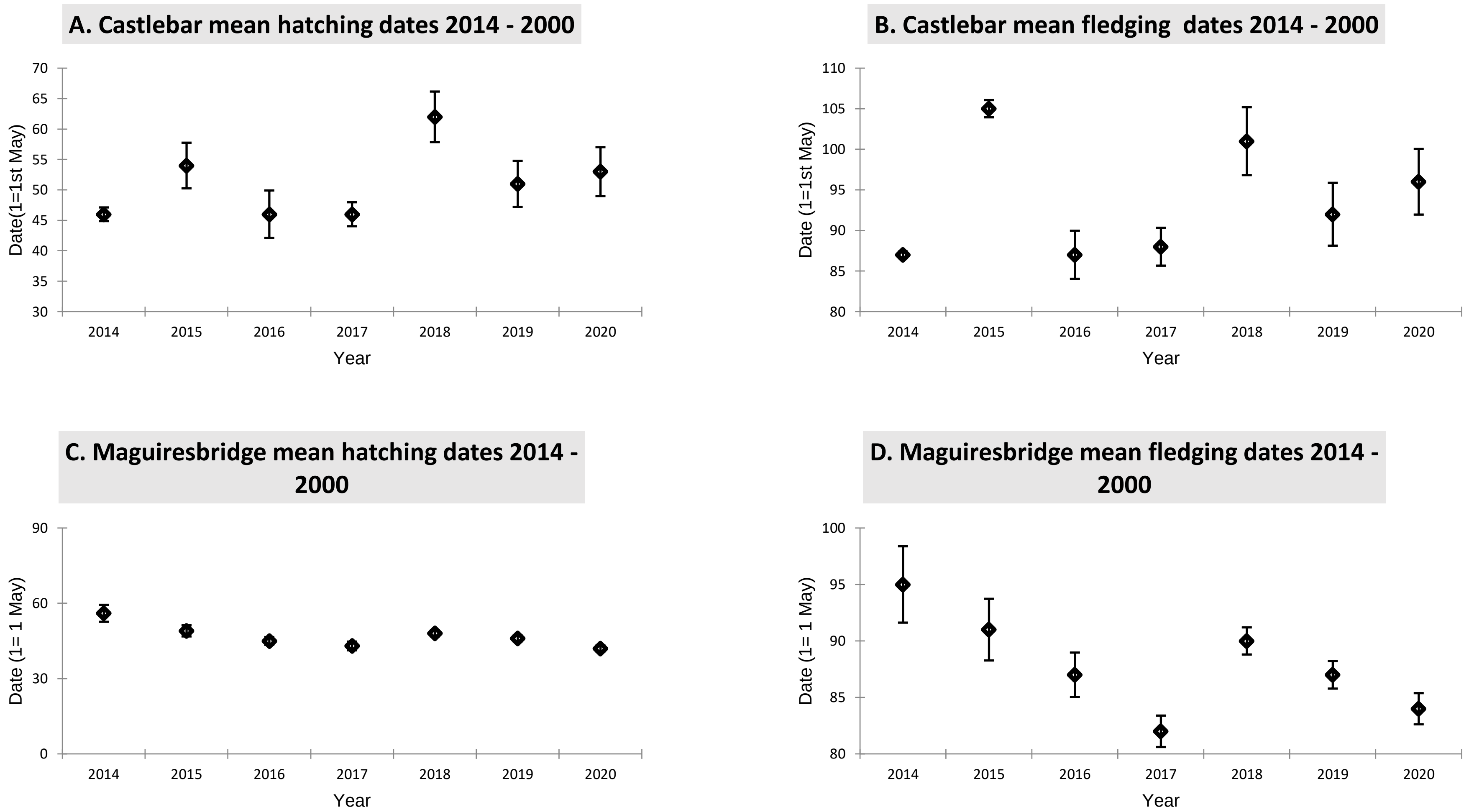


Figure 14. Error graphs illustrating the timing of the hatching and fledging events at both colonies. Error bars illustrate the standard error **(se±)**

4.3.4 Length of the chick-rearing period

The length of the fledging period was measured at Castlebar and Maguiresbridge between 2018 and 2020, by calculating the interval in days between the hatching of the first egg and the observation of the first fledging; second egg and second fledging; third egg and third fledging. This allowed for the average fledging time of each chick at both colonies to be calculated relative to the size of the brood. Samples were eliminated if there was a small number of fledgelings per brood type each season (<5) at any of the studied locations (Table 10). Therefore, the colony in Castlebar provided results only for broods of two, and the colony in Maguiresbrige for broods of two and three chicks.

In Castlebar, the shortest fledging period recorded was in 2018, when a brood of two chicks fledged in 38 and 39 days post hatching. The longest fledging period at the same colony was recorded in 2020, when two chicks both fledged at 48 days post hatching. The average age of the individual chick at fledging ranged from 40.83 (se± 0.37) in 2018 to 42.83 (se± 0.82) in 2020) and there was no significant difference in the mean values in any of the studied years (Kruskal-Wallis, x^2= 3.40, p= 0.182, α= 0.05). In the studied years (2018-2020), there was no significant difference between the fledging periods for the broods of two in any season (Kruskal-Wallis, x^2= 4.64, p= 0.098, α= 0.05).

In Maguiresbridge, for the broods of two, the shortest fledging period in one brood was 39 and 38 days, and the longest was 46 and 43 days. For the broods of three the shortest fledging period in one brood was 40, 40, and 41 days and the longest 43, 44 and 44. The yearly average age of the individual chick at fledging stayed constant and ranged between 41.62 (se± 0.18) and 41.83 (se± 0.33) days with no significant difference in mean values in any of the studied years (Kruskal-Wallis, x^2= 0.16, p= 0.921, α= 0.05). There was no significant difference between the lengths of the fledging periods in any of the studied years for the broods of two (Kruskal-Wallis, x^2= 5.52, p= 0.631, α= 0.05), and broods of three (Kruskal-Wallis, x^2= 0.16, p= 0.921, α= 0.05).

Table 10. Mean fledging age in days relative to brood size.

A. **Castlebar**

	Fledging age	Brood size		
		1	2	3
2018	40.83 (se± 0.37)	N/A	40.50 (se± 0.50)	N/A
2019	41.00 (se± 0.28)	N/A	41.16 (se± 0.43)	N/A
2020	42.83 (se± 0.82)	N/A	43.50 (se± 0.83)	N/A

B. **Maguiresbridge**

	Fledging age	Brood size		
		1	2	3
2018	41.81 (se± 0.36)	N/A	41.66 (se± 0.32)	41.81 (se± 0.36)
2019	41.62 (se± 0.18)	N/A	41.06 (se± 0.39)	41.61 (se± 0.18)
2020	41.83 (se± 0.33)	N/A	42.58 (se± 0.39)	43.81 (se± 0.33)

4.3.5 Adult departure dates and breeding season length

The colony in Castlebar provided 78 total breeding adult departure dates between 2014 and 2020. The mean departure date of the breeding swifts during the study period (2014-2020) was 16 August (se± 1.10, n=78) and the range extended from 29 July to 08 September (41 days) (Table 11A). Only one adult departure was recorded in July throughout the whole study period at the colony (1.25%, n=1). The highest frequency of departures took place in the first two weeks of August (50.00%, n=39). Departures were less frequent in the last two weeks of August (37.18%, n=29) and in September (11.54%, n=5).

The Maguiresbridge colony provided 152 total departure dates for breeding swifts during the study period. The total mean of all departure dates was 20 August (se± 9.08, n=152) and ranged from 17 July to 18 September (63 days) (Table 11B). Out of all recorded departures, 4.60% (n=7) took place in July; 30.26% (n=46) between 1-15 August; 44.73% (n=68) between 16-31 August; and 20.40% (n=31) in September.

The mean date of all 78 breeding adults departure throughout the whole study period in Castlebar was 16 August (se± 1.10). During the same period, the average timing of 152 departure dates in Maguiresbridge was 20 August, (se± 9.08). Direct statistical comparison of departure dates for both colonies suggests a significant statistical difference between the mean value of two samples (Independent T-test, $t(228) = 4.39$, $p = 0.005$).

Table 11. Yearly mean dates of the departures of the breeding swifts in Castlebar (A) and Maguiresbridge (B)

A. Castlebar

Year	n	Earliest breeding swift departure	Latest swift breeding departure	Mean date of departure	SE±
2014	4	29 July	07 Aug	03 Aug	1.89
2015	6	12 Aug	17 Aug	14 Aug	0.72
2016	10	04 Aug	16 Aug	08 Aug	1.49
2017	10	03 Aug	20 Aug	20 Aug	1.51
2018	14	11 Aug	31 Aug	21 Aug	1.92
2019	16	14 Aug	6 Sep	26 Aug	2.17
2020	18	07 Aug	01 Sep	14 Aug	1.90

B. Maguiresbridge

Year	n	Earliest breeding swift departure	Latest swift breeding departure	Mean date of departure	SE±
2014	6	22 Aug	9 Sep	02 Sep	2.53
2015	9	12 Aug	05 Sep	21 Aug	2.89
2016	N/A	Data missing	Data missing	Data missing	N/A
2017	24	6 Aug	18 Sep	24 Aug	1.97
2018	32	25 Jul	04 Sep	24 Aug	2.21
2019	36	25 Jul	07 Sep	21 Aug	1.54
2020	45	17 Jul	09 Sep	14 Aug	1.61

4.3.6 Length of the nesting period

The length of the nest occupancy each season was measured from first to last overnight roost with at least one swift in the nest. The average occupancy of the nest in Castlebar during the study period was 100 days (se± 1.95, n=39) and individual results ranged between 79 and 121 days. In Maguiresbridge the average nest occupancy was 104 days (se± 1.33, n=77) and ranged between 75 and 127 days (Table 12).

Table 12. Yearly range and mean for the duration of nest occupancy (2014-2020)

A. Castlebar

Year	n	Range	Mean	SE±
2014	2	79-84	82	1.77
2015	3	84-101	95	4.50
2016	5	76-102	87	4.09
2017	6	91-103	98	2.08
2018	7	86-116	100	3.90
2019	8	100-121	112	2.47
2020	9	95-120	105	3.04

B. Maguiresbridge

Year	n	Range	Mean	SE±
2014	3	120-117	118	0.82
2015	5	95-101	100	2.16
2016	9	Data missing		
2017	14	93-120	107	3.09
2018	16	79-118	105	2.93
2019	18	87-122	105	2.37
2020	23	75-127	101	2.75

4.3.7 Phenological calendar summary

During the study period (2014-2020) in Castlebar, the mean dates for all recorded events in the nesting calendar were: arrival 13 May (se±1.04, n= 80); first egg 26 May (se±1.65, n=40); hatching 22 June (se± 1.72, n=61); fledging 3 August (se± 1.79, n=56); adult departure 16 August, se± 1.10; length of nest occupancy 100 days (se± 1.95, n=39) (Figure 15A).

In Maguiresbridge, the recorded mean values for dates in the breeding calendar for all breeding attempts observed between 2014 and 2020 were: arrivals 13 May (se±0.66, n=176); first egg 27 May (se± 1.01, n=88); hatching 16 June (se± 0.58, n=197); fledging 27 July (se± 0.64, n=186); adult departure 20 August (se± 9.08, n=152), length of nest occupancy 104 days (se± 1.33, n=77) (Figure 15B).

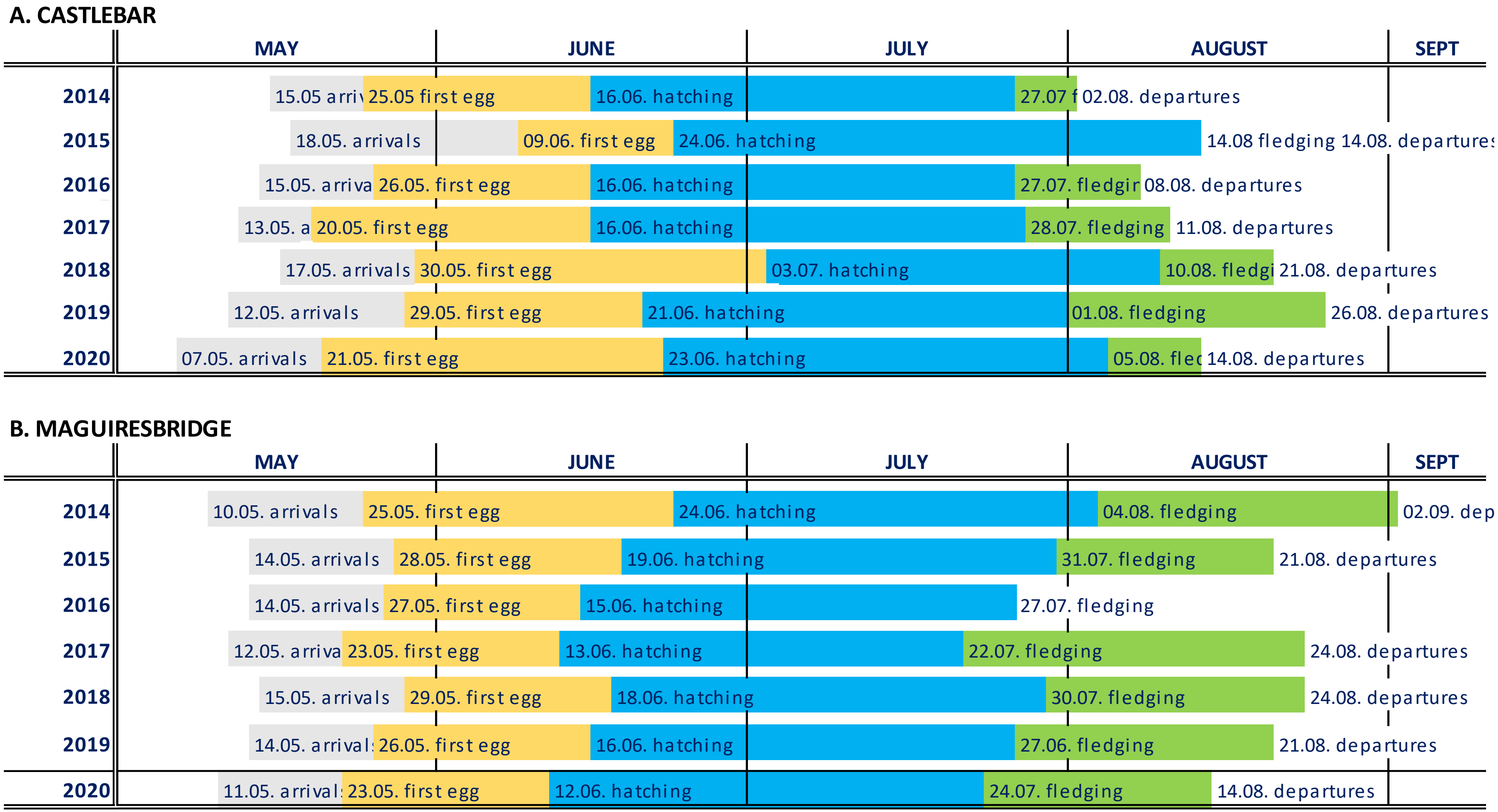


Figure 15. Yearly breeding calendar (2014-2020).

4.4 Breeding success

4.4.1 Clutch size

Overall, during the study period, there were 40 clutches laid in Castlebar and 88 in Maguiresbridge. The average clutch size in Castlebar was 2.33 (se± 0.07, n=40) eggs and 2.41 (se±0.65, n=88) eggs in Maguiresbridge (Table 13). Statistically, there was no significant difference in clutch sizes between the two colonies (Independent T-test, $t(126) = 0.763$, $p= 0.447$).

In Castlebar, there were no instances of one egg clutches in any of the studied years. The most common clutch size was two eggs (67.50%, n=27), with three eggs less common (32.50%, n=13). In Maguiresbridge, one egg clutches were observed in 6.81% (n=6) of all breeding attempts, while two egg clutches in 45.45% (n=40) and three egg clutches in 47.72% (n=42). During this study, there was no evidence of clutches with four eggs or a second clutch in one season.

Egg loss at both colonies affected the success rates of the clutches at both colonies. In Castlebar, 19 out of 40 (47.50%) clutches were lost due to egg loss and this resulted in a total of 12 replacement clutches laid. In Maguiresbridge, 8 out of 88 (9.09%) clutches were lost due to egg loss, and four replacement clutches were laid. However, the number of clutches lost in Maguiresbridge was reduced by human interventions with the returning of ejected eggs back into the nest.

Table 13. Annual mean clutch size per breeding attempt. Clutch success rate presents the percentage of the clutches (excluding replacement clutch) that produced at least one fledgeling.

A. Castlebar

Year	n	Clutch size	SE±	Clutch success rate (%)
2014	2	2	0.00	100
2015	3	2	0.00	66.6
2016	5	2.20	0.18	60
2017	6	2.33	0.30	66.6
2018	7	2.1	1.33	42.8
2019	8	2.6	0.17	62.5
2020	9	2.3	0.16	44.4

B. Maguiresbridge

Year	n	Clutch size	SE±	Clutch success rate (%)
2014	3	1.7	0.27	100
2015	5	2.2	0.18	100
2016	9	2.3	0.25	88.8
2017	14	2.2	0.17	92.3
2018	16	2.4	0.15	81.25
2019	18	2	0.16	92.86
2020	23	2.5	0.12	91.3

There was a negative correlation between the first egg's timing and the size of the first clutch in Castlebar (linear regression, r^2=0.260, p-value =0.001, n=40) (Figure 16A). Early in the season, the probability of a three-egg first clutch was higher than in the later stages of the egg-laying period.

In Maguiresbridge there was a negative correlation between the timing of the first egg and the size of the first clutch at Maguiresbridge (linear regression, r^2=0.217., p-value <0.0001, n=88) (Figure 16B). Three-egg clutches were more likely in the earlier stages of the egg-laying period, during the month of May. One-egg clutches were most likely to occur in June. There were no instances of egg-laying in July. The latest egg at the colony was laid on 10 June, in 2019.

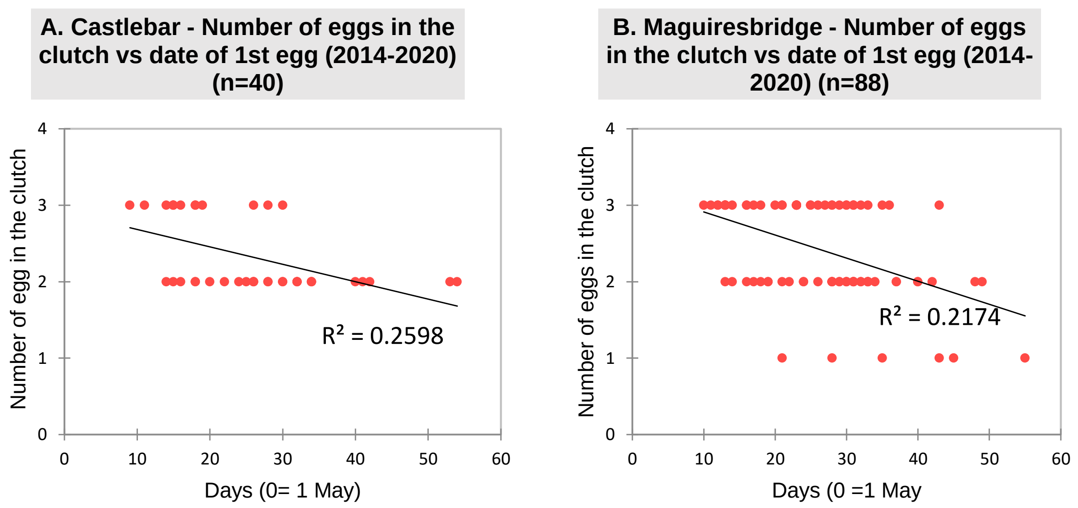


Figure 16. Linear regression graphs illustrate the negative influence of the timing of the clutch and the number of eggs laid.

4.4.2 Brood size and fledging success

In Castlebar, during the study period, the average number of hatchlings per breeding attempt was 1.53 (se± 0.158, n=42). The number of fledgelings was 1.36 (se± 0.152, n=42). Out of a total of 40 breeding attempts, in 22.5% (n= 9) of cases, swift pairs failed to incubate the eggs and therefore did not produce any hatchlings. In 17.5% (n=7) of total breeding attempts, swifts produced only one hatchling, in 45% (n=18) two hatchlings, and in 15% (n=6) three hatchlings. There was no statistical difference in the mean number of hatchlings per breeding attempt across the years studied (Kruskal-Wallis, x^2=1.161, p-value=0.979, α=0.050). In Castlebar, there was a negative correlation between the number of hatchlings and the timing of the first hatching in a breeding attempt (Spearman's, r= -0.475, p=0.010, n=30) (Figure 17). Three-chick broods were only recorded when the first chick hatched before 15 June. For every breeding attempt, pairs produced 1.53 (se± 0.158, n=42) hatchlings. Out of a total of 61 chicks observed at the colony, 55 (90.12%) fledged, and six (9.84%) died in the nest. The was no significant yearly variation in the fledging numbers each season (Kruskal-Wallis, x^2=2.059, p=0.914, α=0.05).

In Maguiresbridge, during the entire study period (2014-2020), a single pair of breeding swifts produced on average 2.28 (se± 0.08, n=88) hatchlings and 2.13 (se± 0.09) fledgelings. Only 5.68% (n=5) of the breeding attempts were unsuccessful; 94.32% (n=83) produced at least one fledgling. Three-chick broods were only recorded when the first chick hatched before 15 June.

Per breeding attempt, each pair of breeders produced 1.53 (se± 0.158, n=42) hatchlings. There was no significant variance in the numbers of hatchlings (Kruskal-Wallis, x^2= 4.946, p=0.551, α=0.05) and fledgelings (Kruskal-Wallis, x^2= 3.203, p=0.783, α=0.05) in any of the studied years.

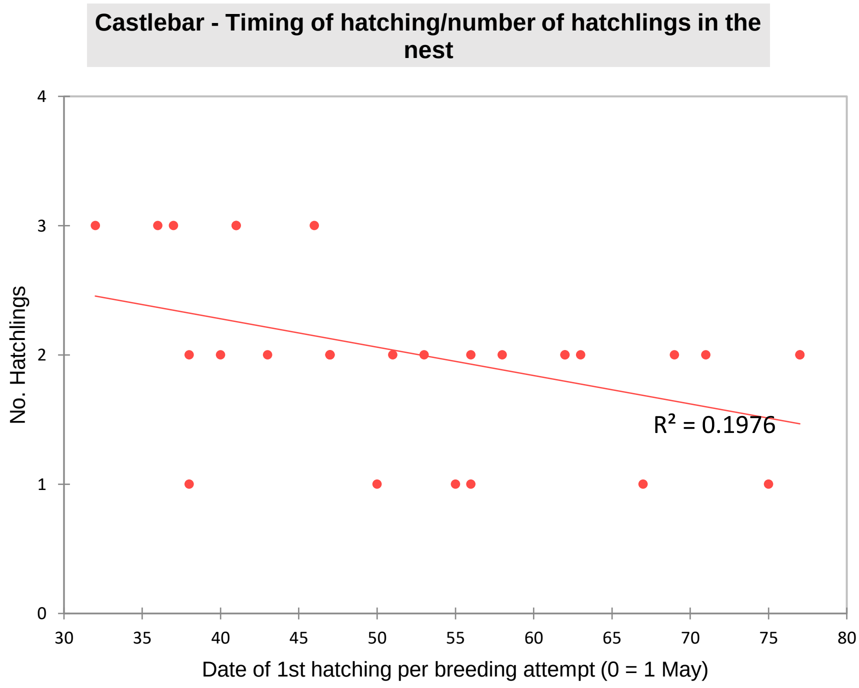


Figure 17. Correlation between the timing of the first hatchling and the number of hatched eggs in the nest.

4.4.3 In-nest chick mortality

During the study period, six chicks at the Castlebar colony and 11 at the Maguiresbridge colony died during the chick-rearing period (Table 14). The ratio of dead to hatched chicks was similar for both colonies: 6% in Castlebar and 5.58% in Maguiresbridge. Four reasons for chick mortality in the nest were identified. These were: adult swifts' failure to provide food for one of the chicks (the youngest) in the brood; adult swifts' failure in feeding the entire brood, leading to breeding failure; nest abandonment due to the disappearance of one of the adult swifts; and an attack from an intruding swift. No predation was recorded.

Table 14. Causes of chick mortality in the nest

	Castlebar (n=60)	%	Maguiresbridge (n=197)	%
Total	6	6%	11	5.58%
Causes				
1. Failed to feed one of the chicks in the brood	4		8	
2. Failed to feed the brood	2		0	
3. Adult abandonment	0		2	
4. Intruding swift	0		1	
5. Predation	0		0	

4.4.4 Productivity

The total productivity for the Castlebar colony during the study period was 45%, while at the same time in Maguiresbridge, a productivity rating of 89% was recorded (Table 15). There was no correlation between the laying of the first egg and the productivity in Castlebar (Spearman's; r= -0.077, p-value= 0.634) or Maguiresbridge (r=-0.143, p-value=0.185). There was no yearly variation in productivity in Castlebar (x^2=7.459; p-value=0.280, α=0.05) or Maguiresbridge (x^2=5.23, p-value =0.515, α=0.05).

Table 15. Yearly egg productivity (Ricklefs, 1973, p. 87) in Castlebar (A) and Maguiresbridge (B).

A. Castlebar

Year	Number of breeding pairs	Number of eggs (successful 1st clutch or replacement)	Chicks fledged in the season	Productivity (%)
2014	2	4	4	100%
2015	3	6	2	33%
2016	5	13	5	38%
2017	6	16	9	60%
2018	7	22	11	50%
2019	8	26	12	46%
2020	9	33	12	36%
Colony (7 years)	40	120	56	45%

B. Maguiresbridge

Year	Number of breeding pairs	Number of eggs (successful 1st clutch or replacement)	Chicks fledged in the season	Productivity (%)
2014	3	5	4	80%
2015	5	11	11	100%
2016	9	21	16	76%
2017	14	36	31	86%
2018	16	38	35	92%
2019	18	44	40	91%
2020	23	57	51	89%
Colony (7 years)	88	212	188	89%

4.5 Patterns of feed frequency

4.5.1 Season totals

With regard to the feeding frequency patterns, only video recordings from the nests in Castlebar were used. Overall, during the three-year research period, 19 breeding attempts were studied throughout the whole chick rearing period (from first observed feed to last). The total number of recorded visits to the nest by all adult swifts in all breeding attempts was 12,491. Food delivery (‘feed’) was clearly identified in 11,527 cases (92.85%). In the remaining 964 cases (7.15%), there was no visible evidence of food exchange between adult and chick (‘no-feed’).

The ratio of ‘feed’ to ‘no-feed’ events was not uniform amongst breeding pairs. From a total of 19 studied breeding pairs, 13 fed their chicks in over 90% of visits to the nest, with the remaining six pairs feeding below that benchmark. The highest ratio was recorded by a breeding pair in 2018, with food deliveries accounting for 99.1% of their visits. The lowest ratio was observed in a breeding pair in 2019, when just 83.8% of visits were recorded as food deliveries.

The number of feeds in a season for a brood of one was on average 501.28 (se± 26.16, n=7) (Figure 18). The lowest number of food deliveries was 427 and the highest was 605. Chicks from single-brood nests fledged between 40 and 42 days after the first recorded feeding event.

Where the broods consisted of two chicks, the parent swifts on average delivered 746.80 feeds (se± 18.15, n=11) during the fledging period. The total number of feeds ranged from 669 to 805, and the chicks fledged between 41 and 49 days after the first recorded feeding event. The average number of feeds for nests with two chicks was 32.87% higher than of nests with a single chick.

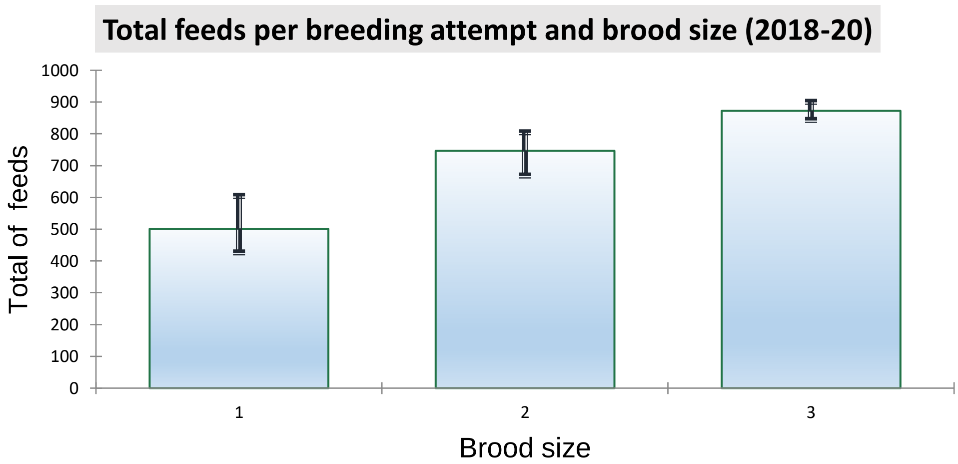


Figure 18. Influence of brood size on the number of feeds per breeding attempt. Columns represent the averages and brackets represent the range. Broods with one chick (n=7), two chicks (n=10) and three chicks (n=2).

Only two nests produced broods with three chicks, and the average feeding number in the season was 872.5 (se ± 20.15, n=2). The first pair fed their chicks 901 times and the second 844 times in a season. Chicks from these broods fledged between 40 and 46 days after the feeds began. The average number of feeds for a nest with three chicks was 42.5% higher than a nest with one chick and 14.4% higher than nests with two chicks.

4.5.2 Hourly feeding patterns

Adult swifts fed their chicks at different rates, depending on the time of day. Three periods of increased activity were identified. These were: early morning (before 6 a.m.), around mid-day to 1 p.m., and late evening before roost (9 p.m. to 10.30 p.m.) (Figure 19).

During the chick-rearing period, adult swifts left the nest as early as 4.30 a.m. and provided the first food delivery before 5 a.m. This took place in 1.42% of all recorded feeding events during the research period.

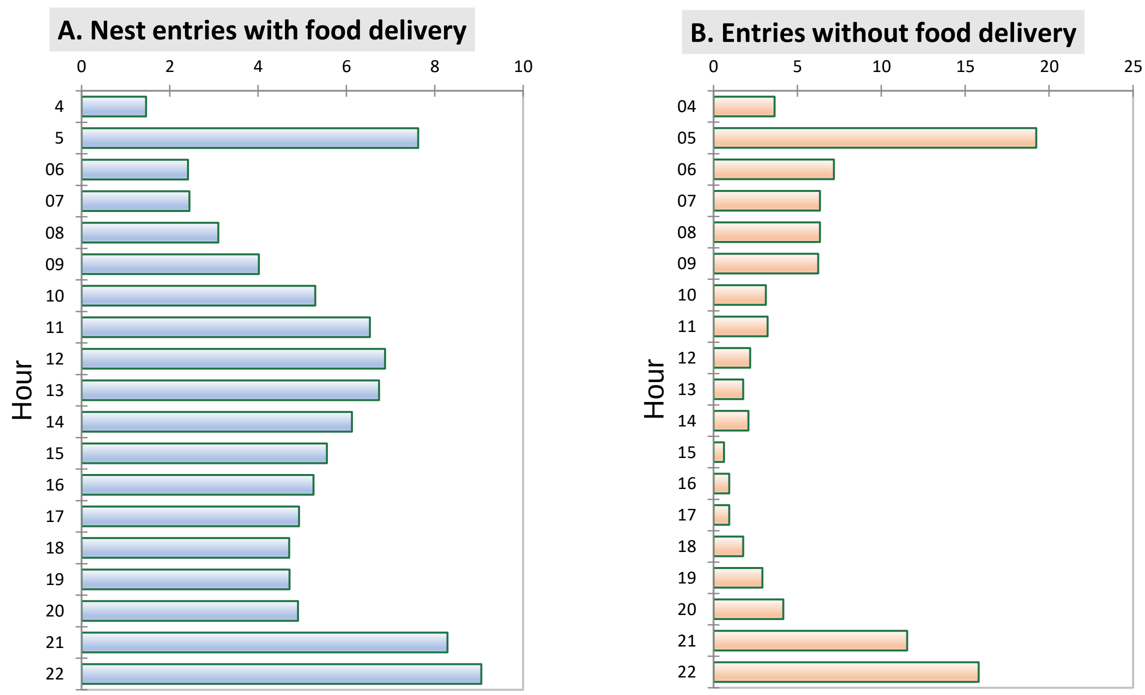


Figure 19. Hourly breakdown of "feed" (A) and "no-feed" (B) visits during the study period (2018-2020). X axis represents the percentage (%) number of total feeds, the Y axis represents hours of the day. There were no entries into the nest recorded at night (11 p.m. to 4.30 a.m.).

Morning activity at the colony peaked between 5 a.m. and 6 a.m. During this hour, adult swifts left and entered the nest frequently, with some excursions lasting no more than a few minutes. Feeding activity increased during this hour, with 7.62% of total food deliveries taking place. In addition, no-feed entries were significant, with 19.23% of the total recorded occurring during this hour. This spike of activity between 5 a.m. and 6 a.m. was recorded in almost all studied breeding pairs and was uniform for different brood sizes. After providing one to four boluses for their chicks, the adults settled back in the nest for a few hours of roosting. Between 6.00 a.m. and 9.00 a.m., feeding visits were at their lowest frequency, during which the interval between feeds was extended. On many occasions, the adult swifts were not active at all during this period, spending a few hours resting, preening, cleaning, and repairing the nest. When this morning lull ended, the adult swifts began to leave the nest more frequently and the number of feeds increased, reaching a mid-day peak between 12 noon and 1 p.m. (6.87% of total feeds). During this period, adult visits to the nest without a bolus were infrequent.

In the afternoon, another lull in feeding was recorded. After the mid-day peak, visits to the nest with a bolus decreased each hour until they reached a low point between 7 p.m. and 9 p.m. However, the most active period for the adult swifts at the colony was in the last 90 minutes before the final entry to the nest before roosting. Between 9 p.m. and 10.30 p.m., adult swifts increased not only their feeding frequency (17.31% of total daily feeds) but also entries into the nest without food provision (27.34% of total "non-feeding" entries). Entries were at times so frequent that one adult entered and exited the nest a number of times in the space of just a few minutes – a behaviour only observed late in the evening.

In general, all swifts were back in their nests for roosting by 10.30 p.m. On occasion, one of the adult swifts would return to the nest after this time, and in two cases an adult did not return to the nest for roosting but reappeared in the nest the following morning.

All of the studied breeding pairs exhibited a very uniform pattern of hourly activity – a large number of feeding visits early in the morning, followed by a low activity period until mid-day, when food provision increased again, followed by another low feeding period until late evening when chicks received the most feeds, just in time for the roost. Chicks were not fed between 11 p.m. and 4.30 a.m.

4.5.3 Stages of parental care and chicks' development before fledging

Considering changes in brooding times during the nestlings' development, coupled with the fact that chicks tend to reduce mass before fledging (Martins & Wright, 1993, p. 215), the following division of the chick-rearing period was determined for further analysis (Figure 20):

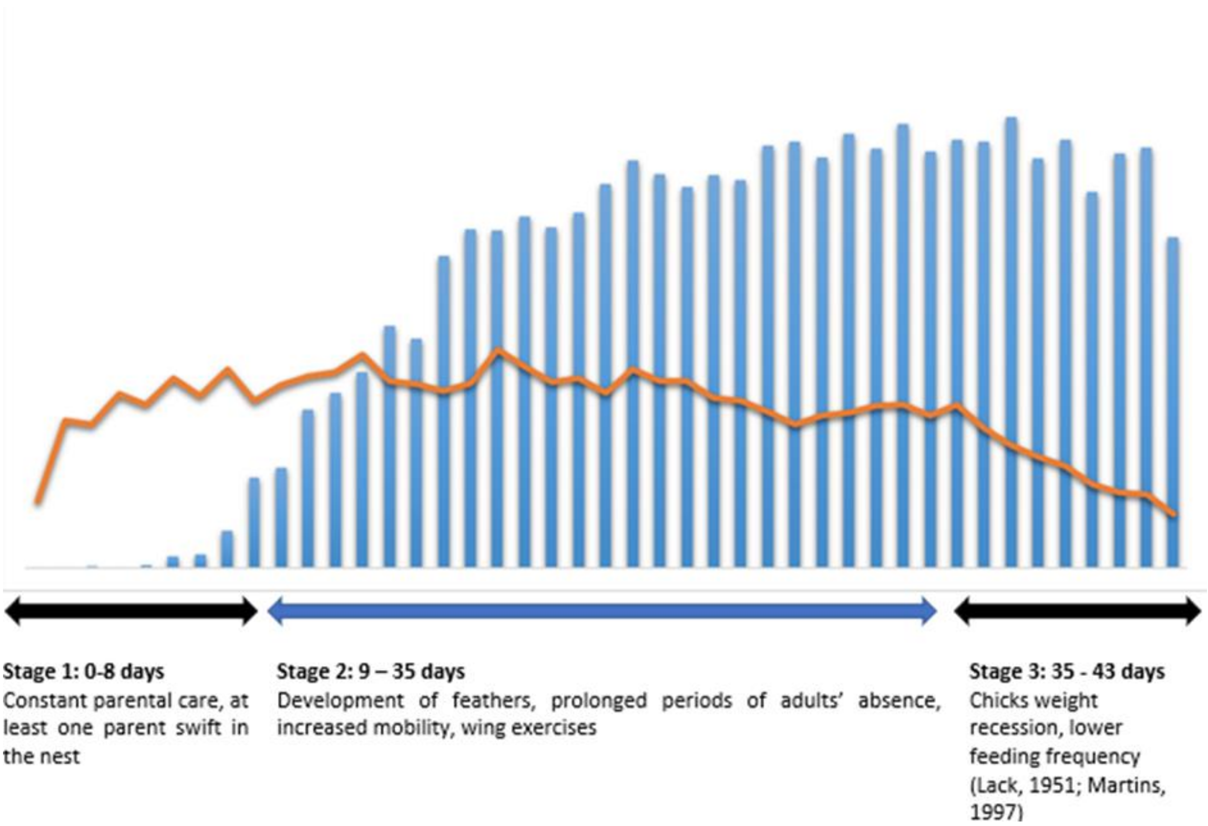


Figure 20. Graph illustrating the stages of chicks' development, based on the level of parental care relative to the age of the brood (measured from the first observed feed). The orange line represents the feeding frequency normalised for all brood sizes. Blue columns represent the average time chicks spent alone in the nest normalised for all brood sizes. Double side arrows represent the range of the stages.

Stage 1: Day 0 to Day 8 – average brooding time was higher than 90% of total day length (24 hours). Chicks were contained in the nest cup and had no plumage (Table 16).

Stage 2: Day 9 to Day 34 – a consistent decrease in average daily brooding time. Chicks began to grow plumage, and during this stage they began to exercise their wings and even leave the nest cup for short periods of time.

Stage 3: Day 35 until fledging – no further decrease in the daily brooding time averages. At this stage, chicks are often as large as adult swifts, and they can only be distinguished by the colour of their plumage on the head and wings. Chicks are also known to reduce mass during this period (Martins & Wright, 1993, p. 215).

Table 16. The relationship between the daily average of brooding time and the age of the brood, calculated from the first observation of feeding in the nest (Spearman's correlation) .

	r	p-value	n (number of days)
Overall (All Stages):	**0.784**	**<0.0001**	**43**
Stage 1: days 0-8	0.604	0.014	9
Stage 2: days 9-34	0.812	<0.0001	26
Stage 3: days 35-42 (average fledging time)	0.453	0.067	8

4.5.4 Relationship between the age of a chick and daily feed numbers

The division of the chick-rearing period into three stages, based on the age of the chicks and the level of parental care, allows for analysis of the average daily feeding patterns for different brood sizes.

Nests with one chick

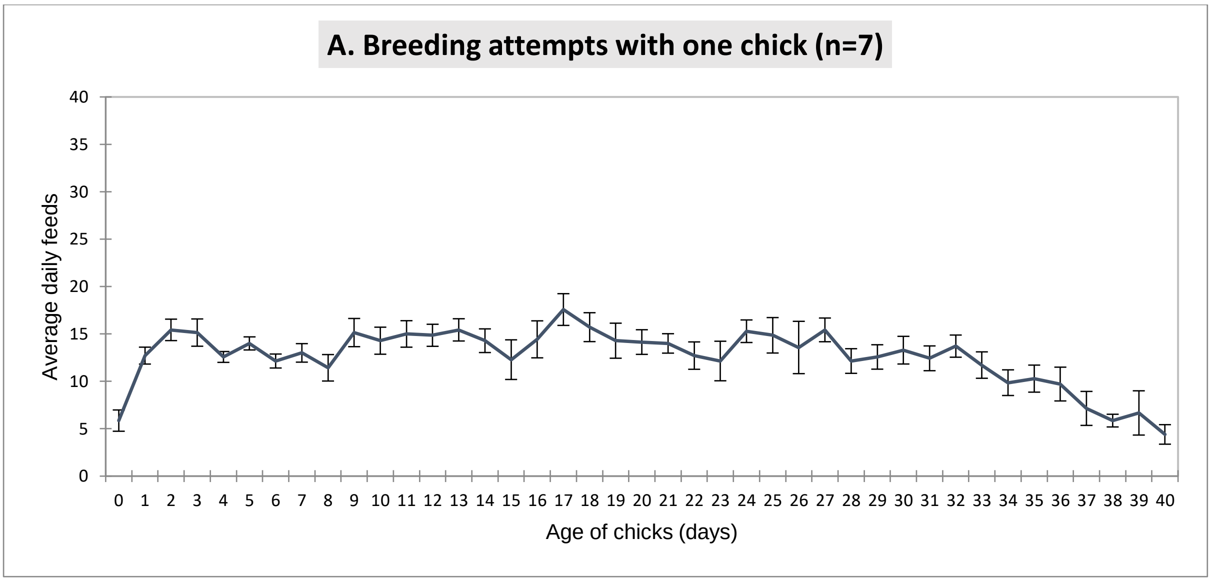
The total number of feeds for a brood with one chick (Figure 21A) was the lowest at 501.28 feeds (se± 26.16, n=7) while the daily mean number of feeds was 12.19 (se± 0.53, n=42). During Stage 1 (0-8 days), the average number of feeds was 12.48 (se±0.88, n=9) and was not related to the age of the chick (Spearman's, r= -0.100, p-value=0.776, α=0.05). In Stage 2 (9-34 days), the mean number of daily feeds was 13.89 (se±0.31, n=26) and it remained constant, but dropped in the last period of Stage 2 (Spearman's, r= -0.591, p=0.002, α=0.05). During Stage 3 (35-42 days), the mean number of feeds decreased to 6.32 feeds per day (se±0.90, n=8), and there was a strong negative correlation between the age of the chick and the number of daily feeds (Spearman's, r= -0.971, p-value=, α=0.05). To summarise the feeding pattern for a brood of one, the number of feeds stays constant until the chick reaches its peak of growth at around Day 34. During the last eight days, when the chick is dropping in mass, adult swifts reduce the number of feeds per day significantly.

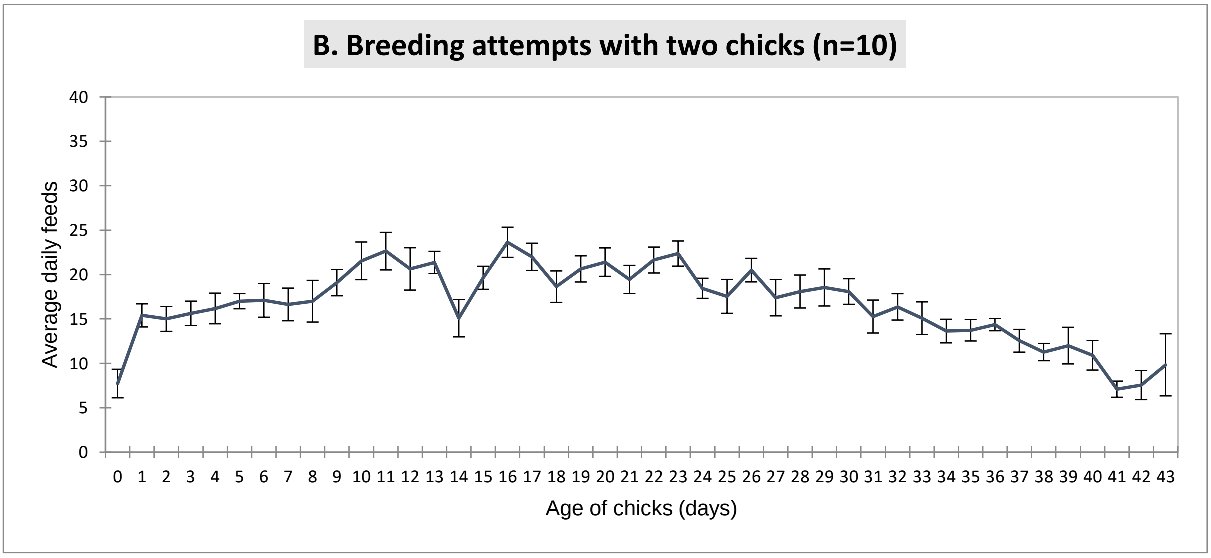
Nests with two chicks

The total mean number of feeds in a season for broods with two chicks (Figure 21B) was 746.80 (se± 18.15, n=11). The mean number of daily feeds was 16.72 (se± 0.62, n=43). The average number of feeds during Stage 1 was 15.30 (se ±0.92, n=9), and increased with the age of the chicks (linear regression, r^2=0.461, p-value= 0.044, α=0.05). The mean number of feeds per day during Stage 2 was 19.18 (se± 0.51, n=26) and reached its peak when chicks were 18 days old at 24.5 feeds (se± 1.86). In the first half of Stage 2 (9-21 days) the feeding frequency was increasing rapidly and reached its peak around day 20 (Spearman's. r=0.698, p-value=0.010, α= 0.05). However, the average number of feeds began to decrease in the final period of Stage 2 (Spearman's, r= -0.659, p-value= 0.017, α= 0.05). A further decrease in average daily feeds was observed during Stage 3 with a mean of 11.03 (se± 0.79, n=9), and expressed a strong negative correlation with the age of the nestlings (Spearman's, r=0.804, p-value= 0.001, α=0.05).

Nests with three chicks

During the study period, only two nests with a brood of three chicks were analysed for feeding frequency (Figure 21C). Therefore, the mean numbers of daily feeds were skewed by a small sample size. However, there were considerable differences between the daily feeding averages of broods of three nestlings and those with one or two. The overall average feeding number in a season was measured at 20.09 (se±1.04, n=43) feeds per day. During Stage 1, the average number of daily feeds was measured at 20.72 (se± 2.64, n=9) and strongly correlated with the age of the brood (Spearman's, r=0.850, p-value= 0.008, α=0.05). Stage 2 reported the highest mean number of daily feeds at 22.92 (se± 0.86), and the correlation test suggests that it remained constant during the first half (9-20 days) (Spearman's, r=0.130, p-value=0.690, α=0.05), but decreased insignificantly in the second half of the Stage 2 (Spearman's, r=-0.222, p-value=0.444, α=0.05). However, during the final stage, daily averages decreased and were strongly (negatively) correlated with the age of the nestlings (Spearman's, r= -0.958, p-value= 0.000, α=0.05).





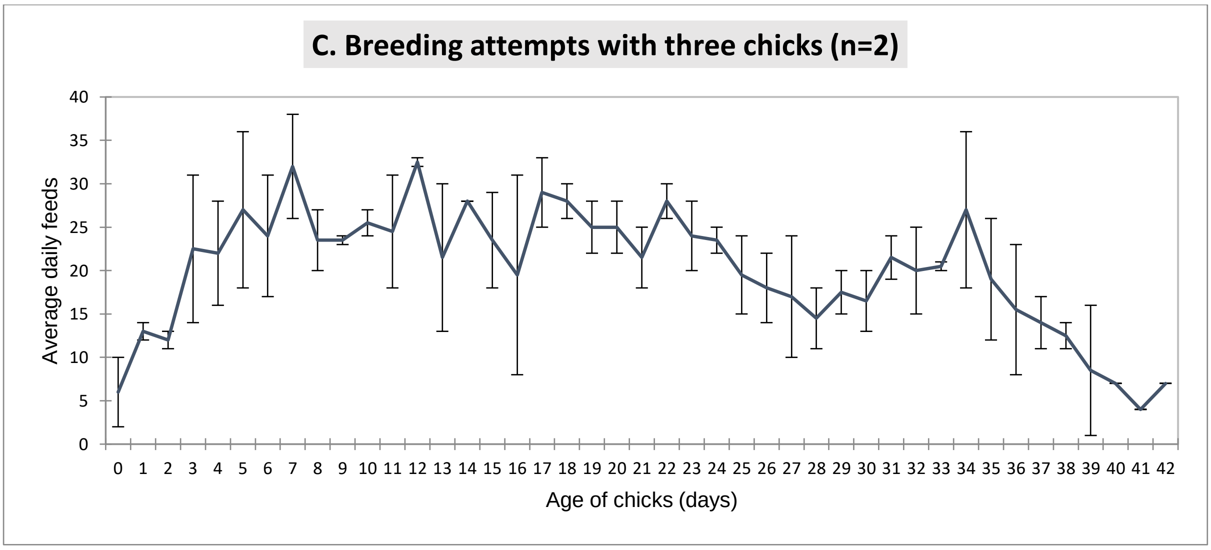


Figure 21. Graphic representation of average daily feeding patterns with regards to the age of the brood (Day 0 = first observed feed) for the broods of different sizes (A, B, C). Brackets represent standard error (se±). Graph C represents a wide range of standard error due to a small sample size (n=2).

4.5.5 DAX (difference of actual to expected feeds) results

To eliminate any skewing of the results, only results from Stage 2 of the chicks' development were used for any further statistical analysis (Tables 17, 18, 19). The analyses of Stages 1 and 3 were eliminated due to the bias caused by small numbers of chicks at the colony (often in the early and late stages of the season), and the differences in the ages at which chicks fledged. Therefore, the decision was made to study only results from Stage 2 with at least two breeding pairs on particular day, as they provided the most reliable data.

The difference between the EXPfeeds and ACTfeeds indicated that there may have been external factors influencing the feeding frequency at the colony. From this point onwards, this difference will be referenced as DAX (difference of actual to expected) and will be represented as a percentage value. The prediction of the equation is that if the result is positive, then the feeding activity of the colony was higher than expected. When negative, the swifts' ability to forage may have been impaired.

The distribution of DAX number between studied years was not significant (Kruskal-Wallis, x^2= 0.700, p-value= 0.705, α=0.05). While daily DAX numbers fluctuate through the research period, with prolonged periods of positive or negative results, the total seasonal mean stayed constant each year.

In 2018, the mean DAX number was recorded at 2.06% (se± 0.02, n=52), with DAX highest during the month of June at 20.14% (se± 0.04, n=5), stable in July at 1.83% (se± 0.03, n=27), and in August at 0.24%% (se±0.05, n=20). During the 2018 breeding season, there were periods in late June and early July when feeds were higher than predicted, yet this was balanced by prolonged periods of low feeds at the end of July and in August.

During the 2019 breeding season, mean DAX registered at 0.25% (se± 0.03, n=47). During the months of June, the swifts feeding frequencies fell below the expected number at -8.73% (se±0.09, n=11), followed by an above-expected feeds number in July at 2.95% (se± 0.03, n=31), and in August 3.24% (se± 0.08, n=5).

Of all the years studied, daily and monthly DAX patterns in 2020 saw the most variation and highest range, and the season total was the lowest in all studied years at -4.11% (se± 0.04, n=65). Moreover, during the months of June (Table 17) and July (Table 18), adult swifts fed their chicks at below expected levels - -15.23% (se± 0.11, n=14) and -8.86% (se± 0.05, n=31), respectively. This was followed by above expected levels of feeding in August at 20.65% (se±0.06, n=12). This season also saw the most significant discrepancy between the actual and expected feeds numbers. On 28 June 2020, the DAX number was recorded at -100% (no recorded feeds in Stage 2) during the summer storm, the lowest recorded in the colony throughout the study period (2018-2020). The highest DAX recorded was observed on 11 August 2020 at 51.92%. Perhaps more evident than in previous years was a pattern of prolonged periods of low feeds followed by a sharp spike for a few days, followed by another rapid decrease.

Table 17. Daily records of the DAX number in the month of June in all studied years (2018-2020). ACT number represents the daily record of feeds recorded at the colony. EXP represents the predicted number of feeds for the colony of the same size and same age of the brood (measured from the record of the first feed). Δ% represents DAX number**.**

	2018			2019			2020		
Date	ACT	EXP	Δ%	ACT	EXP	Δ%	ACT	EXP	Δ%
17-Jun							42	39	8.45%
18-Jun							48	45	6.24%
19-Jun							41	45	-8.15%
20-Jun				38	34	11.94%	23	39	-41.44%
21-Jun				39	37	5.48%	50	42	19.05%
22-Jun				33	37	-10.62%	33	36	-9.57%
23-Jun				5	33	-84.81%	39	39	-0.23%
24-Jun				33	36	-7.80%	60	45	32.53%
25-Jun				21	33	-35.71%	64	44	44.26%
26-Jun	78	64	22.48%	38	35	7.49%	34	37	-8.33%
27-Jun	83	68	22.80%	44	38	16.03%	18	38	-52.86%
28-Jun	90	78	15.72%	40	36	10.67%	0	42	-100.00%
29-Jun	83	63	32.22%	36	33	10.31%	5	37	-86.43%
30-Jun	76	71	7.46%	27	33	-19.04%	49	59	-16.69%
TOTAL	**410**	**343**	**19.69%**	**354**	**385**	**-7.96%**	**506**	**588**	**-13.93%**

Table 18. Daily records of the DAX number in the month of July in all studied years (2018-2020). ACT number represents the daily record of feeds recorded at the colony. EXP represents the predicted number of feeds for the colony of the same size and same age of the brood (measured from the record of the first feed). Δ% represents DAX number.

	2018			2019			2020		
Date	ACT	EXP	Δ%	ACT	EXP	Δ%	ACT	EXP	Δ%
1-Jul	50	54	-6.86%	27	34	-19.51%	54	62	-13.54%
2-Jul	74	59	25.91%	39	35	12.26%	59	59	-0.31%
3-Jul	90	76	18.00%	40	36	9.61%	33	53	-38.27%
4-Jul	77	72	6.94%	29	36	-19.30%	36	58	-38.17%
5-Jul	74	62	18.83%	47	49	-4.13%	10	67	-85.00%
6-Jul	75	66	13.17%	47	44	6.88%	71	73	-2.62%
7-Jul	70	64	8.86%	54	48	12.33%	35	65	-46.00%
8-Jul	66	67	-1.36%	42	46	-7.78%	61	61	0.45%
9-Jul	68	67	1.08%	46	46	0.11%	65	55	17.60%
10-Jul	67	68	-1.80%	44	47	-5.47%	70	52	34.38%
11-Jul	48	56	-14.91%	59	61	-3.57%	78	56	38.97%
12-Jul	63	53	18.66%	81	80	1.00%	58	57	2.24%
13-Jul	66	58	13.79%	100	78	28.01%	54	44	23.75%
14-Jul	48	49	-2.64%	103	74	39.04%	29	41	-29.27%
15-Jul	46	54	-14.31%	83	70	18.70%	32	39	-18.14%
16-Jul	52	54	-2.97%	62	51	22.54%	51	54	-5.71%
17-Jul	66	58	14.42%	45	49	-7.65%	42	54	-22.57%
18-Jul	66	51	30.58%	52	56	-7.12%	87	69	25.76%
19-Jul	57	53	7.09%	52	58	-10.00%	85	70	22.13%
20-Jul	47	57	-17.81%	57	56	1.93%	94	87	8.65%
21-Jul	22	27	-19.33%	35	54	-35.34%	85	86	-1.53%
22-Jul				56	56	0.71%	53	86	-38.46%
23-Jul				62	56	10.16%	78	83	-6.15%
24-Jul				73	68	6.76%	68	84	-19.43%
25-Jul				56	71	-20.97%	67	77	-13.45%
26-Jul	24	34	-29.89%	71	69	2.74%	57	70	-18.09%
27-Jul	30	36	-16.27%	71	63	12.19%	56	69	-18.56%
28-Jul	46	53	-12.84%	80	67	19.07%	60	67	-9.98%
29-Jul	54	50	8.48%	69	64	7.98%	46	61	-24.07%
30-Jul	46	52	-11.18%	66	58	14.52%	66	60	9.24%
31-Jul	30	44	-32.18%	54	51	5.75%	48	49	-2.83%
TOTAL	**1522**	**1495**	**1.83%**	**1802**	**1730**	**4.18%**	**1788**	**1969**	**-9.18%**

Table 19. Daily records of the DAX number in the month of August in all studied years (2018-2020). ACT number represents the daily record of feeds recorded at the colony. EXP represents the predicted number of feeds for the colony of the same size and same age of the brood (measured from the record of the first feed). Δ% represents DAX number.

	2018			2019			2020		
Date	ACT	EXP	Δ%	ACT	EXP	Δ%	ACT	EXP	Δ%
1-Aug	43	47.4	-9.19%	40	46	-12.90%	66	53	25.36%
2-Aug	70	52.4	33.71%	37	46	-18.86%	29	44	-34.34%
3-Aug	69	51.9	33.06%	43	43	0.64%	52	46	14.17%
4-Aug	62	48.8	27.10%				55	46	19.75%
5-Aug	60	52.5	14.30%				54	42	27.36%
6-Aug	47	51.3	-8.31%				67	45	48.59%
7-Aug	44	47.7	-7.83%				57	43	33.53%
8-Aug	45	48.5	-7.20%				42	42	0.81%
9-Aug	45	48.5	-7.23%				41	27	51.92%
10-Aug	47	46.5	1.17%				34	26	29.67%
11-Aug	49	44.5	10.00%						
12-Aug	68	49.4	37.77%						
13-Aug	39	47.7	-18.21%						
14-Aug	25	43.8	-42.93%						
15-Aug	36	46.5	-22.66%						
16-Aug	29	43.5	-33.36%						
17-Aug	28	40.3	-30.47%						
18-Aug	48	43.4	10.69%						
19-Aug	49	39.2	24.89%						
20-Aug	37	37.2	-0.56%						
TOTAL	**903**	**894**	1.05%	**120**	**134**	-10.61%	**497**	**413**	20.24%

4.5.6 Influence of weather on feed frequencies

The relationship between the recorded daily feeds (ACT_{feeds}) and predicted (EXP_{feeds}) provided a number (DAX) that could be used to measure the response of swifts to external factors such as weather. The prediction was that DAX fluctuations may correspond with the changes in daily means of precipitation, temperature, and wind. As the swifts in Castlebar did not leave the nest during the night, weather readings from the hours between 11 p.m. and 4 a.m. were excluded from the analysis. This approach eliminated potential skewing of the results for days where heavy rainfall or strong winds were present at night, but not during the chicks' feeding hours.

According to the linear model of regression, the average daily mean of temperature during feeding hours is responsible for 15.00% of the changes in DAX number (linear regression, r^2=0.150, p-value<0.0001, n=156) (Figure 22). For every increase of one mean daily degree (C) the DAX number is expected to increase by 6.88% (linear regression trendline equation: y= -0.044x + 0.6888) Furthermore, on days when the mean daily temperature was higher than 18.45ºC (top 10% of daily temperature means, n=18), the DAX average was 13.94% (se±4.07, n=18). When the average daily temperature was recorded as being lower than 12.97ºC (bottom 10% of daily temperature means, n=18), the DAX average was negative at -20.03% (se±11.08, n=18). Additionally, the lowest recorded daily DAX number (-100%) coincided with the coldest day during the study period (mean daily temperature at 11.03ºC).

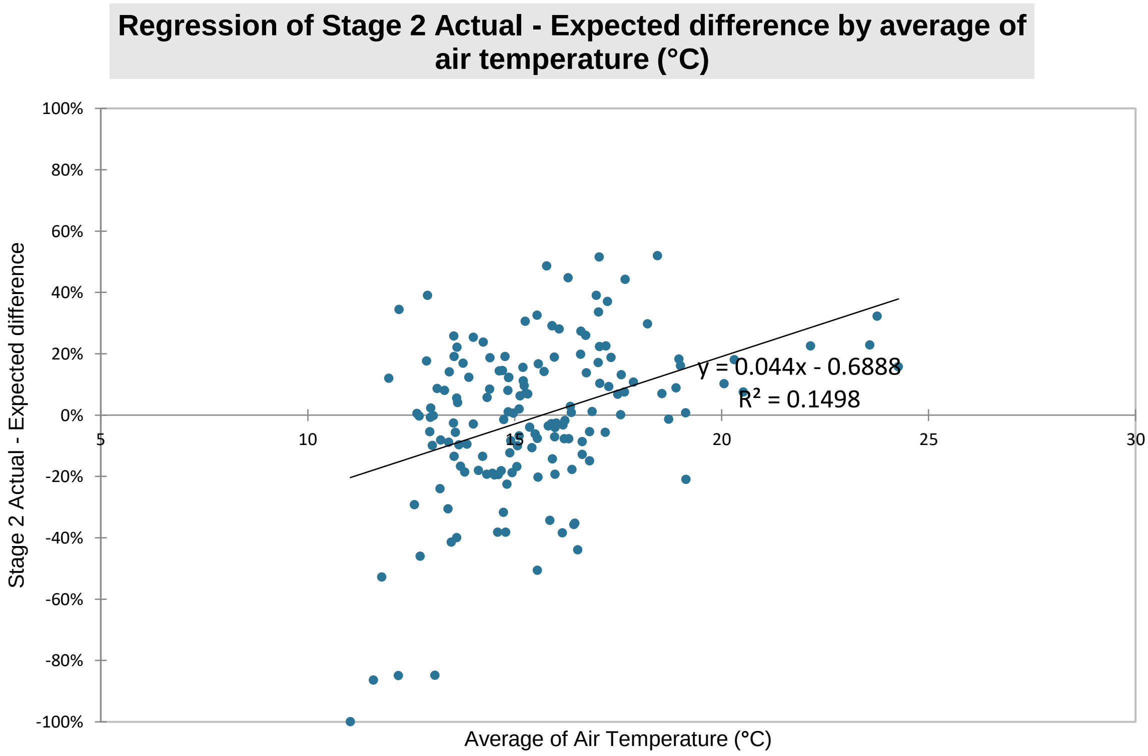


Figure 22. Regression analysis of the relation between DAX and average daily temperatures (2018-2020). Only Stage 2 of chicks' development was included in the statistics (n=182)

The daily total precipitation was responsible for a 12.4% drop in the daily DAX figure (linear regression, r^2=0.124, p-value<0.00001, n=156) (Figure 23). Therefore, if a daily precipitation amount increased by a millimetre, the DAX number was predicted to fall by 3.9% (linear regression trendline equation: y= -0.0147x + 0.0388). When no rain was recorded during the daily feeds window, the DAX figure was 13.47% (se±2.20, n=61). On days with low levels of precipitation (> 0.1mm and < 5.0mm) the average of DAX was -3.71% (se±2.67, n=65). When the total amount of daily precipitation was equal to or higher than 5.0mm, the average DAX ratio was -22.95% (se±5.29, n=35). The lowest feeds ratio (-100% DAX) was recorded on a day with 12.4mm of rain, and the highest feeds ratio (51.92% DAX) on a day with 0.0mm rain recorded.

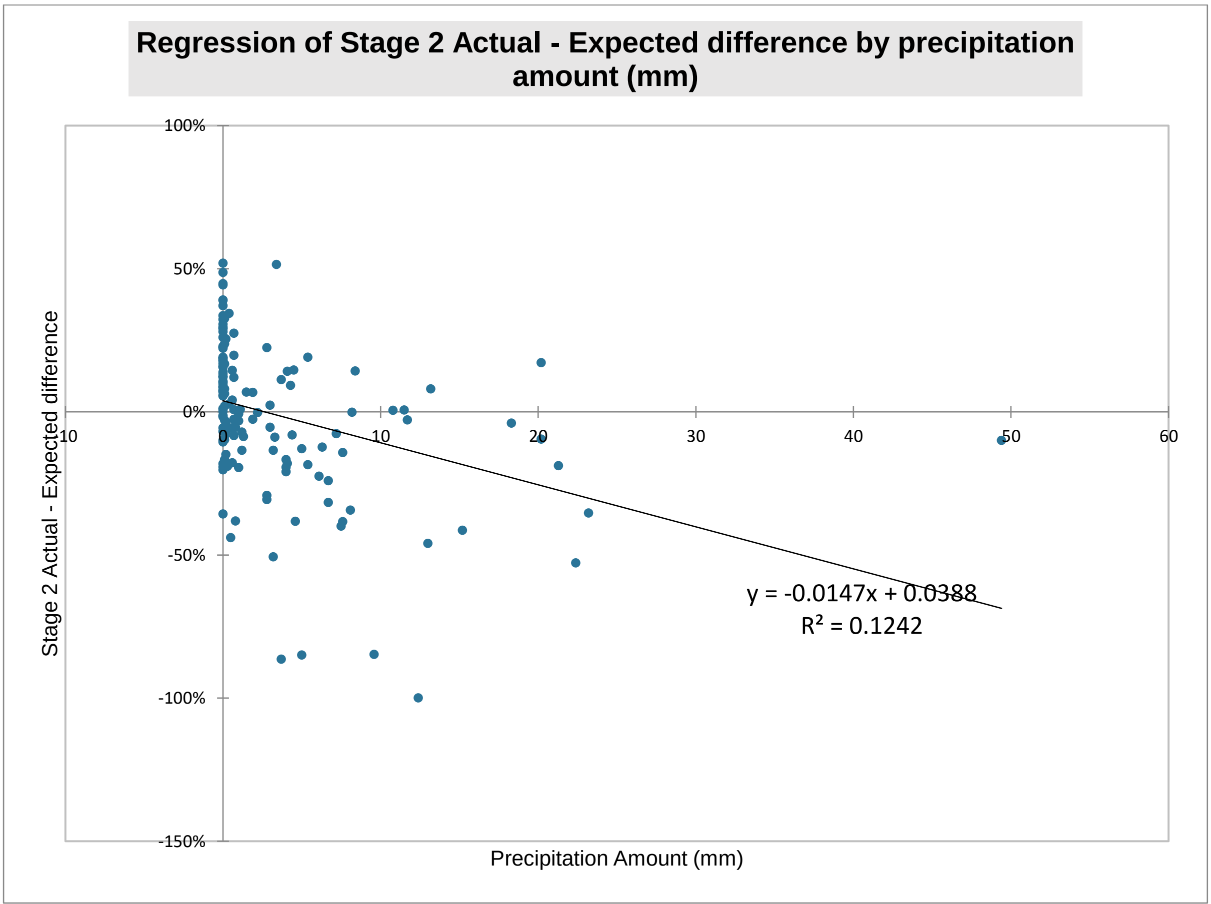


Figure 23. Regression analysis of the relationship between DAX and total daily rainfall (2018-2020). Only Stage 2 of chicks' development was included in the statistics (n=182).

The daily average wind speed was responsible for a 38.3% change in the daily DAX figure (linear regression, r^2=0.383, p-value<0.0001, n=156) (Figure 24). The linear regression between the two variables predicts that for every 1kt. increase in the average daily wind speed, the DAX figure decreases by 4.35% (linear regression trendline equation: y= -0.0595x + 0.4354). Feeding frequency was high when daily mean wind speed was below 4.42kt (low 10% of daily recordings, n=15), with DAX at 24.389% (se±4.57, n=15). Moreover, when daily wind speed was higher than 11.16kt (top 10% of daily recordings, n=15), the feed average was low at -25.90 (se±9.63, n=15). The lowest daily DAX figure recorded (-100%) coincided with the date with the highest mean wind speed (18.21kt).

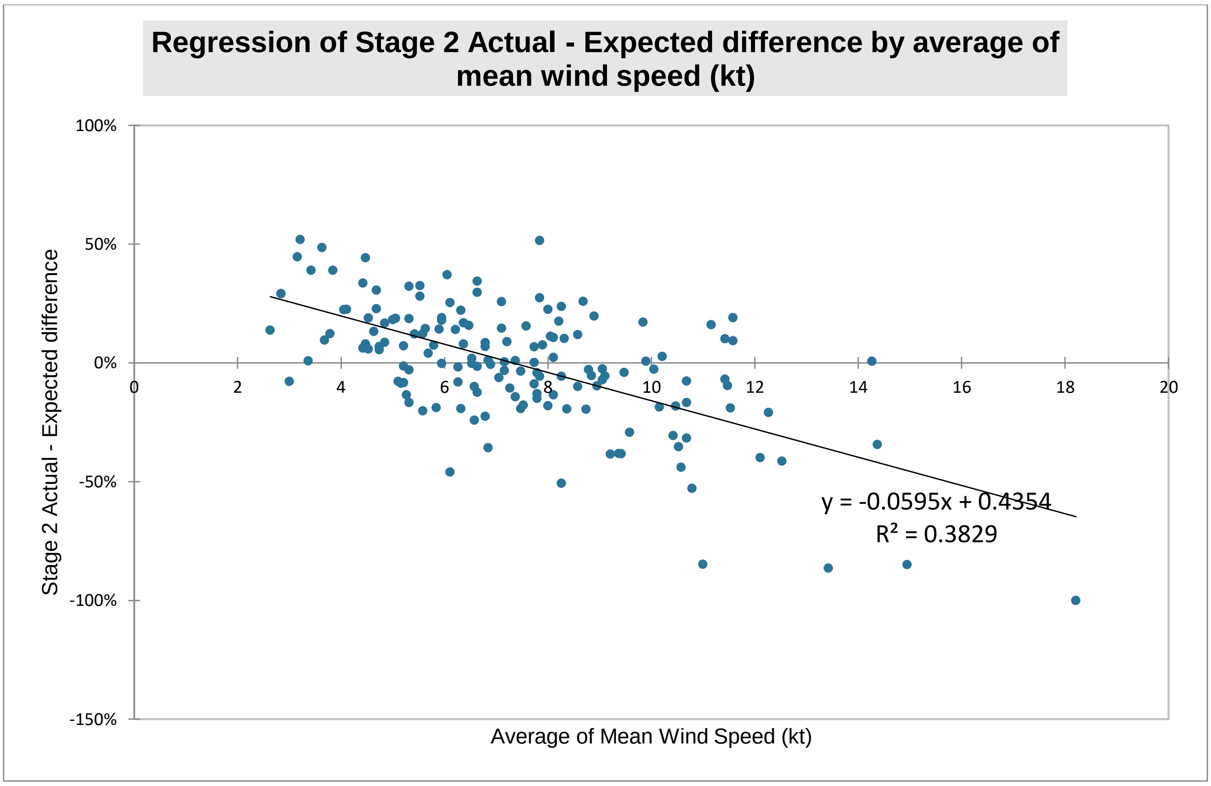


Figure 24. Regression analysis of the relation between DAX and mean daily wind speed (2018-2020). Only Stage 2 of chicks' development was included in the statistics (n=182).

4.5.7 Heatwaves and storms

According to Met Éireann (2020, p. 10), the colony in Castlebar experienced a heatwave during the 2018 season, lasting for six days (26 June 2018-30 June 2018). The colony in Castlebar experienced daily maximum temperatures of between 27.2°C and 30°C with no precipitation. Each day during the heatwave, adult swifts fed their chicks above the expected frequency, with a daily DAX average of 30% (se±0.04, n=5) (Table 20).

In 2020, the Castlebar colony experienced a severe summer storm lasting three days (27.06.2020-29.06.2020). During this period, the daily DAX number averaged at -79.76% (se±0.11, n=3) (Table 21). The temperatures fell each day to a minimum daily low of 10°C, with strong winds averaging 18.1kt on the second day of the storm. Feeding frequency on the second day of the storm was observed to be the lowest during the whole study period. Three out of seven swift breeding pairs (including pairs that at the time were incubating) did not leave the nest during the day. The remaining four exited the nest between two and six times. Chicks in one nest were not fed for 42 hours during this storm. No feeds were recorded in the Stage 2 on 6 June.

Table 20. DAX number recorded during the heatwave in June of 2018. Weather data from Met Éireann Claremorris weather station (Met Éireann, 2020).

Date	Δ %	Precipitation (mm)	Mean Temp (°C)	Max Temp (°C)	Mean Wind (kt)
26 June 2018	22.48%	0	22.1	27.2	4.1
27 June 2018	22.80%	0	23.6	29.2	4.7
28 June 2018	15.72%	0	24.3	30.0	6.5
29 June 2018	32.22%	0	23.8	29.1	5.3
30 June 2018	7.46%	0	20.5	26.8	5.8

Table 21. DAX number recorded during the storm in June of 2020. Weather data from Met Éireann Claremorris weather station (Met Éireann, 2020).

Date	Δ %	Precipitation (mm)	Mean Temp (°C)	Min Temp (°C)	Mean Wind (kt)
27 June 2020	-52.86%	22.4	11.8	10.2	10.79
28 June 2020	-100.00%	12.4	11.0	10.4	18.21
29 June 2020	-86.43%	3.7	11.6	10.6	13.42

4.6 Egg loss and replacement clutch

4.6.1 Egg loss results

The issue of egg loss during incubation was investigated by analysing video footage recorded during the 2018 to 2020 seasons in Castlebar and the 2020 season in Maguiresbridge. A total of 43 egg loss events were observed. The majority of these were recorded in Castlebar (n=38). Only four egg loss events were observed in Maguiresbridge, but the egg loss was reduced by the owner of the Maguiresbridge colony returning ejected eggs back into the nest cup.

4.6.2 Nest quality assessment

All of the studied breeding attempts in Castlebar and Maguiresbridge took place in nest boxes that were fitted with artificial, concave-shaped nest moulds. All of the observed breeding pairs used the nest mould that was provided to construct the nest. The colony in Castlebar used shallow moulds with narrow concave hollow, while Maguiresbridge used broader and deeper moulds. The shape of the nest mould influenced the quality of the nest cup constructed by the adult swift at both colonies. During the first few days after the clutch was laid, each nest was assessed for the amount of nest material collected at the start of the incubation period. Five specific gradings of nest quality were observed: “good” – nest with a large amount of nest material, deep construction of the nest cup; “moderate” – clear shape of a nest cup, but less material and clearly visible nest mould at the bottom of the nest cup; “poor” – a small amount of nest material collected, but nest cup not shaped (Figure 25); “very poor” – minimal amount of nest material collected and no visible nest cup shape; “no material” – no evidence of any nest material (Figure 26)

In Castlebar, of the 23 observed breeding attempts which produced eggs, eight nests were categorised as “good” (32.78%), six were “poor” (26.08%), eight were “very poor” (34.78%), and one had no nest material (4.34%) by the time the first egg was observed.

In Maguiresbridge, out of 22 breeding attempts that produced eggs, none of the nests were categorised as “good” (0.00%), one was “moderate” (4.54%), five were recorded as “poor” (22.72%), four as “very poor” (18.18%), and 12 had no nest material (54.54%) by the time the first egg was laid.

Figure 25. Screenshots illustrating the grading of the nest quality: Top left – "good"; Top right – "moderate"; Bottom – "poor";

Figure 26. Screenshots illustrating the grading of the nest quality: Right – “very poor”; Left – “no material”;

4.6.3 Egg loss

In Castlebar, the loss of at least one egg was observed in 15 out of 23 breeding attempts (65.2%). (Table 22) In Castlebar 38 eggs were lost in one of two ways – "deliberate" (by one of the adult swifts removing the egg out of the nest using its beak and throwing it outside of the nest box) and "accidental" (when the egg is misplaced by the adult swift body or a wing and without the use of its beak). Five eggs (13.16%) were lost due to deliberate removal of the egg by an adult swift, a behaviour observed only after a sudden disappearance of one of the parent swifts during the incubation period. The analysis of the video footage revealed that the remaining egg losses were caused by the movement of adult swifts in the nest, causing the eggs to roll out of the nest cup. Such events were categorised as accidental as there was no evidence of deliberate interaction with the egg. Accidental egg displacement was responsible for 86.84% (n=33) of egg loss in Castlebar. Most of the accidental egg loss in Castlebar (93.5%) took place in nests where the construction of the nest cup was either poor, very poor, or where there was no nest material at the time of the first egg-laying. In 34.8% (n=8) of all breeding attempts at the colony, the nest cup was well constructed at the time of the first egg, and the probability of the egg loss in those nests was 6.5% (n=2).

In Maguiresbridge, egg loss was observed in three out of 22 (13.6%) breeding attempts in 2020. Four out of 59 eggs laid by all breeding pairs were lost (6.78%). Three of the egg ejections were accidental during brooding, while one egg was ejected deliberately after a fight with an intruding swift. The results from Maguiresbridge do not include instances when the eggs were accidentally displaced, but the person that manages the site returned the eggs back into the nest cup.

Table 22. Analysis of egg loss and nest construction at the time of the first egg in the nest in Castlebar

A. Castlebar 2018

Nest	Date of 1st egg	Nest at laying	Nest at hatching	Egg loss	Reason	Outcome
Box 1	27/05/2018	Good	Good	0		
Box 2						
Box 3						
Box 4						
Box 5	04/06/2018	Poor	Good	2	Accidental	Improvement of the nest, replacement clutch successful
Box 6						
Box 7	28/05/2018	Poor	Good	0		
Box 8						
Box 9	29/05/2018	Good	Good	0		
Box 10	04/06/2018	Very poor	Good	2	Accidental	Improvement of the nest, replacement clutch successful
Box 11	25/05/2018	Very poor	Good	2	Accidental	Improvement of the nest, replacement clutch successful
Box 12		Unknown	unknown		unknown	

B. Castlebar 2019

Nest	Date of 1st egg	Nest at laying	Nest at hatching	Egg loss	Reason	Outcome
Box 1	17/05/2019	Good	Good	0		
Box 2	29/05/2019	Very poor	Good	2	Accidental	Improvement of the nest, replacement clutch successful
Box 3						
Box 4						
Box 5	31/05/2019	Very poor	Good	2	Accidental	First and second eggs lost, third egg incubated successfully
Box 6						
Box 7						
Box 8	27/05/2019	No material	Breeding failure	5	Accidental	Initial and replacement clutch lost
Box 9	16/05/2019	Very poor	Good	1	Accidental	First-laid egg was lost, second and third egg incubated
Box 10	12/06/2019	Poor	Good	0	0	
Box 11	17/05/2019	Very poor	Good	1	Accidental	First-laid egg was lost, second and third egg incubated
Box 12	13/06/2019	Very poor	Good	2	Accidental	Replacement clutch with one egg successful.

C. Castlebar 2020

Nest	Date of 1st egg	Nest at laying	Nest at hatching	Egg loss	Reason	Outcome
Box 1	10/05/2020	Good	Good	5	Adult lost+ accidental	New adult, new clutch laid and lost, replacement clutch of one egg laid and successful (total of three clutches in the nest)
Box 2	19/05/2020	Good	Good	0		
Box 3						
Box 4						
Box 5	02/06/2020	Poor	Breeding failure	2	Accidental	No replacement clutch laid – breeding failure
Box 6						
Box 7	04/06/2020	Good	Good	0		
Box 8	19/05/2020	Poor	Breeding failure	4	Accidental	Replacement clutch lost – breeding failure
Box 9	12/05/2020	Good	Good	0		
Box 10	02/06/2020	Very poor	Good	2	Accidental	Replacement clutch successful
Box 11	11/05/2020	Poor	Good	4	Accidental	Replacement clutch successful
Box 12	15/05/2020	Good	Good	2	Adult lost	New adult, new clutch laid and successful

Table 23. Analysis of egg loss and nest construction at the time of the first egg in the nest in Maguiresbridge.

Maguiresbridge 2020

Nest	Date of 1st egg	Nest at laying	Nest at hatching	Egg loss	Reason	Outcome
Gable 1	14/05/2020	Poor	Good			
Gable 2	04/06/2020	Moderate	Good			
Gable 3	14/05/2020	Very poor	Good	1	Accidental	Returned to the nest and hatched
Gable 4	15/05/2020	Very poor	Good			
Gable 5	18/05/2020	Poor	Good			
Gable 6	01/06/2020	Poor	Moderate			
Gable 7	18/05/2020	Poor	Good			
Gable 8						
Gable 9						
Gable 10	02/06/2020	No material	No material			
Gable 11	01/06/2020	No material	No material			
Gable 12	17/05/2020	No material	Good			
Gable 13						
Gable 14	03/06/2020	No material	No material			
Attic 15	12/05/2020	Very poor	Poor			
Attic 16	01/06/2020	Very poor	Poor			
Eaves 1						
Eaves 2						
Eaves 3	30/05/2020	Poor	Good			
Eaves 4						
Eaves 5	13/05/2020	No material	No material			
Eaves 6	14/05/2020	No material	Moderate			
Eaves 7	11/05/2020	No material	No material			
Hi Eaves 1	20/05/2020	No material	No material	2	Accidental	Fostered in different nests and failed
Hi Eaves 2						
Hi Eaves 3						
Hi Eaves 4						
Back 8	31/05/2020	No material	Very poor			
Back 9						
Back 10	14/05/2020	No material	Poor			
Back 11	13/06/2020	No material	No material			
Back 12	19/05/2020	No material	Poor	1	Ejected after a fight	Returned to the nest but failed

4.6.4 Replacement clutch

The loss of a whole clutch was observed in 53.1% (n=12) of all breeding attempts in Castlebar. As a consequence, replacement clutches were laid in 91.6% (n=11) of those events. The averages size of the replacement clutch was 1.83 (se±1.83, n=11), while the mean date of the first egg in the replacement clutch was 16 June (se± 3.14, n=11), and the range was 28 May to 28 June.

In Maguiresbridge, the loss of the whole clutch took place in two breeding attempts out of the observed 22 (9.09%, n=2). Out of these, only one pair laid a replacement clutch of two eggs, with the first egg laid on 3 June 2020.

4.7 Conclusion

The foregoing chapter contains all the results of all statistical analyses of the data collected during the study period. Firstly, data from Castlebar and Maguiresbridge colonies were used to map out the breeding calendar of the Common Swift in Ireland. Secondly, results from both locations allowed the breeding success of the swift to be measured. Thirdly, the comprehensive analysis of video footage from 19 breeding attempts in Castlebar provided hourly, daily and seasonal patterns of chick feeding frequencies. Lastly, this chapter provides result from the study of the egg loss phenomena. The content included in this chapter will provide a substantial amount of evidence to support the answers to questions of this research and fill in some of the knowledge gaps of the Common Swift’s breeding biology in Ireland and beyond. The following chapter focuses on the critical analysis of the four themes and provides a discussion on the research results, comparing previous records from other territories.

Chapter 5: Discussion

5.1 Introduction

The data collected during this study for the phenological calendar, breeding performance, feeds frequencies and egg loss of the Common Swift at colonies in Castlebar and Maguiresbridge provided the first comprehensive study of the species in Ireland. The results from this study are comparable to other studies of the species in other territories. As this research was based on data gathered only with video recordings, certain aspects of the breeding biology that were studied elsewhere, such as physical measurements of the egg and bird's body weight, were not available. Moreover, while both studied colonies use artificial nest boxes, they differ in the construction of the cavity type and the nest mould type. Additionally, the colony in Castlebar remained inaccessible for the entirety of the breeding season, while the colony in Maguiresbridge was accessible and managed so as to prevent egg loss. This situation provided two separate sets of results that can be compared and contrasted in terms of nest box construction and conservation management effectiveness.

5.2 The population of studied colonies

A majority of the studies on the breeding biology of the Common Swift are based on the observations of birds occupying artificial nest boxes (Lack, 1956, p. 19; Martins, 1997, p. 100; Tigges, 2006, p. 28; Sicurella, et al., 2015, p. 66). However, this study was unique from the perspective that it was conducted from the moment of inception, rather than already well-established colonies. Therefore, it was possible to observe the yearly growth of swift numbers in artificial colonies.

In Castlebar, nest boxes first installed in 2012 saw their first breeding swifts arrive two years later in 2014. The number of breeding pairs at the colony increased each year by one or two over the course of the research period. By 2020, there were nine breeding pairs occupying 18 available nest cavities (50%). All of the remaining cavities were either occupied by non-breeding pairs or were regularly visited by individual swifts. Therefore, there is the possibility for a continued increase in breeding pairs at the colony. A more rapid growth in breeding pairs occupying nest boxes was observed in the swift colony at Maguiresbridge. Similar to Castlebar, there was a positive growth in numbers each year across the study period. The colony began in 2014 with three breeding pairs, and by 2020, there were 23 breeding pairs, occupying 33 available nest cavities (69.7%) with the potential for future increases owing to the presence of a number of non-breeding pairs. Therefore, both colonies successfully established large (relative to the numbers of the available nests) colonies quickly, pointing out the suitability of the nest box projects to provide substitute nesting opportunities. The fact that both colonies continue to grow is contrary to the reports of a decrease in numbers of the Common Swift on a national level, as the species is currently on the Red List of Conservation Concern (Gilbert, et al., 2021, p. 8).

The yearly growth of both colonies raises a question regarding colony recruitment and where the new swifts come from. The survival rate of the Common Swift in Oxford was reported by Perrins (1971, p. 65) to be oscillating around 79%. In Scotland, Thompson et al. (1996, p. 34) estimated the survival rate at 76.16%. In northern Italy, the mean annual survival rate was 78% as reported by Boano et al. (2020, p. 7923). Therefore, if the annual mortality rate (21-24%) was actual for the studied breeding sites, the colony in Castlebar would lose yearly between 4-5 adult swifts and the colony in Maguiresbridge between 10-12 adult swifts. The age of the first breeding for the Common Swift is believed to be four (Perrins, 1971, p. 65). Therefore, assuming the reported average survival rate applies to all swifts regardless of age and age of the first breeding was four, only around 25.5 - 30% of the Common Swift chicks would reach a reproductive stage. In 2020, the colony in Castlebar consisted of nine breeding pairs and produced 12 chicks. Assuming that the survival rates are true, the colony will lose four breeding swifts before the next breeding season, and only three fledgelings will reach the productive age. In Maguiresbridge in 2020, 23 breeding pairs produced 51 fledgelings. Using the same assumptions, the colony will lose ten adult swifts, and 16 fledgelings will reach reproductive age. Therefore, the assumptions suggest that, even though the numbers of breeding swifts increase each year, the colony in Castlebar is currently not sustainable (sink). In contrast, the colony in Maguiresbridge produces enough chicks to be considered a source colony (Seward, et al., 2018, p. 144).

Due to the nature of the methodology, it was not possible to confirm if the same pairs returned each season to the same nest. Still, there is strong evidence from other studies that swifts tend to return to the same nest hole (Perrins, 1971, p. 66). Therefore, if the same was true for both of the studied colonies, five pairs bred continuously for seven years, three pairs for six years, and six pairs for at least five years. Once breeders occupied the nest cavity, there was a very high probability that the same cavity would be occupied again next year (89%). Moreover, many swift pairs attempted to breed in the first year of using the nest box, and this was more pronounced in Maguiresbridge.

The percentage of occupied nests in this study was much higher than in some of the previously published studies. Shaub et al. (2016, p. 167) recorded a nest box occupancy level of 24.3% from a city in Germany, while Luniak & Grzeniewski (2011, p. 5) placed this at 26.5% in Poznan, Poland. The difference in results may be due to the survey method of the two mentioned studies, which focused on surveying large numbers of boxes by observations of swifts entering into a nest hole, while this study reported only on the boxes with breeding pairs at only two nest box project sites. However, Newell (2019, p. 25) published a study highlighting differences in occupancy levels between swift box designs with and without artificial nest forms. The boxes with an artificial nest form reported a 48.4% occupancy level (range 25-58%) while boxes without a nest form reported only a 15% occupancy level (7.5%-25%). New nest boxes installed in Castlebar in 2019 didn’t include artificial nest forms, and as of 2020, none of them had hosted a breeding pair. Shaub et al. (2016, p. 170) also reported on additional factors influencing the occupancy of the nest box. Firstly, he found that boxes that provided a single nest cavity, just like the ones in Maguiresbridge, were much more frequently occupied than one’s with the triple entry boxes, identical to ones in Castlebar. Moreover, Shaub et al. (2016, p. 170) reported that the swifts are less likely to occupy the nest cavity in close proximity to other swifts (<1m). This may explain the fact that the first occupied boxes in Castlebar were “Box 1” and “Box 12” – the ones further apart, and that, in general, the edge cavities of the triple entry boxes appeared to be favoured by the swifts. This wasn’t considered to be a factor in Maguiresbridge, where all boxes are further apart than the ones in Castlebar. However, more evidence from additional sites would be needed to confirm a correlation between the nest box type and the occupancy levels.

5.3 Breeding calendar

5.3.1 Timing of spring arrival

Previous studies of the spring arrivals of the Common Swift claimed that the timing of the event is rigid, with minimal yearly variation recorded at studied colonies in England (Lack, 1958, p. 478; Mason, 1995, p. 183), Scotland (Jenkins & Watson, 2000, p. 245) and Ireland (Carroll, et al., 2009, p. 121). For the most part, the results in this study confirm these statements, as there was no yearly variation in the range of the timing of spring arrivals and the annual average in most of the study's years at the colonies in Castlebar and Maguiresbridge. The exception to this however was observed in 2020 when birds arrived earlier than in previous years. Between 2014 and 2019 at both colonies, the spring arrival times saw almost no variation. The first birds appeared in their nests in the first week of May, then the majority of breeders arrived in the second week of May, and the remaining swifts arrived in late May and early June. However, in 2020 at both colonies, the pattern of arrivals took place a week early, with some arrivals in late April and the majority returning in the first week of May. The mean arrival date in 2020 in Maguiresbridge was five days earlier than in any other studied year. The evidence suggests two possible reasons. Firstly, the early arrivals in 2020 may be associated with the fact that the colonies are well established, and that the majority of breeding pairs have bred for a number of years consecutively. Secondly, the weather in April 2020 was hot across the European continent for that time of year. Countries on the migration pathway for swifts destined for Ireland such as Spain and France, experienced above average monthly temperatures. Spain also had very little rainfall. Moreover, relatively dry and warm conditions were recorded in Ireland at the end of April 2020. It is possible then that the combination of an established breeding population and favourable weather conditions allowed some swifts to start the breeding season early in 2020.

The mean arrival times in early to mid-May were consistent with those recorded for the Common Swift breeding at similar latitudes across the European continent (Lack, 1956, p. 27; Tigges, 2007, p. 29; Åkesson, et al., 2020, p. 2381, Kalaykina, 2007, p.1). Gordo et al. (2007, p. 1072) stated that the arrival times may differ across relatively close regions and may be caused by environmental factors such as differences in weather and geographical constraints. However, colonies in Castlebar and Maguiresbrige experience very similar weather conditions. The distance between the colonies would not be such to influence a difference in the timing of the swifts' spring arrival.

The return of both breeding swifts (in a breeding pair) on the same day was rare (7.5% in Castlebar and 10.2% in Maguiresbridge) and should be considered as accidental. In most cases, there were several days between the arrivals, confirming previous observations that the swifts are unlikely to migrate in pairs and instead only meet to breed (Lack, 1956, p. 38). Pairs thought to have bred in previous years assembled first, usually in the first and second week of May. However, there were also records showing a gap in arrivals, by as much as three weeks (9 May and 31 May). Pair assemblies in the last week of May and the first week of June were the least frequent but are recorded each year at both colonies. Unfortunately, due to the limitations of the research, it was not possible to determine if these late arrivals were returnees or new partners of experienced breeders. In one instance, the first bird arrived on 9 May 2019, and for an extended period, was seen roosting in the nest on its own. Three weeks later, on 31 May 2019, another swift began roosting in the nest, and the pair eventually laid their first egg on 12 June. It is possible that in this scenario, the experienced bird was waiting on the return of its partner but eventually was forced to search for a new mate. If both birds in a breeding pair appeared in the nest in the last few days in May and early June, they were always new breeding pairs in the previously unoccupied box. Therefore, both observations confirm that the late arrivals are probably, in most cases, first-year breeders.

The behaviour of swifts' upon returning to the nest was noted in Castlebar and provided some interesting insights. As already mentioned, the pair assembly is in most cases separated by a few days. The behaviour of the first returning swift was characterised by inactivity in the nest, spending most of the time outside, in some cases only returning to roost. However, the behaviour changes upon arrival of the partner. The first meeting appears almost hostile, but the birds appear to recognise each other and settle after a few seconds. From that moment on there was an immediate increase in activity within the nest with frequent exits and entries. The majority of activity was concentrated on accumulating nest-building material. Rarely was a single swift collecting nest material, those incidents were rare. Nest material collection continued even after the first egg is laid, as reported previously by Lack (1956, p. 51). In the last three years of the research, the inspection of footage from Castlebar and Maguiresbridge revealed that swifts collect airborne plastic to construct their nest (Figure 27). This was first observed in 2018 when one pair brought what looked like a piece of a single-use plastic bag. Similar observations were made in the following years. During the maintenance of the nests at the end of the 2019 breeding season, a small pieces of plastic candy wrapper and other small pieces of plastics were found in at least two of the eight breeding pairs nests'.

Figure 27. Evidence of plastic being used as a nest construction material.

5.3.2 Timing of egg-laying and incubation period

When discussing the egg-laying dates recorded in this study, it is crucial to begin by stating that both colonies, but particularly the colony in Castlebar, experienced extensive egg loss during the incubation period. In many cases, this led to the loss of the whole clutch, sometimes of three eggs. If this happened, the pair usually laid a replacement clutch, usually in mid to late June. The explanation for the egg loss will be discussed later in this chapter, but for the purpose of the study of the timing of egg laying the replacement, clutches were not taken into consideration and will be discussed separately.

The yearly average timing of the first egg in the clutch did not change across the study period (not including averages skewed by a low number of breeding birds), confirming the hypothesis of the rigid phenological cycle of the Common Swift. In Castlebar, the yearly mean dates of the first egg fell between 21 May and 30 May. Similarly, in Maguiresbridge, the average first egg dates range was 23 May to 29 May. The range of timing of the first egg at both studied colonies fell between 10 May and 25 June (not inclusive of replacement clutches). The average and range of the timing of the first egg is consistent with ones reported at similar latitudes in England (Lack & Lack, 1951, p. 514; O'Connor, 1979, p. 133) and Germany (Tigges, 2006, p. 29).

Lack & Lack (1951, p. 514) and O'Connor (1979, p. 133) claimed that the onset of egg-laying may be delayed due to periods of low temperature, rain and strong wind. While they may have reported on the influence of weather on individual pairs, our study focused more on the performance of the colony. Therefore, the weather in either of the studied colonies did not affect the average timing of the first egg in the clutch. The only factor that caused a slight variation in the results of the timing of egg-laying was the timing of the spring arrivals of the breeding swifts. In years with the earliest annual average arrival times, the mean date of the first egg occurred earlier. This connection may appear obvious, but it was omitted in some of the previous studies.

The interval between the laying of consecutive eggs in the clutch was, in most cases, two days between the first and second egg, while the gap between second and third was often extended to three or four days, consistent with previous studies (O'Connor, 1979, p. 133). The incubation period in Castlebar and Maguiresbridge ranged between 18 to 24 days, similar to observations by Lack & Lack (1951, p. 514).

5.3.3 Timing of hatching and fledging

At both colonies, the average timing of hatching and fledging did not show any significant yearly variation, further confirming that the phenological breeding cycle of the Common Swift is hardwired to a very precise calendar. The onset of the chick feeding period coincides with the highest temperatures and the most prolonged daytime hours.

There was a significant difference between the average seasonal timing of all hatching and fledging times at both colonies. When all of the hatching and fledging events were taken into consideration throughout the whole of the study period, the average for both events was delayed in Castlebar by seven days. On average, hatching in Castlebar took place on 22 June while in Maguiresbridge it occurred on 15 June. Similarly, the average fledging time in Castlebar was 3 August while in Maguiresbridge it was 26 July. This delay was even more pronounced in later years of the study when both colonies were well established. In 2018, 2019 and 2020 the mean hatching date in Castlebar was delayed by 14, 5, and 11 days respectively when compared to Maguiresbridge. For the mean fledging times in the same three years, the colony in Castlebar was delayed by 11, 5 and 12 days. As there was no significant difference between the spring arrivals and timing of the first egg at both colonies, the delay of colonies hatching and fledging in Castlebar could not have been accidental. Both locations experience similar weather conditions, and both did not record any events of predation. The only apparent difference between both colonies was the level of egg loss at the colony in Castlebar. The delays in 2018 and 2020 coincided with the colony's extremely low initial clutch success rate (42.8% in 2018, 44.4% in 2020). While the egg loss was also observed in Maguiresbridge, the success rate of the initial clutch was 81.2% in 2018 and 91.3% in 2020. The multiple failures of the whole first clutch in Castlebar forced breeding swifts to lay a replacement clutch later in the season. Therefore, the hatchings and consequential fledglings from eggs laid in the replacement clutch caused the delays. To further illustrate the level of impact of the loss of a clutch on the timing of hatching and fledging in Castlebar, in 2019, the last egg hatched on 15 July, and the first chick fledged on 17 July. Similarly, in 2020 the last recorded hatching was recorded on 13 July and first fledging on 16 July. Therefore, some chicks were fully developed and ready to fledge, while some in the same colony only hatched. Previous studies suggest that chicks from late broods tend to fledge later and weigh less than chicks from earlier broods (Lack & Lack, 1951, p. 519). On that account, the chicks who fledge from replacement clutches may have lower fitness levels, and are forced to migrate later than those who fledged earlier in the season. A combination of those two factors may cause them to compete for lower quality feeding grounds during wintering, affecting their fitness upon returning north the following season, as per the chain migration theory of the Common Swift presented by Åkesson et al. (2020, p. 2388).

5.3.4 Length of the chick-rearing period

In previous studies in England, Lack & Lack (1951, p. 93) reported that chicks fledge on average 42.5 days after hatching, with a range of 37 to 56 days. Martins (1997, p. 100) further noted that the chick-rearing period's average time was between 41.3 to 43.6 days, depending on the brood size. In Germany, Tigges (2007, p. 136) recorded the medial value of the age of the chick at fledging as 43 days. In this study, the average fledging period was consistent with those reported by Lack & Lack (1951, p. 93) and Martins (1997, p. 100) and Tigges (2007, p. 136). The shortest recorded chick-rearing time period in this study was 38 days and the longest was 48, a ten days difference. Contrary to Lack & Lack (1951, p. 93), who concluded that weather had a significant effect on the prolonging of the chick-rearing period for the young swifts, there was no evidence that the weather conditions affected the average length of stay of the nestlings in the nest. The same results were presented by Martins (1997, p. 101). At both studied colonies, there was no recorded yearly variance in the average chick-rearing period. Therefore the weather conditions during this study were not as severe as in Lack & Lack (1951, p. 93). However, the average chick rearing period in 2020 at both colonies for the broods with two chicks was delayed by three days in Castlebar but only by one day in Maguiresbridge compared with the results from 2018. The months of June, July and August in 2020 were on average colder and wetter than in 2018 (Met Éireann, 2000). Therefore, it is possible that weather played a role in delaying the fledging periods by a few days, but during this study, the adult swifts were able to control the impact of this variable on the length of the chick-rearing period.

5.3.5 Adult departure dates

For the breeding swifts, the departure dates are mainly determined by the timing of fledging of young and not by the availability of food (Tigges, 2007, p. 136). Departure dates may also be a determining factor in the competition for the best wintering grounds in Africa (Åkesson, et al., 2020, p. 2385). At the same time, raising a brood requires a high energy output, and parent swifts are known to drop in weight when feeding young, significantly when raising large broods (Martins & Wright, 1993, p. 213). Lack (1956, p. 156) observed that the average interval between the last fledging and the adults' departure was influenced by the weather. The study of swifts in Castlebar and Maguiresbridge does not confirm this observation. The interval time of adult departures was recorded and ranged from 0 to 42 days. In the case of one nest in 2020 in Maguiresbridge the adults left on 3 and 4 September, when the last fledgling had left the nest on 23 July. The weather in August 2020 happened to be relatively dry and warm. In addition, even though the average timing of fledging occurred later in Castlebar (3 August to 27 July in Maguiresbridge), the average departure dates were recorded earlier (16 August in Castlebar to 20 August in Maguiresbridge). As the difference in weather between Castlebar and Maguiresbridge was not significant, the reason for the delayed departures in Maguiresbridge may be due to the much higher average number of raised chicks per breeding attempt (1.53 in Castlebar to 2.13 in Maguiresbridge). Therefore, in this study, the departure dates may have been related to the size of the brood raised and its impact on the fitness of the parent swifts. The prolonged stay in the nest after the last chick fledge may be related to the need for recovery time before the journey commences the wintering grounds. The average timing of the departure falls in mid to late August and is similar to departure dates for the Common Swift recorded in Scandinavian countries and later than observations made in other areas on a similar latitude to Ireland (Tigges, 2007, p. 133; Åkesson, et al., 2020). As there was no significant yearly variation in the mean departure dates, the evidence points to later departure dates for Irish swifts in comparison to those breeding in the UK, or eastern and central Europe.

5.3.6 Breeding calendar summary

The evidence collected during this study on all aspects of the breeding calendar of the Common Swift suggests that the phenological breeding cycle for the species is quite rigid, with minimal variation in yearly means of arrival dates, egg-laying, fledging, hatching and departures. The arrival dates in Ireland can be slightly affected by the weather conditions in Europe. The timing of hatching and fledging in one of the studied colonies was greatly influenced by the egg loss. Colony departure dates are affected by the average number of fledglings per breeding attempt. Overall, weather conditions had no major influence on the timing of any events in the breeding calendar for the Common Swifts during the study.

5.4 Breeding success

5.4.1 Clutch size

The average number of eggs in the clutch at both studied colonies was similar. However, the composition of the clutch sizes varied. The colony in Castlebar reported no one-egg clutches, and they were rare in Maguiresbridge (6.81%). There was a significant difference between the colonies when it came to the occurrence of two and three egg clutches, with the higher number much more common in Maguiresbridge. As the weather conditions experienced by the colonies does not vary significantly, the leading cause of such difference may be due to two factors. The size of the nest box and nest mould in Castlebar was much smaller when compared to the ones provided for the swifts in Maguiresbridge. Another possible factor can be related to the locations of the two studied colonies. The colony in Castlebar is located in an urban area with a large local swift population.

In contrast, the colony in Maguiresbridge is situated rurally in a landscape characterised by farmland, and away from an urbanised area with a small local swift population. O'Connor (1979, p. 143) stated that the breeding habits of the Common Swift are adapted to the exploitation of the food supply. Therefore, if the food supply is of lower quality in Castlebar, a brood of two may be more productive. A similar scenario was observed by Lack & Lack (1951, p. 510) in England.

In Castlebar and Maguiresbridge, there was a slight correlation between the timing of the first egg and the clutch size, with larger clutches more likely to be laid early in the season. This level of correlation, while not majorly significant, is consistent with observations in England (Lack & Lack, 1951, p. 510; O'Connor, 1979). There was no evidence of four egg clutches or a second clutch (not including replacement clutches caused by egg loss), a common occurrence for the Pallid Swift breeding in southern Europe and rare in Alpine Swift (Antonov & Atanasova, 2001, p. 543).

5.4.2 Brood size and productivity

There was a significant difference between the productivity of the two studied colonies: 45% in Castlebar and 89% in Maguiresbridge. The colony in Castlebar experienced severe egg loss each season, often leading to the loss of the whole clutch and breeding failure if the replacement clutch was not laid. Throughout the entire study period (2014-2020), the average number of hatchlings per breeding attempt in Castlebar was 1.53 (se± 0.158) and fledglings 1.38 (se± 0.15). During the same period, the colony in Maguiresbridge produced an average of 2.28 (se± 0.08, n=88) hatchlings and 2.13 (se± 0.09) fledglings per breeding attempt. When those results are compared with ones recorded in other territories, the averages in Castlebar were below the mean values for northern regions of Scandinavia (2020, p. 2383). In contrast, the mean averages of hatchling and fledgelings from Maguiresbridge are comparable to ones recorded in areas at lower latitudes such as Spain and Italy (Sicurella, et al., 2015, p. 70; Åkesson, et al., 2020, p. 2382).

As discussed previously (**5.2**), the low productivity and low number of fledgelings recorded in Castlebar may result in the colony not producing enough chicks and may be considered a sink site. Therefore, the recruitment of new breeding swifts to the colony may be detrimental the local population. However, it is only an assumption based on the previous calculations regarding annual survivability rates (Perrins, 1971, p. 65; Thomson, et al., 1996, p. 34; Boano, et al., 2020, p. 7923). In contrast, the colony in Maguiresbridge produces enough fledgelings in a season to be considered a source site.

5.4.3 Brood reduction and chicks' mortality

Predation was not a factor in chicks' mortality in our study. In other territories, the predation of swifts is caused by other birds, or rodents (Antonov & Atanasova, 2002, p. 5). In this study swifts were occupying purpose build nest boxes that may have reduced or perhaps eliminated the predation factor. This does not mean that the chicks in the nest boxes were not prone to death from intruders. We recorded one event in which a chick was killed following a fight between its parents and a third adult swift. As this was the only remaining chick in that brood, the parents abandoned the nest shortly after. A similar event took place when an intruding adult swift entered an unattended nest and attacked a single chick for almost an hour before both parents returned. After a further hour of fighting, the intruder left the nest, but the chick survived.

The more common cause of death in swift chicks' before fledging is falling out of the nest before they are ready to take on their first flight. Those cases were not recorded during this study. However, there is anecdotal evidence of chicks being found on the ground beneath known natural nesting locations, suggesting accidental falls from the nest cavities.

The most common cause of chick mortality in Castlebar and Maguiresbridge was adult swifts failing to provide sufficient food for the chicks. In most cases, the chick that hatched last in a brood of three or two could not compete for food. This was also observed in other studies (Sicurella, et al., 2015, p. 73; O'Connor, 1979, p. 140). The underfed chick was smaller than its siblings, often didn’t develop plumage, and became progressively passive when adults returned. Most deaths from starvation happen four to ten days post hatching, but chick mortality was also recorded on the 25th day. In one observed instance in Maguiresbridge an entire brood perished not long before fledging, but this was due to one of the parents' disappearing, and the remaining adult could not provide sufficient food to sustain the two chicks.

The evidence suggests that the largest chick mortality ratio was recorded in 2020 in both colonies. In Castlebar, where the number of breeding pairs is smaller in most years, there was either one or no fatality. In 2020 out of 14 chicks that hatched, two died. The ratio may not appear substantial at first, but what needs to be considered is that from 2017 to 2019, there was only one death from 31 hatchlings. Similarly, at Maguiresbridge, a total of six chicks perished in 2020, All fatalities were due to starvation, and there were no deaths in 2018 (35 hatchlings) and one in 2019 (41 hatchlings). The report of high chicks’ mortality in 2020 was also reported in other parts of the country. For example, at one colony in County Kildare, in six breeding attempts, out of 13 hatchlings, eight died before fledging (unpublished records supplied by Dermot Doran). This evidence points out that in 2020 the swifts in Ireland experienced food shortages due to unfavourable summer conditions. This negative influence of bad weather was observed previously in other territories (Kindlmann, 2006, p. 70; Martins & Wright, 1993, p. 69; Sicurella, et al., 2015, p. 74).

5.5 Patterns of feed frequencies

5.5.1 Season totals

The results of this study provided a detailed description of the feeding frequency patterns across all breeding seasons for 19 breeding pairs. Where applicable the results were compared with similar studies of the Common Swift elsewhere in Europe. However, some of the results provided information about the parental care of the Common Swift that was never published before, such as the total number of feeds in a season, detailed hourly feeding patterns, and the relationship between daily feeding frequencies and the age of brood (measured from the first observed feed). Additionally, the use of the proprietary DAX function (difference between actual daily feeds and expected feeds), illustrated the influence of rain, wind and temperature on the daily feeds frequencies of chicks for the whole colony.

The Castlebar colony provided a large sample of adult swift visits to the nest during the chick-rearing period. In 7.15% of all visits, there was no evidence of a bolus exchange between the adult and chick. A similar ratio of ‘feed’ to ‘no-feed’ visits to the nest was recorded in Italy by Carere & Alleva (1998, p. 1384). However, this result is significantly lower than one recorded in Oxford, UK where ‘no-feed’ visits constituted 25% of total visits (Martins & Wright, 1993, p. 216). The difference in the ratio between the Castlebar and Oxford colonies may have been caused by food availability, due to the proximity of better foraging grounds, or smaller competition due to the size of the local swift population. Moreover, some of the breeding pairs rarely returned to the nest without food. In one breeding attempt, one pair of swifts recorded only 0.9% of ‘no feed’ visits, while different pairs recorded 16.2% ‘no-feeds’. The reason for this discrepancy is not clear, but it may be down to poor food availability during the season or the inexperience of the breeding pair. Adult swifts also need to allocate food for themselves to sustain the parental effort of raising a brood. It is possible that higher competition for food resources causes swifts in Oxford to allocate more time to self-feeding (Martins & Wright, 1993, p. 216).

The size of the brood was a determining factor in the total number of feeds during the whole of the chick-rearing period. There was a significant difference in the total number of feeds per breeding attempt between broods of one chick and the broods of two (increase of 32.87%) and between broods of two and those made up of three chicks (increase of 14.4%). This means that at the Castlebar colony, adult swifts raising larger broods were required to increase the frequency of feeds. This increase was not linear, and it was not proportionate to the number of chicks. A similar pattern was observed in Oxford by Lack (1956, p. 188) and Martins & Wright (1993, p. 64). This was also true for the Common Swift breeding in Rome, Italy (Carere & Alleva, 1998, p. 1385). Martins and Wright (1993, p. 215) recorded no significant increase in the mass of food deliveries between different broods. Therefore, the lack of a linear increase in feeding rates and no increase in the size of the bolus for different broods’ sizes could mean that the Common Swift may struggle to provide enough parental care to raise three chicks. As it appears, chicks from broods of three receive the lowest amount of food in the season. Chick mortality in the nest is known to increase with brood sizes (Lack, 1956, p. 186). In Castlebar, chick mortality was observed only in broods consisting of two and three chicks. Moreover, chicks from large broods fledged a few days later than from nests with smaller broods.

5.5.2 Hourly feeding patterns

In the Castlebar colony, no feeds were recorded at night (11 p.m. to 4.30 a.m.). Even though the colony is located in an area where there is artificial lighting, swifts returned to the nest regularly at dusk and left the nest at dawn. Artificial lighting can cause swifts activity throughout the night (Amichai & Kronfeld-Schor, 2019, p. 4), but this was not observed in Castlebar.

Chicks were fed at different rates during the day. Three periods of high feeding activity were observed: early morning, afternoon, and late evening. Morning rush happened after sunrise and lasted for about one to two hours. During this time, the ‘feed’ and ‘no-feed’ visits to the nest were most frequent, pointing out the need for the necessity to replenish lost energy reserves following a night of fasting and possibly a heightened level of competition for food during that time. A similar pattern of high ‘feed’ and ‘no-feed’ visits was observed during the last two hours before dusk when swifts presumably attempt to forage as much as possible before the roost. However, the same pattern was not observed for the peak in ‘feeds’ in the afternoon, when a very small number of ‘no-feed’ visits were recorded. This may mean that during mid-day, the food was plentiful, and competition was low. The heightened periods of morning, afternoon and evening activity can be disrupted by unfavourable weather conditions, when the intervals between visits was often extended, or adult swifts may decide to stay in the nest for longer. The evening is also witness an increase in the frequency a period of increased frequency of social behaviour - of “screaming parties” and “banging” (Lack & Lack, 1951, p. 192; Oloś, 2017, p. 47). Therefore, increased observation of adult ‘no-feed’ entries in the evening may be a result offrom participation in the social activities or as a form of defence from the intruders.

5.5.3 Daily brooding, feeding and stages of chicks’ development

During the research, every minute of a chicks’ life in the nest was observed for a total of 19 breeding attempts over a three-year period, revealing significant differences in parental care by the adult Common Swift at different times of a chicks' development. In general, brooding time decreased significantly with the age of the brood, and it was not related to the size of the brood. This was not true for the patterns of daily feedings frequencies. For the broods of two and three, the number of daily feeds increased with the age of the brood during the first few weeks after hatching and decreased significantly before fledging. However, in the broods with one chick, feeding frequency stayed constant from hatching until two weeks before fledging, when it began to decrease. This behaviour was observed previously in international studies and was explained by chicks' weight recession before fledging (Sicurella, et al., 2015, p. 71), and changes in adult swifts' food allocation to replenish fat stores lost during the chick-rearing period (Martins & Wright, 1993, p. 220). The number of feeds, even for large broods, can decrease to as low as one or two feeds during the day when chicks are ready to fledge. A similar pattern was also recorded in the Pallid Swift, where the number of daily feeds also decreases with the age of the brood (1992, p. 210). However, one pair raising a brood of two fed their chicks at a constant rate of 10 to 15 feeds until both chicks fledged at 49 days old, even though their growth rate appeared to be normal.

The levels of parental care in the Common Swift changes with the age and size of the brood. Changes are not linear but display a pattern, and accordingly but three stages of a chicks' development in the nest were recognised: Stage 1, Stage 2, and Stage 3 (Fig. 4).

Stage 1: 0-8 days

After the first chick in the brood hatched, the behaviour of parent swifts shifts towards the provision of food for the chicks and brooding. For the first few days the pattern of one adult brooding while the other forages do not change, and chicks are rarely left unattended. If chicks were left alone, it was only for a very short time, lasting no longer than a few minutes. The total daily brooding time began to decrease toward the later period of Stage 1, when chicks were visually larger. For the broods with one chick, the feeding frequency stayed constant through this stage. However, this was not true for broods with two and three chicks. For larger broods, the feedings increased each day significantly, pointing out the difference in parental care required. At the end of Stage 1, adult swifts began to forage at the same time more frequently.

Stage 2: 9-34 days

After day nine, the total amount of brooding time decreased quickly and continued to decline until the chicks were 32-34 days old. During Stage 2, chicks develop feathers, begin to exercise their wings and leave the nest cup. The increased caloric requirements of the chicks', forced both adult swifts to leave the nest more frequently, and the number of daily average feeds for the broods with two and three chicks continues to increase with age, but stays constant for broods with one chick. During the later period of Stage 2, daily feeding frequencies began to decrease for all broods. When chicks were 32-34 days old, visually, they were the same size as adults and were only distinguished by some visual cues (fresh plumage and behaviour).

Stage 3: 35-42 (average fledging time)

During Stage 3 of the chicks' development, the average brooding time stayed low, and the frequency of feedings decreased significantly. This was uniform for all brood sizes and in all studied years. However, during this stage, the highest number of individual variations between pairs was observed. Some broods of two fledged as early as 38 days, and some broods of two as late as 49 days post-hatching. As mentioned previously, most pairs reduced the number of feeds during Stage 3, but some fed chicks at a continuously high rate until fledging. No definite explanation for this difference was observed, but a possible reason may be the lack of experience of the breeding pair or the level of fitness of the individual swifts.

5.5.4 Influence of weather on daily feeds

Currently, there is no published detailed study on the Common Swifts' daily feeding patterns with regards to weather throughout the entire length of the chick-rearing period. Previous publications provided either a small sample of data or described weather ambiguously (Lack & Owen, 1955, p. 123; Lack, 1956, p. 188; Martins & Wright, 1993, p. 54). Therefore, the influence of weather factors on the daily feeding frequency was measured by using proprietary DAX number, which represented the value between the actual and expected number of feeds at the colony as a whole rather than measuring the response of an individual nest. As the DAX equation takes into account the age and size of the brood, it eliminated errors that may have been a result of swift parental care plasticity at different stages of the chicks' development.

The analysis of the DAX number for the whole of the study period indicates that the Common Swift regulates the frequency of feeds in response to the weather, but the response is greater for some of the weather variables than others. Daily average wind speed was found to have the most significant effect on the feeding frequencies of the Common Swift. The explanation for this result may be due to the fact that prey may be less plentiful, harder to detect and catch. Also, the adult swifts may require higher energy output during periods of strong wind. The highest daily feeding rates in Castlebar were observed on days when the mean wind speed was low. Moreover, the highest feeding number was recorded by the colony (DAX +51.92%), with the lowest daily wind speed average (3.21kt). Also, the highest number of feeds during the day by a single pair (33 feeds) was recorded with low daily wind mean values (5.53kt). To further confirm the effects of wind on the Common Swift feeding frequencies, the foraging performance dropped to very low levels on days with very high winds. During a summer storm on 28 June 2020, the feeding was completely abandoned (DAX -100%) and most of the adult swifts did not leave the nest at all on that day. Some of the chicks were not fed for 42 hours (brood of two, 26 days old), confirming the previous observation in the species that the Common Swift chicks' torpidity allowing them to survive prolonged periods without food, even at a very young age (Lack, 1956, p. 82). On the same day, one brood of two chicks who were only three days old were fed three times; another aged eight days was fed only twice.

Mean daily temperatures also affected the feeding frequencies of the Common Swift in Castlebar, but to a lesser extent than mean daily wind speeds. The overall increase in the daily mean temperature was slightly correlated with an increase in daily feeds at the colony (15.0 % of influence). In general, the lowest recorded daily feeds coincided with the lowest recorded daily temperatures during the study period. This could be caused by a reduced availability of insect prey at lower temperatures and a greater need to preserve calories. On days with low temperatures brooding time was generally longer, and swifts often did not feed in the early morning and returned to the nests earlier.

An increase in daily precipitation also correlated to a decrease in feeding frequencies, but similar to the daily mean temperatures, the influence was lower than the impact of daily mean wind speed. In general, the increase in daily rainfall amounts was responsible for a 12.4% drop in feeds frequency. For the Common Swift in the West of Ireland, the rain may not be a determining factor in the decrease in daily feeds because swifts may fly long distances to forage, therefore avoiding localised rain showers. Also, on many occasions in the Castlebar colony, the rainfall events only persisted for short periods of time during the day. In this situation, the adult swifts often adjusted their behaviour and increased the number of feed visits to the nest when conditions improved. To illustrate this, on 29 July 2019, the total amount of rain during the day (night-time hours excluded) was recorded as 13.2mm but it was restricted to a few hours in the afternoon. The conditions were dry for the rest of the day, with low mean wind speeds and a high-temperature average. Therefore, the total daily feeds were unaffected by the few hours of rain, and adult swifts were able to forage effectively in the morning and the evening of the same day.

5.6 Egg loss

Previous observations regarding the Common Swift's breeding biology have reported the issue of egg loss during the incubation period (Lack & Lack, 1951, p. 200; Lack, 1956, p. 76; Cutcliffe, 1951, p. 53; O'Connor, 1979, p. 136). Cutcliffe (1951, p. 53) and O'Connor (1979, p. 136) suggested that egg ejection may be related to spells of bad weather and linked to the brood reduction adaptation. Lack & Lack (1951, p. 201) found no evidence to support these claims and left the issue without providing an explanation. Newell (2019, p. 26) claimed that ejections may be deliberate and caused by nest disturbance accidental due to poor nest construction.

The colony in Castlebar experienced egg loss in 15 out of 23 studied breeding attempts (64.5%), while the colony in Maguiresbridge only experienced three out of 22 (13.6%). Three factors were recognised to have caused a significant difference between the two colonies. Firstly, the colony in Maguiresbridge is located on a private property, where the owner has access to the nest boxes and regularly checks the video footage for any egg loss during the incubation period. Therefore, ejected eggs are often returned to the nest, while the adult swifts are absent, and usually, on their return incubation resumed. The fact that returned eggs are incubated and successful suggest further that the egg loss may be accidental. Swift boxes in Castlebar are not accessible during the summer, and any egg loss is not managed. Secondly, nest boxes at both colonies differ in construction. Boxes in Castlebar (17A Schwegler model) provide a smaller cavity than boxes used in Maguiresbridge (16 Schwegler model). Boxes in Maguiresbridge are wider, deeper and taller. Therefore, they provide more space for the swifts to manoeuvre while adjusting their positions while incubating. Lastly, the colony in Maguiresbridge is equipped with larger and deeper nest moulds than the ones used in Castlebar.

The analysis of egg loss during the study period began with the examination of the nest quality. The Common Swift construct their nests each season by collecting airborne material. Many nest boxes are equipped with artificial nest moulds to entice newcomers and aid swifts with nest construction. The feeling among the community of people passionate about swift conservation is strongly positive towards deeper nest moulds. However, as observed at both colonies, this often led to adult swifts laying clutch without gathering any nest material. At the time of the first egg in Castlebar, 32.78% of breeding pairs gathered a substantial amount of material to construct a nest categorised as ‘good’, and the remaining nests were either of ‘poor’ or ‘very-poor’ build. In contrast, none (0%) of the breeding pairs in Maguiresbridge constructed a ‘good’ nest at the time of laying, and 54.5% did not bring any material. The remaining pairs constructed either a ‘poor’ or a ‘very poor’ nest. Therefore, by providing a deeper nest mould, the issue of accidental egg loss was minimised, but this resulted in the swifts ignoring the evolutionary behaviour of collecting nest material. It is not clear if this caused any damage to the health of egg or chick. High productivity at the colony in Maguiresbridge may lead to a conclusion that as long as the nest mould is deep enough to protect the eggs from rolling out and allow for safe incubation and brooding, the nest material may not be necessary.

In Castlebar, a small and shallow nest mould required swifts to forage for nest material more often than in Maguiresbridge, but it did not prevent a large number of accidental egg losses. During the study period (2018-2020), 33 eggs were lost due to the accidental rolling out of the nest cup while incubating swifts were adjusting the nest. Swifts in Castlebar were more likely to collect nest material than in Maguiresbridge. Despite this only 32.78% of breeding pairs constructed a nest with a large among of material, and those nests for the most part avoided egg loss. Only 6.5%(n=2) of total egg loss events were observed in the nests with “good” construction of the nest cup. In contrast 93.5% (n=31) of egg displacement happened when the nest was either poorly constructed or had no nest material. As the nest moulds in Castlebar were shallow the eggs would roll out following movements by the adults. For the most part the adult swifts appear oblivious to knocking the egg out of the nest. However, on occasion if the egg did not roll out too far and stayed just outside of the nest mould, the adult swift would appear to push the egg back underneath its body gently with its beak. This behaviour was observed a number of times. However, if the egg rolled to the corner or the front of the nest box, adult swifts ignored it.

Loss of the clutch due to accidental egg loss was prevalent in Castlebar and took place in 53.1% (n=12) of all studied breeding attempts. In 91.6% (n=11) pairs laid a replacement clutch. In all 100% of breeding attempts when the clutch was lost and replacement clutch was laid, the construction of the nest improved in the interval period. This reduced the ration of the accidental egg loss and out of all 11 replacement clutches eight were successful and three resulted in additional egg loss.

The results from both colonies suggests that careful consideration is required when providing nesting opportunities for the Common Swift both in terms of the nest box and the artificial nest mould. Shallow nest moulds may result in an increased frequency in accidental egg loss, leading to lower productivity levels for the colony. However, deep nest moulds may cause the swifts to ignore the need to gather nest material. The consequences of this behaviour are unknown, but this research's result may suggest that deep nest moulds increase productivity. Newly installed swift boxes at the colony in Castlebar in 2019 are not equipped with the nest mould to imitate a natural nest site and to allow future observations of the issue of egg loss.

5.7 Conclusion

The foregoing chapter discusses the analysis of data collected in this research, answers the research questions, and examines the findings of this study. Firstly, the comprehensive study of the important dates during the breeding season of the Common Swift provided a detailed breeding calendar of the species in Ireland. Secondly, the study of productivity enabled an evaluation of the breeding success of the Common Swift in the nest box projects in Ireland. Thirdly, the detailed analysis of the chicks feeding frequencies allowed for a measuring of the weather impact on the Common Swift colonies. Lastly, the discussion and results from the egg loss observations provided some answers to this previously understudied behaviour. Chapter 6 summarises and highlights the most important findings of this study.

Chapter 6: Conclusion

6.1 Introduction

This study was conducted at two artificial nest locations in Ireland – Castlebar and Maguiresbridge to provide first detailed description of the breeding season of the Common Swift in Ireland and to study some of the previously under-researched aspects of the breeding biology of the species, such as patterns of chick feeding frequencies in regards to weather conditions and the issue of egg loss. This chapter will conclude the study by summarizing the key findings concerning the goals of this study. Additionally, this chapter will discuss how this study contributes to the knowledge of the Common Swifts' breeding biology, reflects on limitations of the research and provides recommendations for future research.

6.2. Key findings

The current study identifies the following conclusions that contribute to the knowledge of the breeding biology of the Common Swift in Ireland – the most north-westerly edge of the nesting habitat.

Nest boxes are a viable option for the conservation efforts of the Common Swift in Ireland and a successful substitute in the event that natural nest sites are lost. Careful consideration needs to be given to the management of nest sites and in particular the type of nest moulds so as to reduce the levels of egg loss during the incubation period.

The phenological breeding cycle of the Common Swift is rigid, and there is a little variation in the values of mean arrival, egg-laying, hatching, fledging and departure dates each year. Seasonal weather conditions did not significantly affect the timing of the events during the breeding season of the Common Swift. Any yearly variation in the timing of the breeding events was not statistically significant. In Ireland, the arrival of the breeding swifts in the nests begins in late April and early May. The egg-laying period stretches from the second week in May to the last week in June (replacement clutches). Fledging takes begins in the third week of July, culminates in early August and concludes in the last week of August (late broods from replacement clutches). Adult swifts departure takes place from late July to early September.

Fledging age of individual chicks ranged from 38 to 48 days. The mean value of age at fledging was related to brood size, with chicks from large broods fledging on average 2 days later than chicks from smaller broods. The average clutch size in Castlebar was 2.33 (se± 0.07) and 2.41 (se± 0.65) in Maguiresbridge. The average brood size in Castlebar was 1.53 (se± 0.16) and 2.28 (se± 0.08) in Maguiresbridge. The average number of fledglings in Castlebar was 1.38 (se± 0.15) and 2.13 (se± 0.09) in Maguiresbridge. Productivity in Castlebar during the entire study period (2014-2020) in Castlebar was 45% and 89% in Maguiresbridge. A low average brood size, number of fledgeling and productivity in Castlebar were a result of significant egg loss during the incubation period. Mortality of chicks during chick-rearing period was low: 6% in Castlebar and 5.58% in Maguiresbridge. The most common cause of death was starvation.

The total number of chicks feeding visits to the nest during the entire chick-rearing period was dependant on the size of the brood, but the relationship is not linear. On average: broods of one were fed 501.28 (se± 20.15) times in the season; broods of two were fed 746.80 (se± 18.15) times; broods of three were fed 872.5 (se± 20.15) times. Hourly chick feeding patterns show a pattern of high activity within an hour from sunrise, during mid-day, and two hours before sunset. Daily patterns of chick-feeding frequencies were related to the brood's size and age. For broods of one the feeding remained constant throughout the period and was reduced only in the last ten days before fledging. For the broods of two and three, the feeding increased linearly during the first eight to ten days since hatching and dropped during the last ten days before fledging. Weather factors influenced the daily number of feeds. Daily average wind speed was found to have the most significant negative effect on the feeding frequencies of the Common Swift. To a lesser extent, temperature (positive) and rainfall (negative) also had an impact on the number of daily feeding events.

Egg loss was the most influential factor in the low fledging numbers and low productivity in the Castlebar colony. Due to this, the colony can be considered as a sink site. Egg loss for the most part was accidental with the adult swift knocking out the incubated egg. At both nest box project, the size of the nest mould was crucial in either influencing (Castlebar) or eliminating (Maguiresbridge) egg loss.

6.3 Limitations and recommendation for future studies

While this study provided some critical information about the adaptations of the Common Swift in Ireland and provided some previously unknown knowledge of the species breeding behaviour there are still areas that are not well researched. Information gathered in this research along with some additional information about the swifts may allow for a pattern-oriented modelling approach to estimate survival rates in the Common Swift population in the region. The estimation of the population dynamics would further support the conservation effort of this at-risk species.

Another missing parameter in the knowledge of the species is the determination of the natal origin of birds occupying the Irish nesting habitat. This could be achieved by analysing stable tissue isotopes or DNA from feathers collected at the nest box projects in the region.

6.4 Implications

This research provides the first detailed study of the Common Swift in Ireland. The results prove that the Common Swift is well adapted to breed in the country, even when some previous publications asserted that regions in which both studied colonies are located would be too challenging for the species (Lack & Lack, 1951, p. 502). During the study, there was no evidence of Irish climate having a strong influence on the breeding success of the Common Swift. The current trend places the Common Swift on the Red List of Conservation Concern in Ireland (Gilbert, et al., 2021, p. 8). Therefore, the decline of the species in recent decades may be less influenced by the lack of food supply and more by the loss of natural nest sites. The result of this study may suggest that as long as nesting opportunities are provided, the colony can be sustainable. However, careful considerations need to be placed on the provision of the nest moulds in the swift boxes. Shallow moulds may increase egg loss and cause low yield in the artificial colonies. Therefore, the author's recommendation is to provide the deep nest moulds or none at all.

Bibliography

Ahmed , R. & Adriaens, P., 2010. Common, Asian Common and Pallid Swift: colour nomenclature, moult and identification. *Dutch Birding,* Volume *32,* pp. 97-105.

Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K., Lehikoinen, E., 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology,* Volume 10, pp. 1610-1617.

Åkesson, S., Atkinson, P., Bermejo, A., de la Puerte, J., Ferri, M., Hewson, C., Holmgren, J., Kaiser, E., Kearsley, L., Klaassen, R., Kolunen, H., Matsson, G., Minelli, F., Norevik, G., Pietiainen, H., Singh, N., Spina, F., Viktora, L., Hedenström, A., 2020. Evolution of chain migration in the aerial incectivorous bird, the common swift *Apus apus*. *Evolution*, Volume 74(10), pp. 2377-2391.

Åkesson, S., Bianco, G. & Hedenstöm, A., 2016. Negotiating an ecological barrier: crossing the Sahara in relation to winds by common swift. *Philosophical Transactions of the Royal Society B Biological Sciences*, Volume 371, pp. 1-12.

Åkesson, S., Klaassen, R., Holmgren, J., Fox, J.F., Hedenström, A., 2012. Migration Routes and Strategies in a Highly Aerial Migrant, the Common Swift *Apus apus*, Revealed by Light-Level Geolocators, *Plos One*, Volume 7(7), pp. 1-9.

Amar, A., Butler, S. J., Lindsell, J. A. & Smith, K. W., 2007. Recent charges in British Woodland Bird Populations. *Ibis,* Volume 149, pp. 14-28.

Ambrosini, R., Orioli, V., Massimino, D. & Bani, L., 2011. Identification of Putative Wintering Areas and Ecological Determinants of Population Dynamics of Common House Martin (*Delichon urbinum*) and Common Swift (*Apus apus*) breeding in Italy. *Avian Conservation and Ecology,* Volume 6(3), pp. 1-15.

Amichai , E. & Kronfeld-Schor, N., 2019. Artificial Light at Night Promotes Activity Throught the Night in Nesting Common Swift (*Apus apus*). *Scientific Reports,* Volume 9(11052), pp. 1-8.

Ansonge, K., 2015 Sexual dismorphism of acoustic signals in the Common Swift *Apus apus*. *APUSlife,* 5457.
Available at: http://www.commonswift.org/5457Ansorge.html
[Accessed 12 November 2021].

Antonov, A. & Atanasova, D., 2001, Second Clutches in the Alpine Swift *Apus melba, Ardea,* Volume 89(3), pp. 543-544.

Antonov, A. & Atanasova, D., 2002a. Breeding biology of the alpine swif *Apus melba* in Sofia, Bulgaria. *Avian Science,* Volume 2, pp. 1-8.

Antonov, A. & Atanasova, D., 2002b. Cohabitation and nest-site selection of Common Swift (*Apus apus*) and Pallid Swift (*A. pallidus*). *Die Vogelwarte,* Volume 41, pp. 231 - 239.

Appleton, G., 2012. Swifts start to share their secrets. *British Trust for Ornithology News,* May-June 2012, pp. 16-17.

APUSlife, 2021. *Common Swift Worldwide.* [Online]
Available at: http://www.commonswift.org/swift_english.html
[Accessed 1 December 2021].

Aristotle, 1883. *History of Animals in Ten Books. Translated by Richard Cresswell.* London: George Bell & Sons.

Ashton, K. G., 2002. Patterns of within-species body size vatiation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography,* Volume 11(6), pp. 505-523.

Bäckman, J. & Alerstam, T., 2001. Confronting the winds: orientation and flight behaviour of roosting swifts, *Apus apus*. *Proceedings of the Royal Society B: Biological Sciences*. Volume 268, pp. 1081-1087.

Bäckman, J. & Alerstam, T., 2002, Harmonic oscillatory orientation relative to the wind in nocturnal roosting flights of the swift *Apus apus. Journal of Experimental Biology*, Volume 205, pp. 905-910.

Balmer, D. et al., 2013. *Bird Atlas 2007-11; the breeding and wintering birds of Britain and Ireland.* Thetford: BTO Books. *The Condor,* Volume 59(3), pp. 145-155.

Bartholomew, G. A., Howell, T. R., Cade, T. J., 1957. Torpididy in the White-Throated Swift, Anna Hummingbird and Poor-Will.

Belon, P., 1555. *Les Observations de Plvsievrs.*. Paris: NP.

BirdLife International, 2015. *European Red List,* Luxembourg: European Commission.

BirdLIfe International, 2017. *European Birds of Conservation Concern,* Cambridge, UK: BirdLife International.

BirdLIfe International, 2017. *European Birds of Conservation Concern,* Cambridge, UK: BirdLife International.

BirdLife International, 2020. *Data Zone BirdLife International Common Swift Apus apus.* [Online]
Available at: http://datazone.birdlife.org/species/factsheet/common-swift-apus-apus
[Accessed 29 2 2020].

BirdLife International, 2021. *Species factsheet: Apus apus.* [Online]
Available at: http://datazone.birdlife.org/species/factsheet/common-swift-apus-apus/distribution
[Accessed 27 07 2021].

Bize, P., Diaz, C., Lindström, J., 2012. Experimental evidence that adult antipredator behaviour is heritable and not influenced by behavioural copying in a wild bird. *Proceedings of the Royal Society B.* Volume 279, pp. 1380-1388.

Boano, G. & Cucco, M., 1989, Breeding biology of the pallid swift (*Apus pallidus*) in north-western Italy. *Le Gerfaut,* Volume 79, pp. 133-148.

Boano, G., Pellegrino, I., Ferri, M., Cucco, M., Minelli, F., Åkesson, S., 2020, Climate anomalies affect annual survival rates of swifts wintering in sub-Saharan Africa. *Ecology and Evolution,* Volume 10, pp. 7916-7928.

Brandi, R. & Nelsen, I., 1988. Feeding frequency of Black-headed Gull chicks. *Bird Study.* Volume 32(2), pp. 137-141.

Bretagnolle, V., 1993. Call types of the Common Swift *Apus apus:* adult call given at the nest. *Avocetta,* Volume 17, pp. 141-146.

Bryant, D.M., 1975. Breeding biology of House Martins *Delichon Urbica* in relation to aerial insect abundance. *Ibis,* Volume 177, pp. 180-216.

Calvert, A. M., Walde, S. J. & Taylor, P. D., 2009. Non-breeding drivers of population dynamics in seasonal migrants: conservation parallels across taxa. *Avian Conservation and Ecology,* Volume 4(2).

Carere, C. & Alleva, E., 1998. Sex differences in parental care in the Common Swift (*Apus apus*): effect of brood size and nestling age. *Canadian Journal of Zoology,* Volume 76, pp. 1282-1287.

Carroll, E., Sparks, T., Donnelly, A. & Cooney, T., 2009. Irish phenological observations from the early 20th century reveal a strong response to temperature. *Biology and Environment: Proceedings of the Royal Irish Academy,* Volume 109B(2), pp. 115-126.

Chantler, P. & Driessens, G., 1995. *Swifts, A Guide To The Swifts and Treeswifts of the World.* Robertsbridge, East Sussex: Pica Press.

Church, H. F., 1956. The Roosting Times of the Swift. *Bird Study,* Volume 3(3), pp. 217-220.

Cucco, M., Bryant, D. M., Malacarne, G., 1993. Differences in diet of Common (*Apus apus*)and Pallid (*A. pallidus*) Swifts. *Avocetta*, Volume 17, pp. 131-138.

Cocco, M. & Malacarne, G., 1995. Increase of parental effort in experimentally enlarged broods of Pallid Swifts. *Canadian Journal of Zoology*, Volume 73(8), pp. 1387-1395.

Cocco, M. & Malacarne, G., 1996a. Reproduction of the pallid swift (*Apus pallidus*) in relation to weather and aerial insect abundance. *Italian Journal of Zoology,* Volume 63(3), pp. 247-253.

Cocco, M. & Malacarne, G., 1996b. Effect of food availability on nestling growth and fledging success in manipulated pallid swift broods. *Journal of Zoology*, Volume 240, pp. 141-151.

Cocco, M. & Malacarne, G., 1996b. Factors affecting egg mass in the Pallid Swift *Apus pallidus*. *Bird Study,* Volume 43(3), pp. 314-319.

Cocco, M., Malacarne, G., Orecchia, G. & Boano, G., 1992. Influence of weather conditions of Pallid Swift Apus pallidus Breeding Success. *Ecography,* Volume 15(2), pp. 184-189.

Colhoun, K. & Cummins, S., 2013. Birds of Conservation Concern in Ireland 2014-2019. *Irish Birds,* Volume 9, pp. 523-544.

Colombo, A. & Galeotti, P., 1992. Nest-hole selection as the defence measure in breeding Swits *Apus apus*. *Avocetta*, Volume 17, pp. 1-6.

Corrales, L., Bautista, L. M., Santamaria, T., Mas, P., 2013. Hole selection by nesting swifts in medieval city-walls of Central Spain, *Ardeola,* Volume 60(2), pp. 291-304.

Cramp, S. & Simmons, K., 1985. *Handbook of the birds of Europe, the Middle East and North Africa. Volume 4. The Birds of the Western Palearctic.* Oxford: Oxford University Press.

Crowe, O., Coombes, R.H., Lysagh, L., O'Brien, C., Choudhury, K.R., Walsh, A.J., 2010. Popular trends of widespread breeding birds in the Republic of Ireland 1998-2008. *Bird Study,* Volume 57(3), pp. 267-280.

Crowe, O., Coombesm, R.H., Tierney, T.D., Walsh, A.J., O'Halloran, J., 2017. *Countryside Bird Survey Report 1998-2016,* Wicklow: BirdWatch Ireland.

Cutcliffe, A. S., 1951. Notes on the breeding habits of the swift. *British Birds,* Volume 44, pp. 47-56.

de Margerie, E., Pichot , C. & Benhamou, S., 2018. Volume-concentrated searching by an aerial insectivore, the common swift, Apus apus. *Animal Behaviour,* Volume 136, pp. 159-172.

Dell’omo, G., Alleva, E., Carere, C., 1998. Parental recycling of nestling faeces in the Common Swift, *Animal Behaviour,* Volume 56(3), pp. 631-637.

Dokter, A. M., Åkesson, S., Beekuis, H., Bouten, W., Buurma, L., van Gasteren, H., Holleman, I., 2013. Twillight ascents by common swift, *Apus apus,* at dawn and dusk: acquisiotion of orientation cues?. *Animal Behaviour,* Volume 85(3), pp. 545-552.

Dulisz, B., Stawicka, A. M., Knozowski, P., Diserens, T. A., Nowakowski, J. J., 2021. Effectiveness of using nest boxes as a form of bird protection after building modernisation. *Biodiversity and Conservation,* pp. 1-18.

Eaton, M. et al., 2015. Birds of Conservation Concern 4: the population status of birds in the UK, Channel Islands and Isle of Man. *British Birds,* Volume 108, pp. 708-746.

European Parliament and Council, 2010. DIRECTIVE 2009/147/EC OF THE EUROPEAN PARLIAMENT AND OF THE COUNCIL. *Directive 2009/147/EC of the European Parliament and of the Council,* 30 November, Volume 20(7), pp. 1-19.

Evans, K.L., Newton, J., Mallord, J.W., Markman, S., 2012. Stable Isotope Analysis Provides New Information on Winter Habitat Use of Declining Avian Migrants That Is Relevant to Their Conservation, *Plos one*, Volume 7(4), pp. 1-7.

Finney, S. K., Wanless, S. & Harris, M. P., 1999. The Effect of Weather Conditions on the Feeding Behaviour of a Diving Bird, the Common Guillemot *Uria aalge*. *Journal of Avian Biology,* Volume 30, pp. 23-30.

Freitag, A., Martinoli, A., Urzelai, J., 2001. Monitoring the feeding activity of nesting birds with an autonomous system: case study of the endangered Wryneck *Jynx torquilla. Bird Study.* Volume 48, pp. 102-109.

Gangloff, B. & Wilson, K., 2004. Feeding frequency, meal size and chick growth of Pycroft's Petrel (*Pterodroma pycrofti*): preparing for chick translocation in *Pterodroma* species. *Notornis,* Volume 51, pp. 26-32.

Garg, K. M., Tizard, R., Ng, N., Cros, E,. Dejtaradol, A., Chattopandyay, B., Pwint, N., Packert, M., Rheindt, F., 2016. Genome-wide data help identify an avian species-level lineage that is morphologically and vocaly criptic. *Molecular Phylogenesis and Evolution,* Volume *102* , pp. 97-103.

Geiser, S. & Arlettaz, R., 2008. Impact of weather variation on feeding behaviour, nestling growth and brood survival in Wrynecks *Jynx torquilla*. *Journal of Ornithology,* Volume 149, pp. 597-606.

Gessner, C., 1554. *Medici Tigurini Hiftoriae Animalium Liber II. de Quadru Pedibus ouiparis.* Zurich: NP.

Gilbert, G., Stanbury, A. & Lewis, L., 2021. Birds of Conservation Concern in Ireland 4: 2020-2026. *Irish Birds,* Volume 43, pp. 1-22.

Gill, F. & Donsker, D., 2020. *IOC World Bird List Version 11.2.* [Online]
Available at: https://www.worldbirdnames.org/

Gordo, O., Brotons, L., Ferrer , X., Comas, P., 2005. Do changes in climate patterns in wintering areas affect the timing of spring arrival of trans-Saharan migrant birds?. *Global Change Biology,* Volume 11, pp. 12-21.

Gordo, O. & Sanz, J. J., 2008. The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distace Iberian migrants. *Journal of Ornithology,* Volume 149, pp. 199-2010.

Gordo, O., Sanz, J. J. & Lobo, J., 2007. Environmental and geographical constraints on the common swift and barn swallow spring arrival patterns throughout the Iberian Peninsula. *Journal of Biogeography,* Volume 34, pp. 1065-1076.

Günther, E., Hellmann, M. & Nicolai, B., 2004. Baumbrütende Mauersegler Apus apus – Relikte uralter Waldqualitäten?. *Vogelwelt*, Volume 125, pp. 309-318.

Hahn, A, & Yosef, R., 2020, Inducted alloparental care in Common Swift (*Apus apus*). *European Journal of Ecology,* Volume 6(2), pp. 18-22.

Halupka, L. & Halupka, K., 2017. The effect of climate change on the duration of avian breeding seasons: meta-analysis. *Proceedings of the Royal Society,* Volume 284, pp. 1-9.

Harris, S. J. et al., 2019. *The Breeding Bird Survey 2018. BTO Research Report 717,* Thetford: British Trust for Ornitology.

Hedenström, A., 1992, Flight Performance in Relation to Fuel Load in Birds, *Journal of Theoretical Biology*. Volume 158, pp. 535-537.

Hedenström, A., 2006. Scalling migration and the annual cycle of birds. *Ardea,* Volume 94(3), pp. 399-408.

Hedenström, A. & Åkesson, S., 2017, Adaptive airspeed adjustment and compensation for wind drift in the Common Swift: differences between day and night. *Journal of Animal Behaviour,* Volume 127, pp. 117-123.

Hedenström, A., Norevik, G., Warfvinge, K., Andersson, A., Bäckman, J., Åkesson, S., 2016. Annual 10-Month Aerial Life Phase in the Common Swift Apus apus. *Current Biology,* Volume 26, pp. 3066-3070.

Henningsson, P., Johansson, L. C. & Hedenstrom, A., 2010. How swift are swifts *Apus apus*? *Journal of Avian Biology,* Volume 41, pp. 94-98.

Henningsson, P. & Hedenström, A., 2011. Aerodynamics of gliding flight in Common Swift. *Journal of Experimental Biology,* Volume 214, pp. 382-393.

Henningsson, P., Spedding , G. & Hedenström, A., 2008. Vortex wake and flight kinematics of a swift in cruising flight in a wind tunnel. *Journal of Experimental Biology,* Volume 210, pp. 717-730.

Holmgren, J., 2004. Roosting in tree foliage by the Common Swift *Apus apus*. *Ibis,* Volume 146, pp. 404-416.

Hudson, P.J., 1979. The Parent-Chick Feeding Relationship of the Puffin, *Fratercula arctica*. *Journal of Animal Ecology*, Volume 48(3), pp. 889-898.

Huxley, L., 2017. *We Are Swifts - We Are in Trouble,* Mayo: Carra Books.

Ieronymidou, C., Pople, R., Ian , B. & Ivan , R., 2015. The European Red List of Birds 2015. *Bird Census News,* Volume 28(1), pp. 3-19.

Jaroszewicz, B., Cholewska, O., Gutomski, J. M., Samojlik, T., Zimny, M., Latalowa, M., 2019. Białowieża Forest - A Relic of the High Naturalness of European Forests. *Forest,* Volume 10(849), pp. 1-28.

Jenkins, D. & Watson, A., 2000. Dates of first arrival and song of birds during 1974-99 in mid-Deeside, Scotland. *Bird Study,* Volume 47(2), pp. 249-251.

Jobling, J. A., 2010 . *Helm Dictionary of Scientific Bird Names.* London: A&C Black Publishers Ltd.

Johansson, L. C., Henningsson , P. & Hedenstrom, A., 2010. How swift are swifts *Apus apus*?. *Journal of Avian Biology,* Volume 41(1), pp. 94-98.

Kaiser, E., 1997. Sexual recognition of the Common Swift, *British Birds*, Volume 90, pp. 167-174.

Kalyakina, N. M., 2007. Phenology of the Common Swift in Moscow. *APUSlife,* No. 3165. [Online]
Available at: http://www.commonswift.org/3165Kalyakina.html

Khaleghizadeh, A., 2005. Phenology of the Common Swift *Apus apus* in the Middle East - Tehran, Iran. *Sandhouse,* Volume 27(1), pp. 79-82.

Kindlmann, P., 2006. Long-term decline in Common Swift Apus apus annual breeding success may be related to weather conditions. *Ornis Fennica,* Volume 83, pp. 66-72.

Klvanova, A., Vorisek, P., Gregory, R. D. & Van Strien, A. J., 2009. Wild birds as indicators in Europe: latest results from the Pan-European Common Bird Monitoring Scheme (PECBMS). *Avocetta,* Volume 33, pp. 7-12.

Koskimies, J., 1948. On Temperature Regulation and Metabolism in the Swift: *Micropus a. apus L.,* during fasting, *Experientia,* Volume 4(7), pp. 274-276.

Koskimies, J., 1950. On movement of the swift, *Micropus a. apus L.* during the breeding season (Preliminary publication). *Annales Academiæ Scientiarum Fennicæ,* Volume 15, pp. 106-111.

Lack , D. & Lack, E., 1951. The Breeding Behaviour of the Swift. *British Birds,* Volume XLV, pp. 186-215.

Lack, A. & Lack, E., 1950. The breeding biology of the swift *Apus apus*. *The Ibis,* Volume 93(4), pp. 501-546.

Lack, D., 1947. The significance of clutch size, part III - some specific comparisons. *Ibis,* Volume 90(1), pp. 25-45.

Lack, D., 1955. The Summer Movements of Swifts in England, *Bird Study,* Volume 2(1), pp. 32-40.

Lack, D., 1956. *Swifts in a Tower.* London: Methuen & Co Ltd.

Lack, D., 1958. The return and departure of swifts *Apus apus* at Oxford. *The Ibis,* Volume 100, pp. 473-502.

Lack, D., 1966. *Population Studies of Birds.* I ed. Oxford: Clarendon Press.

Lack, D. & Owen, 1955. The Food of the Swift. *Journal of Animal Ecology*, Volume 24(1), pp. 120-136.

Leader, P.J., 2011, Taxonomy of the Pallid Swift, *Apus pacificus*, Latham, 1802, complex. *Bulletin of the British Ornitologists' Club,* Volume 131, 81-83.

Lewis, L., Coombes, D., Burke, B., O'Halloran, J., Walsh, A., Tierney, D., Cummins, S., 2019. *Countryside Bird Survey: Status and Trends of Common and Widespread Breeding Birds 1998-2016*, Kilcoole, Wicklow: BirdWatch Ireland.

Linnaeus, C., 1758. *Systema naturae per regna tria naturae :secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* Stockholm: Laurentius Salvius.

Lockley, R. M., 1969. Non-stop flight and migration in the Common Swift *Apus apus. Ostrich: Journal of African Ornithology,* Volume 40, pp. 265-269.

Lundbegr, S. & Alerstam, T., 1986. Bird Migration Patterns: Conditions for Stable Geographical Population Segregation. *Journal of Theoretical Biology,* Volume 123, pp. 403-414.

Luniak, M. & Grzeniewski, M., 2011. Nest-boxes for the Common Swift *Apus apus* - experience from Poland. *Ecologia Urbana*, Volume 23, pp. 3-5.

Lynas, P., Newton, S. F. & Robinson, J. A., 2007. The status of birds in Ireland: an analysis of conservation concern 2008-2013. *Irish Birds,* Volume 8, pp. 149-166.

Malacarne, G. & Cucco, M., 1991. Chick mortality and hatching asynchrony in the PallidSwift *Apus pallidus*, *Avocetta*, Volume 15, pp. 19-24.

Malacarne, G. & Cucco, M., Bertolo, E., 1994. Sibling competition in asynchronously hatched broods of the Pallid Swift (*Apus pallidus*). *Ethology Ecology & Evolution*, Volume 6, pp. 293-300.

Malacarne, G.M., Cucco, M. & Orecchia, G., 1992. Nest attendance, parental roles and breeding success in the Pallid Swift (*Apus pallidus*). Die Vogelwarte 36, pp. 203-210.

Malacarne, G., Palomba, I., Griffa, M., Castellano, S., Cucco, M., 1989. Quantitative analysis of differences in the vocalizations of the Common Swift *Apus apus* and the Pallid Swift *Apus pallidus*. *Avocetta,* Volume 13, pp. 9-14.

Marin, M., 1997. Some Aspects of the Breeding Biology of the Black Swift. *The Willson Bulletin*, 109(2), pp. 290-306.

Marra, P. P., Hobson, K. A. & Holmes, R. T., 1998. Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes. *Science,* Volume 282(5395), pp. 1884-1886.

Martins, T. L., 1997. Fledging in the Common Swift, *Apus apus*: weight watching with a difference. *Animal Behaviour,* Volume 54, pp. 99-108.

Martins , T. L. & Wright, J., 1993. Patterns of food allocation between parent and young under differing weather conditions in the Common Swift (*Apus apus*). *Avocetta,* Volume 17, pp. 147-156.

Martins, T. L. & Wright, J., 1993. Brood reduction in response to manipulated brood sizes in the common swift (Apus apus). *Behavioural Ecology and Sociobiology*, Volume 32, pp. 61-70.

Martins, T. & Wright, J., 1993. Cost of reproduction and allocation of food between parent and young in the Swift (Apus apus). *Behavioral Ecology,* Volume 4, pp. 213-223.

Mason, C. F., 1995. Long-term trends in the arrival dates of spring migrants. *Bird Study,* 42(3), pp. 182-189.

Mayr, G., 2003. A new Ecocene swift-like bird with a peculiar feathering. *Ibis,* Volume 145(3), pp. 382-391.

McCarthy, J. P., 2002. The number of visits to the nests by parents is an accurate measure of food delivered to nestlings in Tree Swallows. *Journal of Field Ornithology,* Volume 73(1), pp. 9-14.

Meiri, S. & Dayan, T., 2003. On the validity of Bergmann's rule. *Journal of Biogeography,* Volume 30, pp. 331-351.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mage, F., Mestre, A., Nordli, Ø., Penuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F., Zach, S., Zust, A., 2006, European phenological response to climate change *Global Change Biology,* Volume 12, pp. 1969-1976.

Merriam-Webster, 2020. *Swift.* [Online]
Available at: https://www.merriam-webster.com/dictionary/swift

Met Éireann, 2000. *met.ie.* [Online]
Available at: https://www.met.ie/climate-ireland/1971-2000/claremorris.html
[Accessed 08 December 2020].

Met Éireann, 2019. *Met.ie.* [Online]
Available at:
https://www.met.ie/cms/assets/uploads/2019/08/heatwave_article_met.ie_July2019.pdf
[Accessed 28 June 2021].

Met Éireann, 2020. *Met.ie.* [Online]
Available at: https://www.met.ie/cms/assets/uploads/2020/06/Summer2018.pdf
[Accessed 28 06 2021].

Møller, A. P., 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia,* Volume 159, pp. 849-858.

Møller, A. P., 2020. Quantifying rapidly declining abundance of insects in Europe using a paired experimental design. *Ecology and Evolution,* Volume 00, pp. 1-6.

Møller, A. P., Cuervo, J. J., Barbosa, A. & Merino, S., 1998. Sexual selection and tail streamers in the Barn Swallow. *The Royal Society*, Volume 265, pp. 409-414.

Murray, B. G., 2000. Measuring Annual Reproductive Success in Birds. *The Condor*, Volume 102(2), pp. 470-473.

Murray, B. G., 2006. A new equation for calculating reproductive success of clutches as a function of the day on which incubation starts: some implications., *The Auk*, Volume 123(3), pp. 708-721.

Museum of Natural History, 2020. *Museum of Natural History.* [Online]
Available at: https://oumnh.ox.ac.uk/swifts-diary#/
[Accessed 05 04 2021].

Newell, D., 2015. *Action For Swifts.* [Online]
Available at: http://actionforswifts.blogspot.com/2015/05/beijing-swift-project-preliminary.html
[Accessed 22 October 2019].

Newell, D., 2019. A test of the use of artificial nest forms in common swift Apus apus nest boxes in southern England. *Conservation Evidence*, Volume 16, pp. 24-26.

Newton, I., 2006. Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology*, Volume 147, pp. 146-166.

Newton, I., 2007. Weather-related mass mortality events in migrants. *Ibis*, Volume 149, pp. 453-467.

Newton, I., 2011. Migration within the annual cycle: Species, sex and age differences. *Journal of Ornitology*, Volume 152, pp. 169-185.

Nguyên Quang, P., Voisin, J. F. & Lam Ngoc, T., 2006. Biology of the house swift Apus nipalensis(Hodgson) in Vietnam. *Revolutionary Ecology*, Volume 61, pp. 383-395.

Nice, M. M., 1957. Nesting Success in Altricial Birds. *Auk*, Volume 74, pp. 305-321.

Nilson, C., Backman, J. & Dokter, A. M., 2019. Flocking behaviour in the twilight ascents of Common Swifts *apus apus*. *Ibis* , pp. 1-5.

O'Connor, R., 1978. Brood reduction in birds: Selection for fracticide, infracide and suicide?. *Animal Behaviour,* Volume 26, pp. 79-96.

O'Connor, R., 1979. Egg weigts and brood reduction in the European Swift (*Apus apus*). *Condor,* Volume 81, pp. 133-145.

Ološ, G., 2017. Is "banging" an antipredator behavior in Common Swift (*Apus apus*)?. *Ornis Fennica,* Volume 94, pp. 45-52.

Online Etymology Dictionary, 2020. *Swift.* [Online]
Available at: https://www.etymonline.com/word/swift

Palm, V., Truu, J., Tomingas, O., 2009. The spring timing of arrival of migratory birds: Dependence on climate vatiables and migration route. *Ornis Fennica,* Volume 86, pp. 97-108.

PECBMS, 2017. *Trends of common birds in Europe, 2017 update,* s.l.: European Bird Cencus Council.

PECBMS, 2019. *Trends and indicators.* [Online]
Available at: https://pecbms.info/trends-and-indicators/species-trends/
[Accessed 29 February 2020].

PECBMS, 2020. *PECBMS About Us.* [Online]
Available at: https://pecbms.info/about-us/
[Accessed 29 February 2020].

Pellegrino, I., Cucco, M., Harvey, J.A., Liberatore, F., Pavia, M., Voelker, G., Boano, G., 2017, So simmilar yet so different: taxonomic status of Pallid Swift Apus pallidus and Common Swift Apus apus, *Bird Study,* 2017, pp. 1-9

Pennant, T., 1776. *British Zoology.* London: Warrington, Printed by W. Eyres, for B. White.

Perrins, C., 1964. Survival of young swifts in relation to brood size. *Nature,* Volume 201, pp. 1147-1148.

Perrins, C., 1971. Age of the First Breeding and Adult Survival Rates in the Swift. *Bird Study,* Volume 18(2), pp. 61-70.

Pichorim, M., 2011. The influence of clutch and brood sizes on nesting success of the biscutate swift, *Streptoprocne biscutata* (Aves: Apodidae). *Zoologia,* Volume 28(2), pp. 186-192.

Pliny, 1854. *Natural History (translated by Bostok and Riley).* London: Taylor & Francis.

Pliny, 1967. *Natural History, Volume III, Book VII-XI. Translated by H. Rackham.* London: William Heinemann Ltd. .

Rajchard, J., Prochazka, J. & Kindlmann, P., 2006. Long-term decline in Common Swift *Apus apus* annual breeding success may be related to weather conditions. *Onnis Fennica,* Volume 83, pp. 66-72.

Rattenborg, N., 2017. Sleeping on the wing. *Interface Focus*. Volume 7, pp. 1-14.

Ray, J., 1678. *The Ornitology of Francis Willughby.* London: Royal Society.

Reudnik, M. W. et al., 2015 . Patterns of migratory connectivity in Vaux's Swifts at northern migratory roost: A multi-isotope approach. *Condor* , Volume 111, pp. 670-682.

Reynolds, S. J., Ibáñez-Álamo, J. D., Sumasgutner, P., Mainwaring, M. C., 2019, Urbanisation and nest building in birds: a review of threats and opportunities. *Journal of Ornithology,* Volume 160, pp. 841-860.

Ricklefs, R. E., 1965. Brood reduction in the Curve-Biller Trasher. *The Condor,* pp. 505-510.

Ricklefs, R. E., 1973. Facundity, Mortality, and Avian Demography. In: D. S. Farmer, ed. *Breeding Biology of Birds.* Washington, DC: Natural Academy of Science, pp. 366-435.

Rickliefs, R. E., 1980. Geographical variation in clutch size among passrine birds: Ashmole's hypothesis. *The Auk*, Volume 97(1), pp. 38-49.

Ricklefs, R. E. & Bloom, G., 1977, Components of Avian Breeding Productivity, *The Auk,* Volume 94, pp. 86-96.

Rose, A. P., 2009. Temporal and Individual Variation in Offspring Provisioning by Tree Swallows: A New Method of Automated Nest Attendance. *Plos One,* Volume 4(1), pp. 1-13.

Rowley, S. J. & Orr, R. T., 1965. The Nesting of the White-Naped Swift. *The Condor,* 64(5), pp. 361-367.

Rouaiguia, M., Lahlah, N., Bensaci, E., Houhamdi, M., 2015. Feeding Behaviour and the Role of Insects in the Diet of Northern House-Martin (*Delichon urbica meridionalis*) Nestlings in Northeastern Algeria. *African Entomology,* Volume 23(2), pp. 329-341.

Royama, T., 1966. Factors Governing Feeding Rate, Food Requirement and Brood Size of Nestling Great Tit Parus Major. *The Ibis,* Volume 108(3), pp. 313-347.

RSPB, 2020. *Swift Survey.* [Online]
Available at: https://swiftsurvey.org/Rspb/Home/Index
[Accessed 02 March 2020].

Ruf, T. & Geiser, F., 2015. Daily torpor and hibernation in birds and mammals. *Biological Reviews, Volume* 90, pp. 891-926.

Ruttledge, R. F., 1989. *Birds of Counties Galway and Mayo.* Dublin: Irish Wildbird Conservancy.

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

Sakraoui, R., Dadci, W., Chabi, Y., Banbura, J., 2005. Breeding biology of Barn Swallows *Hirundo rustica* in Algeria, North Africa. *Ornis Fernica*, Volume 82, pp. 33-43.

Schaub, T., Meffert, P. J. & Kerth, G., 2016. Nest-boxes for Common Swifts Apus apus as compensatory measures in the context of building renovation: efficacy and predictors of occupancy. *Birds Conservation International*, Volume 26, pp. 164-176.

Schaub, T., Wellbrock, A. H., Roznan, J. & Witte, K., 2020. Light data from geolocation reveal patterns of nest visit frequency ans suitable conditions for efficient nest site monitoring in Common Swift Apus apus. *Bird Study*, Volume 66(4), pp. 519 -530.

Schmaljohan, H., 2019 . The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: a cross-continental analysis. *Movement Ecology*, Volume 7(25), pp. 1-18.

Scopoli, G. A., 1777. *Introducto ad historiam naturalem.* Prague: Apud Wolfgangum Gerle.

Scribblemaps, 2021,
Available at: https://www.scribblemaps.com/
[Accessed 1 November 2021]

Seward, A., Ratcliffe, N., Newton, S., Caldow, R., Piec, D., Morrison, P., Cadwallender, T., Davies, W., Bolton, M., 2018. Metapopulation dunamics of roseate terns: Sources, sinks and implications for conservation management decisions. *Journal of Animal Ecology*, Volume 88(1), pp. 138-153.

Sharrock, J., 1976. *The Atlas of Breeding Birds in Britain and Ireland.* Berkhamstead, Uk: T. & A.D. Poyser Ltd.

Sicurella, B., Caffi, M., Caprioli, M., Rubolini, D., Saino, N., Ambrosini, R., 2015. Weather Conditions, brood size and hatching order affect Common Swift *Apus apus* nestlings' survival and growth. *Bird Study*, Volume 62(1), pp. 64-77.

Slagsvold, T., 1986. Asynchronous versu synchronous hatching in birds: experiments with the pied flycather. *Journal of Animal Ecology*, Volume 55(3), pp. 1115-1134.

SLN, 2020. *Action for Swifts.* [Online]
Available at: https://actionforswifts.blogspot.com/
[Accessed 02 March 2020].

Smiddy, P. & O'Halloran, J., 2010. Breeding biology of Barn Swallow Hirundo rustica in Countries Cork and Waterford, Ireland, *Bird Study,* Volume 57(2), pp. 256-260.

Sokal, R. R. & Rohlf, J. F., 1969. *Biometry, The Principles and Practice of Statistics in Biological Research.* 3rd ed. New York, NY: W.H. Freeman and Company.

Studs, C. E. & Marra, P. P., 2011. Rainfall-induced changes in food availability modify the spring departure programme of migratory bird. *Proceedings of the Royal Society,* Volume 278, pp. 3437-3443.

Swift Conservation Ireland, 2020. *Swift Conservation Ireland.* [Online]
Available at: http://www.swiftconservation.ie/
[Accessed 02 March 2020].

Szép, T. & Moller, A.P., 2005. Using remote sensing data to identify migration and wintering areas and to analyze the effects of environmental conditions on migratory birds. In: Greenberg, R. & Marra. P.P., ed. *Birds of Two Worlds,* Baltimore, Maryland: Johns Hopkins University, pp. 390-400.

Tarburton, M.K. & Kaiser, E., 2001. Do fledgling and pre-breeding Common Swifts *Apus apus* take part in aerial roosting? An answer from radiotracking experiment, *Ibis*, Volume 143, pp. 255-263.

Tenow, O., Fagerström, T., Wallin, L., 2008. Epimeletic behaviour in airborne Common Swifts *Apus apus*: do adults support young in flight? *Ornis Svecica,* Volume 18, pp. 96-107.

Thompson, D., Douglas-Home, H., Furness, R. & Monaghan, P., 1996. Breeding success and survival in the common swift *Apus apus*: a long term study on the effects of weather. *Journal of Zoology,* Volume 239(1), pp. 29-38.

Tigges, U., 1999. Spartial behaviour of the Common Swift (Apus apus). *APUSlife*, No. 0061. [Online]
Available at: http://www.commonswift.org/0061TiggesU.html

Tigges, U., 2000. On the breeding phenology of the Common Swift (Apus apus) – the last diurnal return to the nest with reference to environmental factors. *APUSlife*, No. 2340. [Online]
Available at: http://www.commonswift.org/2340TiggesU.html

Tigges, U., 2006. The Breeding Cycle in Calendar Form of the Common Swift Apus apus across its Euriasian Breeding Range - A testable Hypothesis?. *Pedoces,* Volume 1(1/2), pp. 27-33.

Tigges, U., 2007. The Phenology of the Common Swift *Apus apus* in Eurasia and the Problem of Defining the Duration of their Stay. *Podoces,* Volume 2(2), p. 127–140.

Tigges, U., Mayer, M., Tucakov, M., 2016. International Swift Seminars Szczecin. Summaries of the presentations. *APUSlife*, No. 6555. [Online]
Available at: http://www.commonswift.org/6555Tigges-Mayer&Tucakov.html

Tompkins, D. M., Jones, T., Clayton, D. H., 1996. Effect of vertically transmitted ectoparasites on the reproductive success of Swift *(Apus apus), Functional Ecology,* Volume 10, 733-740.

Tryjanowski, P., Kuźniak, S., Sparks, T.H., 2005. What affects the magnitude of change in first arrival dates of migrant birds? *Journal of Ornithology,* Volume 146, pp. 200-205.

Tucker, V. A., 1998. Gliding flight: Speed and acceleration of ideal falcons during diving and pull out. *The Journal of Experimental Biology,* Volume 201, pp. 403-414.

Ussher, R. J. & Warren, R., 1900. *Birds of Ireland.* London: Gurney and Jackson.

Walker, M.D. & Rotherham, I.D., 2010a. Characteristics of *Crataerina pallida. (Diptera: Hippoboscidae*) populations; a nest ectoparsite of the Common Swift, *Apus apus* (*Aves: Apodidae), Experimental Parasitology,* Volume 126, pp. 451-455.

Walker, M.D. & Rotherham, I.D., 2010b. The breeding succes of Common Swift *Apus apus* is not correlated with the abundance of their Louse Fly *Crataerina pallida* parasites, *Bird Study*, Volume 57(4), pp. 504-508.

Walker, M.D. & Rotherham, I.D., 2011. No evidence of increased parental investment by Common Swift *Apus apus* in response to parasite load in nests, *Bird Study*, Volume 58(2), 217-220.

Wellbrock, A. H. J., Bauch, C., Rozman, J., Witte, K., 2017. “Same as last year?” – Repeatedly tracked swifts show individual consistency in migration pattern in succesive years, *Journal of Avian Biology,* Volume 48(6), pp. 897-903.

Westray, G. & Partridge, T., 2010. The Common Swift population in the UK is suffering a serious decline but veterinary nurses can help! *Veterinary Nursing Journal,* Volume 25(4), pp. 63-65.

Whelan, R., Hayes, W. & Caffrey, B., 2019. *Saving Swifts,* Wicklow: BirdWatch Ireland.

Whelan, R., Krastev, A., Hayes, W. & Caffrey, B., 2018. A study of the distribution and density of Swift *Apus apus* nest sites in four neighbouring counties (Laois, Offaly, Westmeath and Tipperary). *Irish Birds,* Volume 11, pp. 100-101.

White, G., 1795. *The Natural History of Selborne.* London: Benjamin White.

Wilson, J. S., 2011. Nest site conservation anction for the Common Swift (Apus apus) in Scotland 2000-2010. *APUSlife*, No. 4784. [Online]
Available at: http://www.commonswift.org/4784Wilson.html

Winkler, D. W. & Luo, M. K., 2013. Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). *Oecologia,* Volume 173, pp. 129-138.

Woodward, I. D. et al., 2018. *BirdTrends 2018: trends in numbers, breeding success and survival for the UK breeding birds,* Thetford, Norfolk : BTO.

Zarybnicka, M., Kubiznak, P., Sindelar , J. & Hlavac, V., 2016. Smart nest box: a tool and methodology for monitoring of cavity-dwelling animals. *Methods of Ecology and Evolution*, Volume 7, pp. 483-492.

Zatonski, J., 2016. Population of Common Swift in Poznan (Poland) and ecosystem services provided by it. *Ekonomia i Srodowisko,* Volume 59(4), pp. 265-273.

Appendices

All additional supplementary files listed in this section are available on the attached Appendix USB Flash Drive and at:

https://drive.google.com/drive/u/1/folders/1lZjBB_B3TYJ8MHArJnqN4pW7ahUIG3ms

Contact information for password to the Appendix USB Flash Drive and Google Drive link:
jaroslawmajkusiak@gmail.com
swiftresearchgmit@gmail.com

Additionally, the electronic version of this thesis (.docx) that is available on the Appendix USB Flash Drive provides links to spreadsheets embedded within the file.

Appendix A: Breeding Calendar Data (On USB Flash Drive)

File list:

- 2014-2020 Castlebar - Maguiresbridge Calendar Summary.
- 2018 - 2020 Swift Calendar – Castlebar
- 2018 - 2020 Swift Calendar – Fermanagh
- 2018 - 2020 Swift Calendar – Fermanagh
- Departures Dates Castlebar - Maguiresbridge Data
- Egg Laying Dates Castlebar - Maguiresbridge Data
- Fledging Dates Castlebar - Maguiresbridge Data
- Fledging Hatching Data
- Hatching Dates Castlebar - Maguiresbridge Data

Links:

Hatching Dates Castlebar - Maguire:

Fledging Hatching Data.xlsx

Fledging Dates Castlebar - Maguire:

Egg Laying Dates Castlebar - Maguire:

Departures Dates Castlebar - Maguire:

Arrivals Dates Castlebar - Maguire:

2018 - 2020 Swift Calendar - Fermana(

2018 - 2020 Swift Calendar - Castleba

2014-2020 Castlebar - Maguire:

Appendix B: Productivity and Breeding Success Data (USB Flash Drive)

File list:

- Productivity analysis 2014-2020

Link:

Productivity analysis 2014-2020.x

Appendix C: Feeding frequencies data

File list:

Claremorris Met Éireann Weather Station

- Claremorris Daily Weather Data
- Claremorris Hourly Weather
- Claremorris Weather Data Pivot Tables

Feeding Frequency Analysis

- 2018 Feeding Frequency pivot tables
- 2019 Feeding Frequency pivot tables
- 2020 Feeding Frequency pivot tables
- Daily feeding with the age of the brood
- Hourly Feeding Patterns
- Stage 2 DAX
- Stages of Chicks Development
- DAX Weather Correlations

Video Analysis

- 2017 Video Analysis
- 2018 Video Analysis
- 2019 Video Analysis
- 2020 Video Analysis

Links:

Claremorris Weather Data Pivot

Claremorris Hourly Weather (source).cs

Claremorris Daily Weather Data.xlsx

TOTAL Weather Correlation.xlsx

Stages of Chicks Developement.xlsx

STAGE 2 DAX (all fixed).xlsx

Hourly Feeding Patterns.xlsx

Daily feeding with the age of the broo

2020 Feeding Frequency pivot tab

2019 Feeding Frequency pivot tab

2018 Feeding Frequency pivot tab

2017 Video Analusis.xlsx

2020 Video Analysis.xlsx

2019 Video Analysis.xlsx

2018 Video Analysis.xlsx

Appendix D: Egg Loss Data

File list:

Analysis

- Castlebar (2018-2020)- Maguirebridge (2020) egg loss

Egg Loss Evidence Videos

Castlebar 2018

- 2018 Box 5 - adult tries to pick up knocked out egg-Multi - 2 June, 09-49.f4v-
- 2018 Box 5 - second egg knocked same day (third time overal) -Multi - 2 June, 09-49.f4v-
- 2018 box 5 accidental egg knockout -Multi - 2 June, 09-49.f4v-
- 2018 box 5 adult brings the egg back into the nest - 2 June, 09-49.f4v-
- 2018 Box 5 -Adult knocks the egg that was brought back in-Multi - 2 June, 09-49.f4v-
- 2018 Box 5 another attempt of picking up the egg(failed) -Multi - 2 June, 09-49.f4v-
- 2018 box 5 -brings the egg back in -Multi - 2 June, 09-49.f4v-
- 2018 box 5 knocking an egg out semi-accidentaly Multi - 7 June, 13-09.f4v-
- 2018 Box 10 EGG Knocked out BOX 10-Multi - 12 June, 13-07.f4v-
- 2018 Box 10 Egg knocked out by accident - 1 June, 13-34.f4v-

Castlebar 2019

- 2019 box 8 07.06.2019 Adult interacting with an egg.ts
- 2019 box 8 25.06.2019 4th Egg ejected.ts
- 2019 Box 8 28.05.2019 2nd Egg ejected.ts
- 2019 Box 8 29.05.2019 tries to pick up an egg 2.ts
- 2019 Box 8 29.05.2019 Tries to pick up an egg.ts
- 2019 BOX 8 Egg brought back into the nest and lost -Multi 1 June 9-49.f4v-.ts
- 2019 box 8 egg knocked 27.05.2019.mp4
- 2019 box 9 5.06.2019 Egg ejected 2.mp4

- 2019 box 9 17.05.2019 Egg tossed.mp4
- 2019 Box 9 18.05.2019 Egg laid.mp4
- 2019 Box 12 1st Egg knocked 18 May 2019.mp4
- 2019 box2 29 May 2019 Brings the egg back into nest.ts
- 2019 Box 2 29.05.2019 Egg tossed.ts
- 2019 Box 2 31.05.2019 2nd Egg ejected.ts
- 2019 Box 5 01.06.2019 Egg ejected.ts
- 2019 Box 5 04.06.2019 2nd Egg ejected.ts
- 2019 Box 8 02.07.2019 Egg ejected.ts
- 2019 Box 8 03.07.2019 All 5 eggs visible.ts
- 2019 box 8 05.06.2019 Adult interacting with an egg 3.ts
- 2019 box 8 5.06.2019 Adult interacting with an egg 2.ts
- 2019 box 8 5.06.2019 Adult interacting with an egg.ts

Castlebar 2020

- box8 28.05.2020 egg finally tossed out of the nest 16.mkv
- box8 28.05.2020 egg picked up 15.mkv
- box10 04.06.2020 egg lost.mkv
- box11 21.05.2020 egg brought back.mkv
- box11 21.05.2020 egg knocked.mkv
- box11 22.05.2020 2nd egg lost.mkv
- box11 24.05.2020 3rd egg knocked.mkv
- box11 30.05.2020 4th egg lost.mkv
- box11 31.05.2020 FIGHT.mkv
- box12 01.06.2020 2nd egg tossed out of the nest.mkv
- box12 01.06.2020 egg thrown out.mkv
- box12 01.06.2020 egg tossed out of the nest.mkv
- Box 11 20.05.2020 egg lost.mkv
- box5 09.06.2020 egg picked and tossed out of the nest.mkv
- Box8 01.06.2020 3rd egg lost.mkv
- box8 02.06.2020 egg laid.mkv

- box8 03.06.2020 4th egg lost.mkv
- box8 09.06.2020 egg picked and ends up back in the nest.mkv
- box8 09.06.2020 egg picked up 17.mkv
- box8 09.06.2020 egg picked up 18.mkv
- box8 19.05.2020 egg lost.mkv
- box8 21.05.2020 egg brought back.mkv
- box8 25.05.2020 egg picked up again 5.mkv
- box8 26.05.2020 egg picked up 11.mkv
- box8 26.05.2020 egg picked up 12.mkv
- box8 26.05.2020 egg picked up 13.mkv
- box8 27.05.2020 egg picked up 14.mkv
- box8 28.05.2020 egg finally ejected out of the nest 16.mkv
- box8 28.05.2020 egg picked up 15.mkv
- box10 04.06.2020 egg lost.mkv
- Box11 20.05.2020 egg lost.mkv
- box11 21.05.2020 egg brought back.mkv
- box11 21.05.2020 egg knocked.mkv
- box11 22.05.2020 2nd egg lost.mkv
- box11 24.05.2020 3rd egg knocked.mkv
- box11 30.05.2020 4th egg lost.mkv
- box11 31.05.2020 FIGHT.mkv
- box12 01.06.2020 2nd egg tossed out of the nest.mkv
- box12 01.06.2020 egg thrown out.mkv
- box12 01.06.2020 egg tossed out of the nest.mkv
- box5 09.06.2020 egg picked and ejected out of the nest.mkv
- Box8 01.06.2020 3rd egg lost.mkv
- box8 02.06.2020 egg laid.mkv
- box8 03.06.2020 4th egg lost.mkv
- box8 09.06.2020 egg picked and ends up back in the nest.mkv
- box8 09.06.2020 egg picked up 17.mkv
- box8 09.06.2020 egg picked up 18.mkv
- box8 19.05.2020 egg lost.mkv

- box8 21.05.2020 egg brought back.mkv
- box8 21.05.2020 egg lost again.mkv
- box8 21.05.2020 egg lost.mkv
- box8 23.05.2020 egg picked up.mkv
- box8 24.05.2020 egg picked up again 4.mkv
- box8 24.05.2020 egg picked up again and lost.mkv
- box8 25.05.2020 egg picked up 6.mkv
- box8 25.05.2020 egg picked up 7.mkv
- box8 25.05.2020 egg picked up 8.mkv
- box8 25.05.2020 egg picked up 9.mkv
- box8 25.05.2020 egg picked up 10.mkv

Maguiresbridge 2020

- Gable 3 24.05.2020 egg loss 1
- Gable 3 24.05.2020 egg returned by John 1
- Gable 7 27.05.2020 egg placed

Link:

Castlebar
(2018-2020)- Maguir

Appendix E: Miscellaneous

Captured Video

- box8 28.05.2020 egg finally tossed out of the nest 16.mkv
- box8 28.05.2020 egg picked up 15.mkv
- box10 04.06.2020 egg lost.mkv
- box11 21.05.2020 egg brought back.mkv
- box11 21.05.2020 egg knocked.mkv
- box11 22.05.2020 2nd egg lost.mkv
- box11 24.05.2020 3rd egg knocked.mkv
- box11 30.05.2020 4th egg lost.mkv
- box11 31.05.2020 FIGHT.mkv
- box12 01.06.2020 2nd egg tossed out of the nest.mkv
- box12 01.06.2020 egg thrown out.mkv
- box12 01.06.2020 egg tossed out of the nest.mkv
- Box 11 20.05.2020 egg lost.mkv
- box5 09.06.2020 egg picked and tossed out of the nest.mkv
- Box8 01.06.2020 3rd egg lost.mkv
- box8 02.06.2020 egg laid.mkv
- box8 03.06.2020 4th egg lost.mkv
- box8 09.06.2020 egg picked and ends up back in the nest.mkv
- box8 09.06.2020 egg picked up 17.mkv
- box8 09.06.2020 egg picked up 18.mkv
- box8 19.05.2020 egg lost.mkv
- box8 21.05.2020 egg brought back.mkv
- box8 25.05.2020 egg picked up again 5.mkv
- box8 26.05.2020 egg picked up 11.mkv
- box8 26.05.2020 egg picked up 12.mkv
- box8 26.05.2020 egg picked up 13.mkv
- box8 27.05.2020 egg picked up 14.mkv
- box8 28.05.2020 egg finally ejected out of the nest 16.mkv

- box8 28.05.2020 egg picked up 15.mkv
- box10 04.06.2020 egg lost.mkv
- Box11 20.05.2020 egg lost.mkv
- box11 21.05.2020 egg brought back.mkv
- box11 21.05.2020 egg knocked.mkv
- box11 22.05.2020 2nd egg lost.mkv
- box11 24.05.2020 3rd egg knocked.mkv
- box11 30.05.2020 4th egg lost.mkv
- box11 31.05.2020 Fight.mkv
- box12 01.06.2020 2nd egg tossed out of the nest.mkv
- box12 01.06.2020 egg thrown out.mkv
- box12 01.06.2020 egg tossed out of the nest.mkv
- box5 09.06.2020 egg picked and ejected out of the nest.mkv
- Box8 01.06.2020 3rd egg lost.mkv
- box8 02.06.2020 egg laid.mkv
- box8 03.06.2020 4th egg lost.mkv
- box8 09.06.2020 egg picked and ends up back in the nest.mkv
- box8 09.06.2020 egg picked up 17.mkv
- box8 09.06.2020 egg picked up 18.mkv
- Box 5 20.05.2020 Fight.mkv
- box 10 26.05.2020 fight.mkv
- Box2 2020 28.05.2020 Plastic.mkv
- Box4 01.06.2020 Fight.mkv
- Box4 03.06.2020 Fight.mkv
- box5 26.05.2020 fight.mkv
- box7 19.05.2020 Fight.mkv
- box7 20.05.2020 plastic.mkv
- box9 25.05.2020 plastic.mkv
- box10 20.07.2020 Adult only feeds the stronger chick.mkv
- box10 30.05.2020 parasite.mkv
- box10 31.07.2020 interacting with a carcas of a dead chick.mkv
- box10 31.07.2020 Adult interacting with a carcas of a dead chick 3.mkv

- box10 31.07.2020 adult interacting with a carcas of a dead chick.mkv
- box11 July 11 2019 chick exercising.mkv
- box11 July 11 2019 Chick looking out.mkv
- box11 July 11 2019 Feeding.mkv
- box11 July 11 2019 reaction to bangers.mkv
- Gable 5 27.05.2020 Plastic.mkv
- Gable 7 27.05.2020 Plastic.mkv
- 2019 2 week old falls out of the nest.mp4
- 2019 box1 3rd egg laid.mp4
- 2019 box1 egg laid.mp4
- box 1 June 28 2019 3 chicks feeding.mkv
- Box 5 20.05.2020 Fight 2.mkv

YouTube Compilation Videos

- Day and Night with the Swifts
- Egg interaction video
- Swifts Ti and Rex