

The Feeding Ecology of Little Tern *Sternula albifrons* in the UK

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Abstract

An understanding of feeding and foraging behaviour is an important component of population ecology. Studying feeding and foraging behaviour is particularly important for seabirds where a link between poor breeding success and poor feeding has been identified in several species. This study looks at the feeding ecology of the Little Tern *Sternula albifrons*, a species which has undergone an estimated population decline of 37% in the UK over the last three decades, attributed to reduced productivity and recruitment. The study firstly examines chick diet in the UK and how this varies between colonies and years. It then looks at the factors driving observed patterns of food delivery to chicks and links these to measures of colony success. In doing so it draws on unpublished chick feeding data collected at English and Welsh colonies by the EU LIFE funded Little Tern Recovery Project in the period 2014 to 2018. The study goes on to investigate the potential for using camera trapping and video imagery as an alternative to direct observation for collection of data in chick feeding studies of Little Tern and to examine patterns and locations of foraging by adult Little Tern at the Long Nanny tern colony in Northumberland and at the Seaton Carew tern colony in Hartlepool on Teesside. I review what evidence these provide on the role of diet and food availability on the breeding success and conservation of UK Little Tern and provide recommendations for further areas of study.

Dedication

This thesis is dedicated to my father, Norman Brodin (22nd February 1936 – 6th January 2023).

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Chapter 1. General Introduction

1.1 Foraging and diet of animals

An understanding of animal diet is a fundamental aspect of animal ecology (Gaglio *et al.* 2017, Jordan 2005). Patterns of food availability influence where animals chose to live, breed and forage; they effect survival and productivity, and influence life history and behaviour. A knowledge of what food resources are needed by a species, and of the factors which affect their access to those food resources, is critical when planning conservation action (Ronconi *et al.* 2022).

There is a long and growing history of studies into how animals may respond to changes of availability in prey (Krebs 2022). One early concept was the notion of functional and numeric responses by predators to fluctuating prey availability introduced by Solomon (1949). The numeric response involves changes to predator density in response to prey availability and can be seen through, for example, variations in nesting density or changes in foraging intensity. The functional response may involve changes to the rate at which prey is consumed or to the types of prey taken (Redpath and Thirgood 1999). Andersson and Erlinge (1977) classified predators as being either specialists or generalists with specialists responding numerically to prey availability while generalists respond both numerically and functionally.

One of the key concepts underpinning feeding studies in animals is Optimum Foraging Theory. This predicts that natural selection has shaped foraging animals so that their main aim is to optimize their energy or food intake in the most efficient way possible (Macarthur and Pianka 1966), thereby influencing their choice of prey and their duration and location (Pyke 1984, Pyke *et al.* 1977). One consequence of this is that in patchy environments the distribution of foraging animals is expected to be non-random.

One elaboration of Optimum Foraging Theory is Optimal Diet Theory, sometimes called the Optimal Diet Model. This deals with food choice and predicts that animals should show a preference for selecting prey which maximizes energy or nutritional value per

unit time and ignore prey of lower nutritional value when better prey is available (Pyke *et al.* 1977, Sih and Christensen 2001, Stephens 2019) Decisions on whether to spend time selecting prey which is sub-optimal in energetic or nutritional terms will depend on the availability of more profitable prey items (Davies *et al.* 2012). For generalist predators, the Alternative Prey Hypothesis (APH) predicts that alternative prey will be used when the availability of their main prey resource declines (Breisjøberget *et al.* 2018).

Generalist predators are defined as those that can feed on a wide range of available food resources. In contrast specialist predators feed only on a narrow range of food resources and have limited capacity for prey switching in response to food shortages (Stienen *et al.* 2000). However, generalists may show varying degrees of diet specialism between individuals and between populations in response to prey availability and to individual morphology and life history (Salamolard *et al.* 2000).

1.2. Foraging and diet of seabirds

Globally, seabirds are considered one of the most threatened group of birds with population declines linked to a range of factors including impacts from invasive non-native species, mortality due to bycatch in fisheries, climate change, and overfishing (Dias *et al.* 2019). Food availability has been cited as a key pressure affecting breeding seabird species in the UK (Burnell *et al.* 2023). Seabirds exist at the top end of the marine food chain and changing patterns of feeding and diet variations in both the amount and quality of available food is known to be closely related to their productivity and breeding success (Fayet *et al.* 2021) with low food availability or poor quality of available prey being associated with lowered productivity (Monaghan *et al.* 1992, Monaghan *et al.* 1989, Uttley *et al.* 1989). Seabirds may also act as sentinel species with changing patterns of feeding and observed diet and can be an indicator of wider changes in marine ecosystems (Hazen *et al.* 2019, Parsons *et al.* 2008, Piatt *et al.* 2007).

During the breeding season seabirds are central place foragers in the terminology first defined by Orians and Pearson (1979) – when foraging they must bring food back to a specific location (the central place), in the case the breeding site. Consequently, seabirds are constrained in the distances which they can travel to obtain food before needing to return to the central place (Ronconi *et al.* 2022). Breeding seabirds need to

make decisions about how they balance the time they spend addressing their own feeding needs versus the time they spend in nest attendance or in chick feeding. Optimal Foraging Theory (Macarthur and Pianka 1966) predicts that the result of these decisions should optimise foraging effort and the energy intake their offspring, selecting prey of the highest nutritional quality while minimising the time spent looking for it. As a result, they may adopt a strategy of alternating longer foraging trips to meet their own energetic needs with shorter trips needed to meet the needs of their growing chicks (Shoji *et al.* 2015). The energy demands of chicks increase as they grow (Klaassen *et al.* 1992, Klaassen *et al.* 1989). For birds which are single-prey loaders (i.e. can only return with one prey item per foraging trip), parents can meet these demands through increasing the rate at which food is brought to chicks or by increasing the energetic value of the food which is delivered, for example by bringing larger items or selecting prey species which are more energy-rich (Robertson *et al.* 2016). Adult birds may therefore be more selective about their choice of prey items for chicks than for prey items which they select for themselves (Bugge *et al.* 2010).

Reproductive success in Terns (Sternidae) is considered to be more sensitive to low food availability than is the case for larger species of seabird. This is thought to be due to limits on foraging distances placed on them during the breeding season as central place foragers and limits on the number of prey items they can carry as single prey loaders (Monaghan 1996, Daunt *et al.* 2008, Furness and Tasker 2000). The low body mass of Tern species has also been identified as a factor which may make them species more sensitive to food availability, with small size being one of the variables included by Furness and Tasker (2000) in their modelling of seabird vulnerability to food shortages. The foraging time required to rear a brood of chicks is greater for smaller seabirds than it is for larger seabirds, reflecting the larger biomass of prey capable of being taken by larger birds, leaving smaller seabirds with less opportunity to increase foraging effort to compensate for food shortages during the breeding season (Furness and Monaghan 1987, Pearson 1968)

A number of different environmental factors may influence the ability of seabirds to access food resources and can therefore affect their own survival and the survival of their chicks. Weather conditions can play a major role in the ability of seabirds to forage

for food (Anderson *et al.* 2005, Dunn 1975, Frank 1992, Stienen *et al.* 2000, Taylor 1983) or influence the types of prey available to birds (Frank 1992, Stienen *et al.* 2000). Sea Surface Temperature (SST) is an important driver of habitat use by marine fish (Freitas *et al.* 2021) and can influence their abundance and nutritional quality (Marine Climate Change Impacts Partnership 2018, Mitchell *et al.* 2020b, Wanless *et al.* 2004). Poor breeding success at some seabird colonies has been linked to the impacts of sea temperature on food availability with, for example breeding success in Black Legged Kittiwake *Rissa tridactyla* being negatively correlated with winter sea temperatures (Frederiksen *et al.* 2004). There is also evidence that large-scale climatic phenomena such as the North Atlantic Oscillation (NAO) has an influence on seabird demographics and breeding success, probably through changes in patterns of prey availability (Durant *et al.* 2005, Ramos *et al.* 2013).

It has been argued that for many species of seabirds, demographic parameters such as breeding performance can be relatively insensitive to changes in food availability due to their long life-span and ability to switch between different types of prey (Votier *et al.* 2004, Church *et al.* 2019). In such situations, changes in seabird diet and foraging behaviour are likely to be easier to detect and therefore have the potential to indicate changes in marine ecosystems which may not be apparent from the study of breeding success alone.

1.3 Little Tern

1.3.1 Little Tern Life History

The focus of this thesis is the feeding ecology of the Little Tern *Sternula albifrons*. The Little Tern is a migratory seabird of the family Sternidae (Figure 1.1). It is the smallest of the UK's five breeding tern species weighing approximately 50g and with a total body length of 22-24cm (Cabot and Nisbet 2013). Breeding populations of the species are found in Europe, Africa, Asia, and Australia (Fasola *et al.* 2002), with five distinct sub-species recognised from across this geographical range. Little Tern is one of a group of about seven closely related species in the genus *Sternula*. Other members of this genus include the Least Tern *Sternula antillarum* found in North and Central American and the Damara Tern *Sternula balaenarum* found in southern Africa. The seven species replace

each other geographically and have in the past sometimes been combined into a single species (Cabot and Nisbet 2013).



Figure 1.1 Adult Little Tern feeding chick with Sandeel *Ammodytes* spp. Photograph taken under licence (Ref: 2017-28158-SCI-SCI) at Long Nanny.

Little Terns are long-distance migrants. In the UK they arrive from April onwards and depart from August for their wintering grounds in West Africa. Egg laying takes place in May with the first chicks normally seen in mid-June (Natural England. 2012). In the UK and Ireland, Little Tern are an exclusively coastal species. They breed in colonies on sand or shingle beaches, spits, sandbars and offshore islands. In the western Isles of Scotland and west coast of Ireland birds also breed on short grass swards on Machair grassland (Cabot and Nisbet 2013). In other parts of their range Little Tern also breed on sand or shingle within major river systems such as the Danube or the Po (Fasola *et al.* 2002, Fasola and Bogliani 1984), on man-made habitats such as Saltinas (salt-pans) in Portugal (Paiva *et al.* 2008) and even on flat roofs when suitable substrate is present (Fujita *et al.* 2009). Breeding locations in the UK are generally associated with sparse vegetation cover and low disturbance levels (Ratcliffe *et al.* 2008). Proximity to a good supply of food availability is also believed to play an important role in colony location and may be a more important factor in the selection of breeding location than other

measures of habitat suitability (Perrow *et al.* 2003). Little Tern has widely been described as a generalist feeder (Fasola *et al.* 2002, Eglington and Perrow 2014) in that the species is capable of consuming a wide range of available prey types. Reported prey items from across their global range include marine fish and crustaceans, freshwater fish, annelid worms, molluscs, and terrestrial insects, with different studies usually report different dominant prey species at different locations (Cramp 1985, Eglington and Perrow 2014, Fasola *et al.* 2002). Cabot and Nesbit (2013) have described the available data on Little Tern diet as ‘somewhat contradictory’, with some reports suggesting Little Tern feed almost exclusively of fish while others have indicated that they feed extensively on invertebrate prey items such as crustacea. The location of breeding sites can change from year to year and colonies may be completely abandoned due to pressure from disturbance or predators (JNCC 2016, Brown and Grice 2005). Recent examination of colour-ringed Little Tern in Britain and Ireland has shown extensive exchanges of breeding birds between individual colonies both between and within years, indicating the importance of considering Little Tern breeding colonies as part of a wider network (Wilson *et al.* 2021).

Breeding Little Terns are found around the UK coastline, in around 86 separate colonies or sub-colonies (RSPB 2019a), although the precise number and size of breeding colonies varies from year to year (Natural England. 2012) making an accurate assessment difficult. Little Tern is one of the most intensively managed seabird species in the UK (Wilson *et al.* 2020) with some form of protection, monitoring or wardening presence usually being put in place when breeding locations are identified. Most UK colonies are small, with an average of 30 pairs; only 12 colonies regularly support more than 100 nest (Brown and Grice 2005, Cabot and Nisbet 2013).

Nests are made in shallow bare scrapes in which usually 2 or 3 eggs are laid (Brown and Grice 2005). Scrapes are often located close to high tide marks, making nests and eggs vulnerable to high spring tides (Natural England. 2012). An average of 21 days passes between egg lay and hatching, with chicks taking approximately 20 days to fledge. Only one brood per year is raised to fledging but it is common for a second or a third brood to be laid when eggs or young chicks are lost (Brown and Grice 2005). Both parents share in brooding and chick feeding duties. Young are entirely dependent on their parents for

food with chicks achieving close to their full weight by about 10 days of age (Norman 1992).

Chicks are precocial and semi-nidifugous and can become highly mobile within a few days of hatching (Fasola *et al.* 2002). This, when combined with the sometimes ephemeral nature of breeding locations and often high rates of chick mortality, can make Little Tern a difficult species to study in the field resulting in them being comparatively less well studied than other UK tern species (Cabot and Nisbet 2013).

1.3.2 Conservation status

Little Tern is classified as Least Concern on the IUCN Red List due to its large range and global population size (IUCN 2019) and is an Amber listed Species of Conservation Concern in the UK (Stanbury *et al.* 2021). The overall population trend for Little Tern globally is decreasing, with a number of threats to the species identified including human disturbance of breeding colonies, predation, habitat change and direct habitat loss through coastal development (IUCN 2019). The global population is estimated to be between 190,000 - 410,000 individuals with the European breeding population of Little Terns is estimated at 36,000 - 53,000 pairs (Birdlife International 2024). The UK population size is estimated as 1,900 pairs (Pickerell 2004) with populations showing a 37% decline since the 1990s (Wilson *et al.* 2020). Little Tern is protected as an Annex 1 migratory species under the EC Bird Directive (European Parliament, 2009), and is listed on the Schedule 1 UK Wildlife and Countryside Act 1981 (Eaton *et al.* 2015).

Declines in Little Tern numbers are thought to be driven by low productivity and poor recruitment (Pickerell 2004, Ratcliffe 2004, Ratcliffe N. *et al.* 2000, Wilson *et al.* 2021). Little Tern chicks and eggs frequently suffer from high mortality (Cabot and Nisbet 2013). Reported causes of losses include predation (including from crows, gulls, raptors and mammals), high tides, poor weather, disturbance, and lack of access to food. There are potential interactions between some of these factors, for example food shortages may lead to an increase in the time which parents spend away from their eggs or chicks on foraging trips which may in turn increase the risk of predation or exposure (RSPB 2015b). Wilson *et al.* (2020) identified that the most common causes of losses of eggs and chicks in Little Tern (based on 280 reports of losses from 2014-2018) were predation and

tidal flooding/weather. Food availability only accounted for reported failures at 3% of reports across the period from 2014-2018.

1.4 The EU LIFE Little Tern Recovery Project (“The LIFE Project”)

1.4.1 Background to Project

The EU LIFE-funded Little Tern Recovery Project (hereafter “The LIFE project”) ran from five years from March 2014. The LIFE project was led by the RSPB and was established in direct response to ongoing Little Tern population declines in the UK: details of this have been described by Wilson *et al.* (2020) from whom the details below are taken.

Increased management effort was applied between 2014-2018 at 29 sites in England and Wales. All but two of these sites were within Special Protection Areas (SPAs) with the remaining two believed to be used by Little Terns originating from within adjacent SPAs. Resources were used under four main management themes: (i) an enhanced warden scheme; (ii) predator management; (iii) habitat management and enhancement for existing colonies; and (iv) habitat creation/restoration to support new colonies. These resources provided additional management at existing colonies but were also aimed at providing a more resilient network of sites. Actions undertaken included enhance habitat management, increases numbers of site wardens, fencing, predation control and human disturbance management.

At each participating site, measures of annual breeding success were monitored using methodologies following those set out in the Seabird Monitoring Handbook for Britain and Ireland (Walsh *et al.* 1995). Monitoring undertaken included nest counts fledgling counts and chick feeding surveys.

1.4.2 Monitoring of chick feeding

As part of the ongoing programme of monitoring work undertaken by the LIFE project timed observations of chick feeding were made at twelve participating colonies. Data on chick diet was also available from a thirteenth site using video imagery captured through use of camera traps (Figure 1.2). The timed observations of chick feeding were made by staff and volunteers at participating colonies using a standard methodology. The length of time spent on survey effort varied between colonies with not all locations undertaking surveys in each year. These data were intended to be used to investigate the interaction

between chick feeding rates and colony productivity measures and to compare feeding rates between years (RSPB 2015b).

The data on chick diet collected by the LIFE project represents the first concerted effort in the UK to collect observations from multiple colonies, across multiple years, using a consistent field methodology and provides the widest overview available currently available on chick diet from English and Welsh colonies.

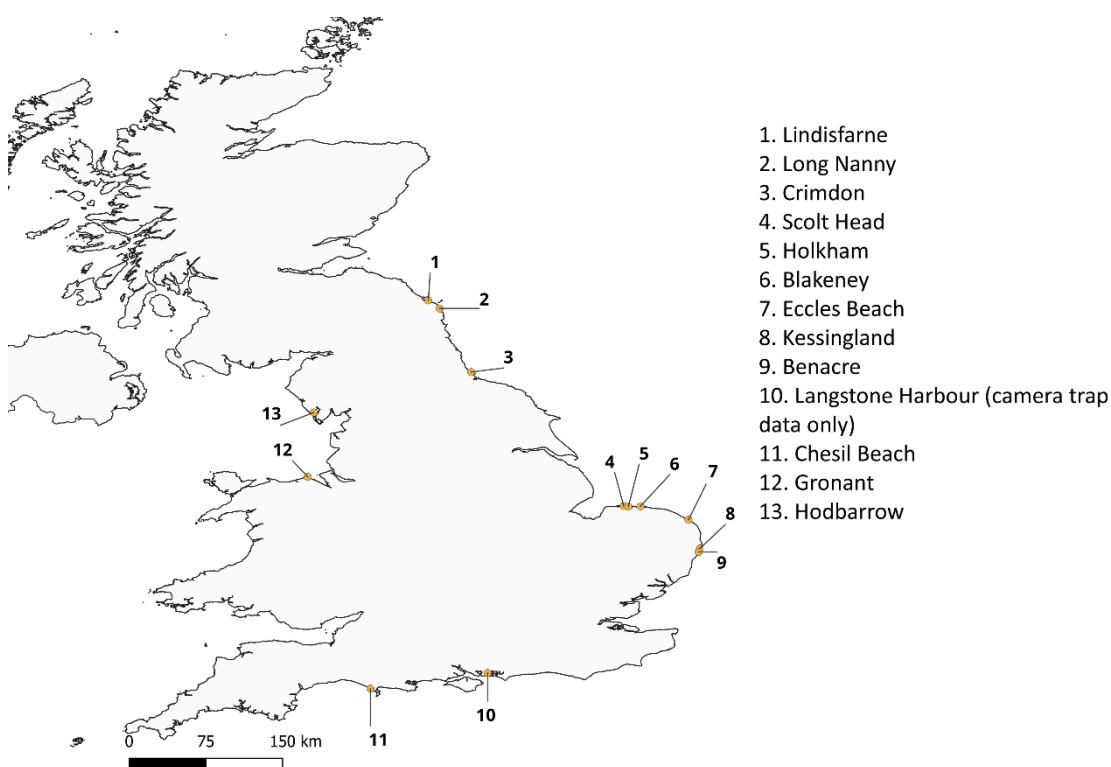


Figure 1.2. Locations of colonies providing chick feeding observations to the LIFE project. Not all colonies provided records in each during the period 2014-2018. See Chapter 2 for a breakdown of the observational effort at each colony and details of colony productivity. All colonies with the exception of Langstone Harbour provided data based on timed observations of chicks. Data from Langstone Harbour was derived from camera trap video footage.

1.4.3 Data collection methodology

Survey and monitoring methodologies were circulated each year to participating colonies by the LIFE project. This included a methodology for chick feeding surveys.

Surveyors were asked to select a brood of chicks to monitor and to observe them for a period of at least 60 minutes using binoculars or a scope, recording the following information:

- the date, start time and end time of observations
- the number of chicks in the brood and the age of the chicks
- the brood identifier or nest reference number if known
- the time when adults return to the nest/brood with food
- the identity of the prey
- the estimated size of the prey relative to bill length.
- the fate of the prey e.g. whether the prey was eaten by chick
- environmental variables such as state of tide, wind direction and strength (Beaufort scale) and wave state (Douglas Sea Scale).

Surveyors were asked to vary observations across different times of day and different stages of the tide. Prey items were only required to be identified to a broad taxonomic level, usually family. The LIFE project produced a photographic guide of the main prey types to aid identification. In practice, not all survey returns from the LIFE project included all contextual information. Estimates of wind speed and wave state were commonly omitted and there were inconsistencies in how individual observers recorded tidal stage and chick age. Tidal stage was recalculated using online tide tables for the closest port or harbour. Chick ages were classified under three different age bands: age band 1 (less than seven days of age), age band 2 (seven to 14 days of age) and age band 3 (older than 14 days).

Survey results were submitted to the LIFE project coordinator at the end of each season. Additional chick feeding surveys carried out as part of the research presented in this thesis also adopted the methodology used by the LIFE Project.

1.5 Study locations for additional fieldwork

In addition to the chick feeding data provided by the LIFE project, this thesis is also informed by independent field work undertaken at the Long Nanny and Seaton Carew tern colonies.

1.5.1 Long Nanny

My main study location was at the Long Nanny, a National Trust owned and managed site on Beadnell Bay in Northumberland (55.539572° N, -1.637723W). The 7.5ha site includes a section of beach and a low-lying sand-spit formed at the mouth of the Long Nanny Burn. The sand-spit forms the main nesting area for Little Tern and is prone to inundation during spring tides (Figure 1.3). Little Tern have bred at the colony since 1977, with initially three breeding pairs using the site growing to around 30-50 pairs during the 1990s (Dorman *et al.* 2016). The site is also home to Arctic Tern *Sterna paradisaea*, which first bred on the site in 1980 and has since grown to be the largest mainland site for species, recording up to 2,443 pairs (Bridge *et al.* 2014). The colony is part of the Newton Links Site of Special Scientific Interest (SSSI) and forms part of the Northumbria Coast Special Protection Area (SPA), whose designation recognises the important breeding population of Little Tern and Arctic Tern found there (Natural England. 2017).



Figure 1.3. Location of the Long Nanny tern colony. Little Tern breed on the sand spit (location identified with pin).

The National Trust employ a small team of staff to provide a 24-hour warden presence on the site during the tern nesting season. Their role includes protecting nesting birds from predation and inundation by the tides, managing human disturbance and carrying out monitoring of the productivity and success of the colony (Arthur *et al.* 2017). The

wardens identify active scrapes and record their location and the number of eggs present. Numbered marker stones are left by scrape locations. Because of the risk of tidal inundation of the sand-spit, scrapes and eggs are routinely lifted on to sand-filled fishing boxes to provide additional height and protection from high tides. Chicks drop from these crates a few days after hatching after a few days and become mobile on the sand-spit. Monitoring of Little Tern chick feeding by site staff has taken place since 1998, with monitoring for 2014-2018 being incorporated into the work of the LIFE project.



Figure 1.4. Views of the Long Nanny tern colony. Image on the right shows examples of nests loaded on to fishing crates.

I collected data from Long Nanny during 2017, 2018, 2019, 2021 and 2022 (Table 1.1). This fieldwork was in addition to the chick feeding surveys undertaken by site wardens as part of the LIFE project.

Table 1.1. Summary of peak colony size and colony productivity at the Long Nanny tern colony during the years when fieldwork was undertaken by the author of this thesis. Colony productivity was calculated by dividing peak breeding pair or Apparently Occupied Nest (AON) by the total number of chicks fledged. Note that LIFE project feeding observations were made separately by site wardens in 2014-2018. A summary of type of work undertaken is given in the final column. Parentheses indicate minor activities for that year.

Year	Peak breeding pairs	Colony Productivity	Data gathered
2017	38	0.11	Chick feeding observations Video imagery of chick feeding
2018	40	0	Chick feeding observations Video imagery of chick feeding (Adult foraging locations)
2019	34	1.59	Chick feeding observations Video imagery of chick feeding
2021	9	0	(Adult foraging locations)
2022	39	1.44	Adult foraging locations Video imagery of chick feeding (chick feeding observations)

1.5.2 Seaton Carew

Seaton Carew beach in Hartlepool (54°39'28.38"N, 1°11'0.19"W) has been the main breeding location for Little Tern on the Teesmouth and Cleveland coast since 2019, following the relocation of birds from Crimdon Denemouth, located approximately 7km to the north, which had been the local breeding stronghold for the species since the mid-1990s (RSPB 2021).

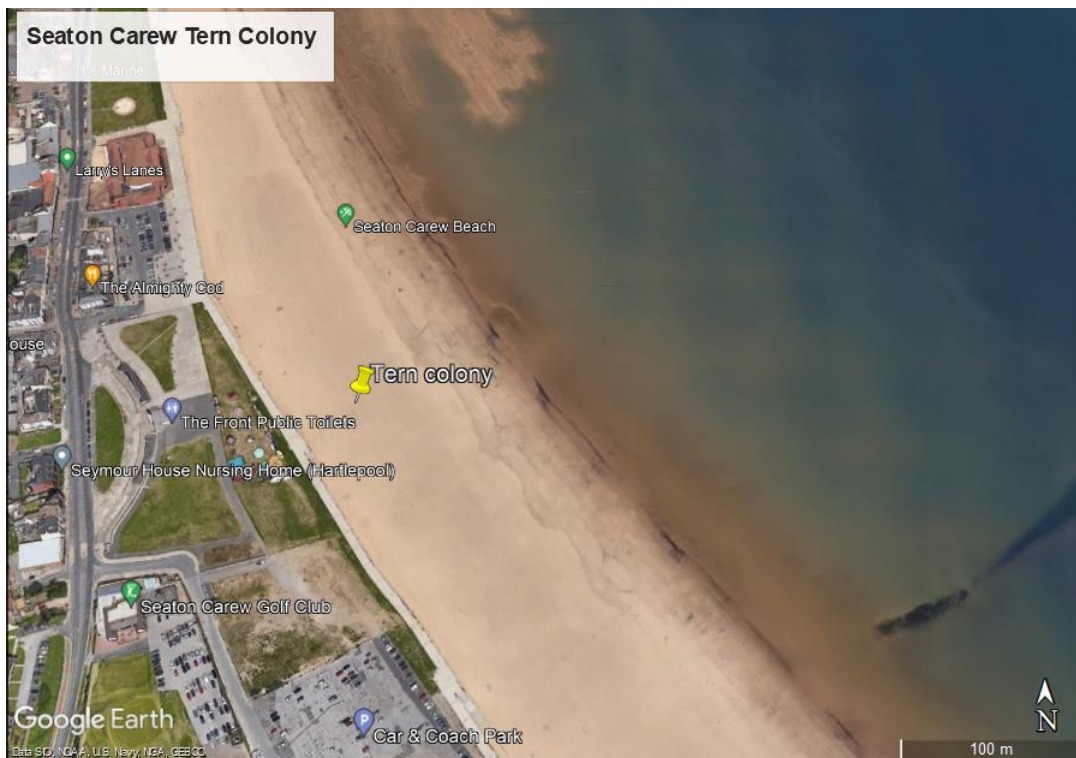


Figure 1.5. Location of the Seaton Carew Little Tern colony.

The location is a recreational beach in an urban location with high visitor numbers. During the breeding season terns are protected by an inner fence consisting of wooden fence posts with two strings below enclosing an area of approximately 2.2ha. An outer “buffer zone” demarcated by traffic cones and thick rope to which safety tape (coloured red and white and yellow and black) is tied so that it is visible to members of the public whilst on the beach. In 2021 this buffer zone was initially 2 metres wide but was later increased when scrapes were discovered in the buffer zone to the north and south of the nest site. The breeding area is backed by a promenade. The stairway leading off this into the nesting area is blocked off by Hartlepool Council in early May. Staff and volunteers from Durham Wildlife Trust act as wardens at the colony during the day time (Durham Wildlife Trust 2021, RSPB 2021).



Figure 1.6. Two views of the Seaton Carew Little Tern colony. The image on the left is looking southeast across the colony and shows the fencing used to deter public entry into the tern nesting areas. The image on the right is looking out to sea and shows the wall of the promenade which backs on to the breeding site.

Fieldwork at Seaton Carew was carried out during the 2021 breeding season. In that year, a peak of 57 pairs of Little Tern were recorded from which three chicks fledged (a productivity of 0.05). These numbers include one chick fledged from a small satellite colony at North Gare, approximately 1.8km to the south. The main cause of losses of eggs and chicks in 2021 was identified as high tides and strong winds on the 25th June (Durham Wildlife Trust 2021, RSPB 2021).

1.6 Aims

The overall aim of this thesis is to examine the feeding ecology of UK populations of Little Tern and understand the role of diet and food provisioning may play in their conservation. In doing so, it draws on my own fieldwork at tern colonies in North East England and on unpublished chick feeding data collected by the LIFE project. A key purpose of the study has been to analyse these data and draw inferences about the drivers of population dynamics in little tern populations, particularly those related to breeding productivity. It is hoped that the analysis will help to make the results of the LIFE project's work on chick feeding more widely available. Specifically, this thesis aims to:

- Elucidate the diet of Little Tern chicks in the UK

- Identify the main factors driving rates of chick provisioning and to understand how differences in chick provisioning rates may relate to Little Tern productivity
- Assess the potential application of camera traps and video capture in feeding studies of Little Tern chicks
- Better understand how adult Little Terns are using the North East coast for foraging

1.6.1 Structure of the thesis

Following this general introduction, the thesis is arranged in 4 chapters which are intended to address each of the main aims presented above. The thesis ends with a general discussion and recommendations for further study.

Chapter 2 looks at chick diet in the UK. I examined the existing literature (published and unpublished) and examine data on chick diet from the LIFE project to assess what additional contribution this makes to our knowledge, particularly about the range of prey types fed to chicks and how this varies across locations and between years. A version of this chapter has been published as **Nicholas Brodin, Mark J. Whittingham and Richard Francksen** (2024) Chick diet in UK Little Terns *Sternula albifrons*. *Bird Study*. Available at <https://doi.org/10.1080/00063657.2024.2326405>

In **Chapter 3**, I analyse the data on food delivery to chicks collected by the LIFE project. I examine what factors have the greatest influence on the observed patterns of chick provisioning and attempts to assess the links between chick provisioning and colony success. An additional analysis looking at variation in food provisioning between separate broods of chick using my own data collected at Long Nanny in 2018 and 2019 is presented as an appendix to the thesis.

Chapter 4 examines the use of camera traps to verify estimates of prey size made in the field. I also examine the potential for using camera traps and video capture as an alternative to field observation as a method of collecting data on the feeding of Little Tern chicks.

Chapter 5 looks at foraging by adult Little Tern at two colonies in North East England. I compare the range and core foraging areas of birds at Long Nanny and Seaton Carew and examine some of the factors which influence the distribution of foraging birds.

These chapters are intended to address the aims set out in Section 1.6. In addition it is hoped that they will help to identify any wider implications for the ongoing conservation management of Little Terns in the UK.

Chapter 2. Chick Diet in UK Little Tern

Note: a version of this chapter has appeared as **Nicholas Brodin, Mark J. Whittingham and Richard Francksen** (2024) Chick diet in UK Little Terns *Sternula albifrons*. *Bird Study*. Available at <https://doi.org/10.1080/00063657.2024.2326405>

2.1 Abstract

The EU LIFE-funded Little Tern Recovery Project ("The LIFE project) undertook feeding surveys of Little Tern *Sternula albifrons* chicks at 12 English and Welsh colonies during the period 2014 to 2018. In this Chapter I look at the dietary data from the project and compared it with the findings from previous studies (both published and unpublished). to assess what additional insight it on chick diet at UK locations.

Chick diets (data from The LIFE project) were dominated by lipid-rich marine fish, principally Sandeels and clupeids species (82% of all recorded prey items). Feeding of chicks with crustaceans or other invertebrates were recorded at 75% of colonies but no evidence was found that these routinely made up a substantial proportion of Little Tern chick diet. No significant inter-annual differences were found in diet composition at individual colonies. However, analysis of records of chick diet over a longer time series (Long Nanny colony in Northumberland, with data available for 17 of the years between 1998-2018) showed some significant differences in diet composition between years.

Although Little Terns are generalist feeders, 82% of the prey diet consisted of two prey types, Sandeels and clupeids (Clupeidae). This may leave existing UK Little Tern colonies vulnerable to any future climate change impacts affecting either the distribution or nutritional quality of the main prey species.

2.2 Introduction

The importance of feeding studies in animal ecology is widely recognised (Nielsen *et al.* 2018). Seabirds are particularly well represented in feeding studies due to their presence at the top of many marine food chains (Paiva *et al.* 2006a, Paiva *et al.* 2006b, Parsons *et al.* 2008), and because changing patterns of feeding may indicate changes in

the wider marine ecosystems such as declines in the abundance or size of certain fish species (Wanless *et al.* 2005).

The Alternative Prey Hypothesis (APH) states that generalist predators will utilise alternative prey as availability of their main prey declines (Angelstam *et al.* 1984, Mckinnon *et al.* 2014, Poysa *et al.* 2016, Reif *et al.* 2001). Diet flexibility in seabirds can reduce the impacts of a shortage of preferred food items if high abundances of poor-quality prey are available, meaning that species which can show flexibility in their choice of diet are considered to be less vulnerable to shortages in food supply than species which specialise on a narrow range of prey items (Gaglio *et al.* 2018a). However, a diet of low quality prey may not be adequate for successful breeding (Pierotti and Annett 1990) and some access to higher prey quality items may still be necessary to ensure chick growth (Paiva *et al.* 2006b). In contrast, the provision of high-quality prey to chicks can bring a range of benefits including reductions in chick stress and low parental foraging effort (Čech and Čech 2013, Čech and Čech 2017).

Little Tern *Sternula albifrons*, is a UK Amber listed species (Stanbury *et al.* 2021) and has seen particular conservation effort in recent years. The species has undergone an estimated population decline of 37% over the last three decades, a reduction that has been attributed to reduced productivity and reduced recruitment (Wilson *et al.* 2020). Food availability has been suggested as an important determining factor in the location and size of breeding colonies (Perrow *et al.* 2003). In the UK, Little Terns breed solely on the coast, forming colonies on sand or shingle and feeding by plunge diving for prey in shallow waters close to shore. The estimated UK breeding population is 1,927 Apparently Occupied Nests (JNCC 2021), with 86 separate colonies or sub-colonies (RSPB 2019a), although the precise number and size of breeding colonies varies from year to year (Natural England. 2012). Little Terns are relatively poorly studied compared to other tern species (Cabot and Nisbet 2013), owing to high nesting failure, shifting colony locations, precocial and semi-nidifugous chick behaviour, and strong legal protection all making studying this species challenging.

Little Tern diet was most recently reviewed by Eglington and Perrow (2014). Data on the diet of this species are available from across its geographic range including Russia

(Snow and Perrins 1998), Portugal (Catry *et al.* 2009, Correia *et al.* 2016, Paiva *et al.* 2006a, Ramos *et al.* 2013), Italy (Bogliani *et al.* 1992), Japan (Fujita *et al.* 2009), and Australia (Taylor and Roe 2004). Little Terns appear to be opportunistic feeders capable of selecting a wide variety of food items reflecting prey available in the local area (Bogliani *et al.* 1992, Catry *et al.* 2006, Paiva *et al.* 2006a). Studies from across the world have identified Little Tern prey items as diverse as marine and freshwater fish, crustaceans, annelid worms, marine molluscs, and insects including dragonflies, beetles and ants (Fasola *et al.* 2002, Eglington and Perrow 2014). Within the UK, Little Tern diet is described as consisting mostly of marine fish and invertebrates (Natural England 2012, Cabot and Nisbet 2013, Eglington and Perrow 2014). Since the review of Eglington and Perrow (2014), the EU LIFE funded Little Tern Recovery Project (2014-2018) has further investigated food provisioning in Little Tern chicks in the UK. The LIFE project focussed on 26 sites in England and Wales with the overall aim of long-term recovery of Little Terns in the UK (RSPB 2019b).

Here, I present data on Little Tern chick diet collected through the LIFE project between 2014 and 2018, and place this in a long-term context by (i) reviewing relevant literature and (ii) presenting 17-years of diet monitoring data from a colony in Northumberland. I examine spatial and temporal differences in diet composition and suggest how these data can aid ongoing recovery efforts for Little Terns in the UK.

2.3 Methodology

This review draws on three data sources which are addressed separately: i) chick feeding records obtained from a literature review of published and unpublished sources, ii) LIFE Project timed observations of chick feeding (from twelve colonies), iii) LIFE Project camera trap observations from Langstone Harbour.

2.3.1 Review of Existing Literature on Chick Diet

Previous reviews by Fasola *et al.* (2002) and Eglington and Perrow (2014) were used to identify pre-existing studies into Little Tern diet at UK locations, with additional information identified through searches of the Web of Science Database, Google Scholar, and by direct approaches to the managers of Little Tern sites. Search terms

used were “Little Tern”, “*Sternula albifrons*” and “diet”, “food”, “foraging” and “provisioning”.

Information on the numbers or relative proportions of prey were extracted from each of the sources, where available, and were assigned to one of the following categories:

- Sandeel *Ammodytes* spp.
- Clupeidae (Herring and Sprat)
- Goby *Gobius* spp.
- Flatfish (Pleuronectiformes)
- Stickleback (Gasterosteidae).
- Other Fish Species
- Invertebrates

Where prey could not be confidently assigned to a taxonomic category the records were classed as ‘unidentified’.

2.3.2 Collation of LIFE Project Data

Between 2014 and 2018 timed observations of Little Tern chick feeding took place across twelve English and Welsh colonies as part of the Little Tern Recovery LIFE Project (henceforth referred to as ‘the LIFE project’). Data were collected by staff and volunteers from each colony using timed observations of chick feeding. Colonies carried out feeding surveys independently of each other leading to variation in the recording effort between locations and between years (see Table 2.1 for details of colony locations and observation effort). It is estimated that 188 separate broods were subject to feeding observations during the duration of the Project. Timed observations of chick feeding is a method widely used with single prey-loading species such as terns and allows for the collection of large numbers of feeding records without any disturbance to the birds (Barrett *et al.*, 2007). A standardised methodology was circulated among monitoring staff at participating colonies (RSPB 2015b), whereby a nest or brood was selected and observed with telescope or binoculars for a recommended period of at least 60 minutes and prey items brought to chicks recorded. Individual prey items were usually recorded to the family level, which reduced the need for detailed taxonomic identification. The

LIFE projected produced a photo identification guide of common species to aid colony staff and volunteers when carrying out the feeding surveys.

Table 2.1. List of colonies which provided timed feeding observations to the LIFE project and the duration (in minutes) of chick feeding observations made in each year.

Location (County)	GPS Coordinate	2014	2015	2016	2017	2018
Benacre (Suffolk)	52°23'8.46"N, 1°43'4.63"E	0	324	0	0	0
Blakeney (Norfolk)	52°58'38"N, 000°57'47"E	1300	800	0	0	0
Chesil Beach (Dorset)	50°36'57"N, 002°32'11"W	0	0	0	180	0
Crimdon (County Durham)	54°43'00"N, 001°13'49"W	0	0	0	1680	0
Eccles Beach (Norfolk)	52°48'07"N, 001°35'05"E	0	0	515	0	0
Gronant (Flintshire, Wales)	53°21'34"N, 003°20'55"W	0	135	1057	271	114
Hodbarrow (Cumbria)	54°11'33"N, 003°16'09"W	0	0	0	0	484
Holkham (Norfolk)	52°58'27"N, 000°48'22"E	330	360	0	300	360
Kessingland (Suffolk)	52°25'41"N, 001°43'52"E	415	0	0	0	0
Lindisfarne (Northumberland)	55°38'45"N, 001°47'08"W	605	1680	660	0	965
Long Nanny (Northumberland)	55°32'24"N, 001°38'16"W	3780	5230	1807	3360	900
Scolt Head (Norfolk)	52°58'52"N, 000°44'43"E	1410	1680	1560	120	330

Feeding data were provided by the LIFE project as Excel spreadsheets or as PDF scans of reporting forms. Design and format of data capture varied between colonies and between years. These were collated into a single database and any queries about data provided were resolved directly with the LIFE Project staff.

Furthermore, chick diet data were collected from an additional colony at Langstone Harbour in Hampshire using camera traps placed at nests during in 2015 and 2016. These surveys were separate to the main feeding surveys undertaken by the LIFE project. The Little Tern colony at Langstone Harbour is located on small islands where the use of

timed feeding observation would be logistically difficult and lead to disturbance of nesting birds.

The camera traps used in surveys were a mixture of Bushnell and Acorn manufacture. They were deployed on the ground close to scrapes and set to record video when triggered by motion. Traps were used at four individual scrapes during 2015, with video footage captured between the 7th June and the 19th July. During 2016, camera traps were deployed at six separate scrapes, with video footage of chick feeding captured between the 4th and 9th of July. Time and date stamped data on individual feeding events, including identification of prey to family level where possible and estimations of prey size, were captured on by the RSPB site warden for Langstone Harbour and made available through the LIFE project.

2.3.3 Long Nanny Feeding Data

Feeding observations of Little Terns have been made by seasonal wardens at the Long Nanny colony in Northumberland (55°32'24"N, 001°38'16"W) since 1998. The methodology used to record feeding has changed throughout this period. In 1998 and 1999, feeding observations were made on a whole colony basis, while from 2000 onwards one or more individual broods were observed for a fixed period of time. Data on chick diet from 2014 to 2018 were collated as part of the analysis of LIFE project data (see Section 2.3.2). Data from before this date was extracted from physical copies of annual colony reports held at the National Trust offices at Low Newton in Northumberland. Items recorded in chick diet were classified using the categories described in section 2.3.1.

2.3.4 Statistical Analysis

Data from the LIFE project were collated for each year and for each of the twelve colonies at which timed observations had been made. Data from the thirteenth colony, Langstone Harbour, did not form part of the analysis as a different field methodology (camera trapping) was used in their collection. Since relative proportions of different prey types found within samples are not independent of each other, compositional analysis was used to examine patterns of chick diet (Aebischer *et al.* 1993). It is important to note that no measure of prey availability was available therefore the results

can be interpreted as dietary differences between or within colonies and years but any patterns could be a result of either prey selection or prey availability or a combination of both.

Prey items recorded in timed observations from the LIFE project were assigned to one of five separate categories: Sandeel, Clupeid, Other Fish, Invertebrates, and Unidentified (comprising unidentified or ambiguously named prey items on recording forms).

Unidentified prey were removed from further analysis and the remaining prey categories were expressed as proportions of total observed prey items, with summed values equal to one.

Log-ratios were calculated for three of the four prey categories. The fourth prey category ('Other Fish') was used as the denominator for the transformation. Any zeros in the dataset were replaced with 0.1 to allow calculation of log-ratios. The analysis does not depend on which group is used as the denominator group (Aebischer et al. 1993). This is because the method analyses relative proportions of components rather than their absolute values. Changes to the choice of denominator do not alter the relative differences or relationships between the proportional components, all of which will sum to a value of 1.

Log-ratio values for different prey groups were compared using MANOVA to examine the effect of colony location and year and any interaction between the two. The model was assessed using the Pillai-Bartlett statistic (Λ) with values of $p < 0.05$ considered as being significant. Data were tested for multivariate normality using Mardia's tests. Data were included in the model from all twelve of the colonies which provided timed observations of chick feeding to the LIFE project. No significant skew ($p = 0.14$) or kurtosis ($p = 0.51$) were found.

Differences between colonies in the proportions of Sandeel, clupeids, and invertebrates relative to other prey was analysed further using ANOVA. Model residuals for each prey category were examined using residual vs fitted value plots, residual histograms, Q-Q Plots and Shapiro-Wilks tests. Model residuals conformed with assumption of normality for Sandeel ($p = 0.39$), Clupeid ($p = 0.09$) and Invertebrates ($p = 0.25$).

Observations of feeding of Little Tern chicks at Long Nanny pre-date the LIFE project and have been made since 1998. Data from individual feeding surveys were available for thirteen of the breeding seasons between 1998 and 2018, while a summary of the overall composition of chick diet (expressed as a percentage of total observed chick diet) was available for an additional four breeding seasons. No quantitative data were available for the years 2000, 2004 and 2006.

Data on chick diet were extracted from annual colony reports and from LIFE project recording sheets and observed prey items from each timed count were assigned to the categories “Sandeel”, “Clupeid”, “Unidentified”, and “Other”. This final category comprised other fish and invertebrates, which were combined due to low numbers of records in most years.

Mardia’s tests suggested significant skewness ($p < 0.001$) in the data from the Long Nanny colony, which could not be addressed by transformation. As such, a Poisson Generalized Linear Model was used to determine if counts of Sandeel within observations varied between years using prey data collected from individual timed observations.

All statistical analyses were carried out using R (R Core Team 2021) .

2.4 Results

2.4.1 Literature Review

Thirty sources of information on Little Tern diet in the UK were identified for the period up to 2014, of which twenty-eight contained details of chick diet (Table 1.A1 in section 2.6 appendix). These include eighteen additional sources not referenced within the most recent literature review of tern foraging ecology by Eglington and Perrow (2014). All but one of these additional sources came from the grey literature of annual colony reports or student dissertations.

Marine fish dominated dietary records for both adults and chicks (Figure 2.1). Within chick diet, the prey items whose presence was most frequently noted in reports were Sandeel (100% of sources) and clupeids (93% of sources). A variety of other fish species were noted in the Literature most notably flatfish, mentioned in 50% of reports, and Goby, mentioned in 28% of reports. Invertebrate prey items were identified as a component of chick diet in 51% of the available studies with the majority of items described as shrimp or crustacea. A median of three different prey types were reported as being present in chick diet (range = 2-6).

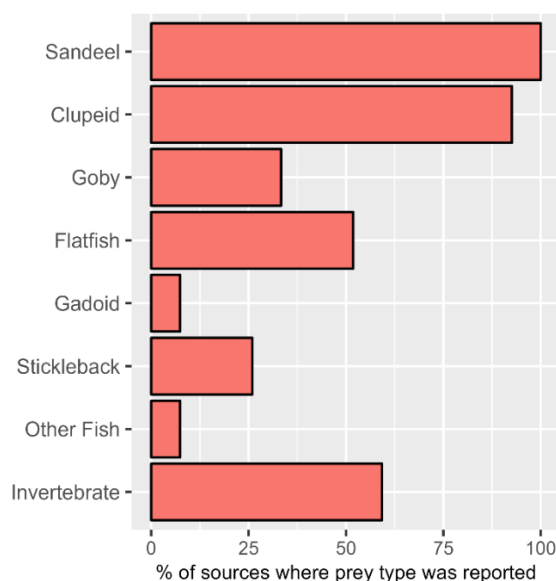


Figure 2.1. Summary of the frequency of prey types mentioned as forming part of chick diet in reports identified by literature review. A total of 28 reports were consulted. Not all reports contained full lists of prey. These dated from 2014 and earlier. See Table 2.A1 (section 2.6) for a list of the sources used.

Only 68% of the sources provided information about the relative abundance of individual prey items within chick diets. Full quantitative data on chick diet could only be confidently derived for three locations: Long Nanny, Easington Lagoons, and the Great Yarmouth and North Denes SPA. Partial quantitative information was given for a fourth site (Gibraltar Point) by Davies (1981) but a complete breakdown of the relative proportions of all observed prey items was not given.

Available numeric data on chick diet showed a dominance by Sandeels and clupeids, although their relative contribution to total diet varied with location. Invertebrate prey made up only a minor component of chick diet where full quantitative data were provided (typically less than 2%) despite being recorded as a component of chick diet in over half the available sources. It should be noted that Davies (1981) found that crustacea made up over 90% of chick diet at Gibraltar Point, but this study was excluded from analysis due to the absence of a full numeric breakdown of the relative proportions of the other prey species mentioned in the paper.

2.4.2 LIFE Project Feeding Observations

Timed observations made through the LIFE project produced a total of 2202 chick feeding records in the period 2014 to 2018 (Figure 2.2a, Table 2.2a). A median of three different prey types were identified at each colony (excluding unidentified items) across the total length of the LIFE Project (range = 2-6).

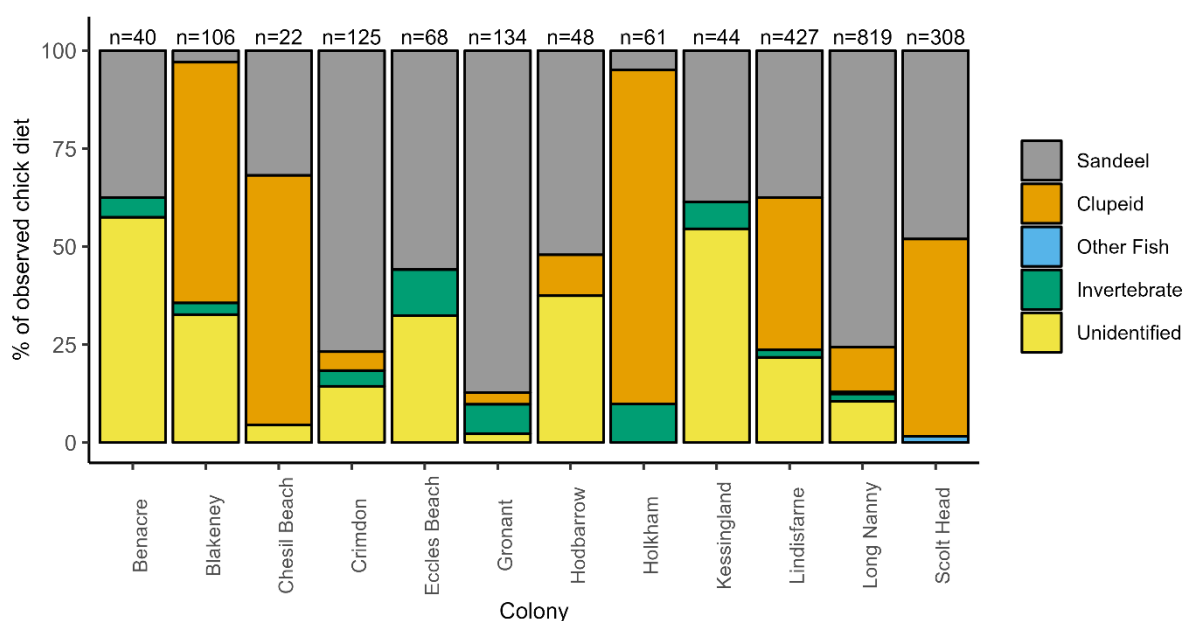


Figure 2.2a. Summary of numbers of individual prey items recorded through timed feeding observations at the twelve colonies from which timed feeding observations were made during the period of the LIFE project (2014-2018). Not all colonies were surveyed in each year. n=total number of prey items recorded at location.

In addition to dietary records obtained through timed observations an additional 442 records of chick feeding were captured through camera trap footage at Langstone Harbour during 2015 and 2016 (Figure 2.2b, Table 2.2b). Records from 2015 identified six prey item types, while records from 2016 identified three types of prey (excluding unidentified prey items in both year).

Table 2.2a Summary of chick diet records collected from timed observations by the LIFE project (2014-2018)

Prey Item	2014		2015		2016		2017		2018		TOTAL	
	N	%	N	%	n	%	N	%	N	%	n	%
Sandeel	368	63.3%	339	49.2%	206	51.0%	244	71.8%	93	49.5%	1250	56.8%
Clupeid	85	14.6%	252	36.6%	126	31.2%	59	17.4%	40	21.3%	562	25.5%
Other named fish species (Goby, Butterfish, Flatfish)	5	0.9%	2	0.3%	0	0.0%	1	0.3%	1	0.5%	9	0.4%
Unidentified fish species	8	1.4%	10	1.5%	23	5.7%	0	0.0%	19	10.1%	60	2.7%
Invertebrate	12	2.1%	29	4.2%	8	2.0%	9	2.6%	2	1.1%	60	2.7%
Item not identified	103	17.7%	57	8.3%	41	10.1%	27	7.9%	33	17.6%	261	11.9%
TOTAL	581	100	689	100	404	100	340	100	188	100	2202	100
Number of colonies from which data collected	6		7		5		6		6		12	

Table 2.2b Chick diet at Langstone Harbour obtained from Camera trap images by RSPB.

Prey Item	2015		2016		TOTAL	
	Number	%	Number	%	Number	%
Sandeel	25	8.6%	5	3.3%	30	6.8%
Clupeid	45	15.4%	37	24.7%	82	18.6%
Goby	69	23.6%	68	45.3%	137	31.0%
Other named fish species (Seabass and Flatfish)	12	4.1%	0	0.00%	12	2.7%
Invertebrate	2	0.7%	0	0.00%	2	0.4%
Item not identified	139	47.60%	40	26.7%	179	40.50%
TOTAL	292	100%	150	100%	442	100%

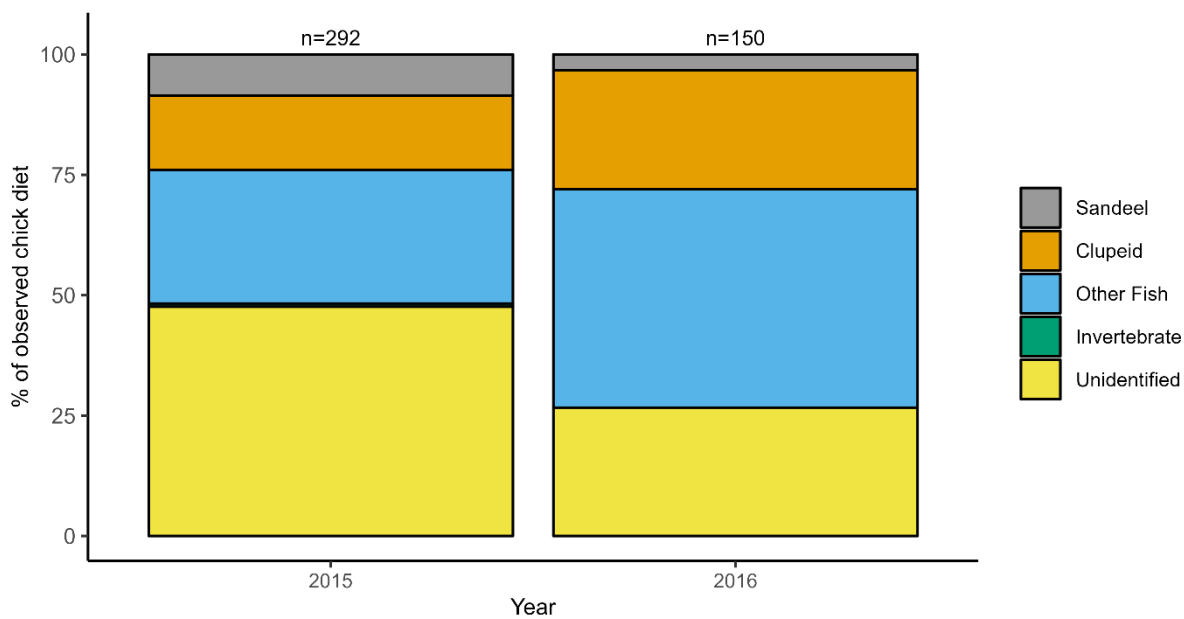


Figure 2.2b. Summary of prey delivered to chicks caught on camera trap footage at Langstone Harbour in 2015 and 2016. n=number of prey items recorded.

The prey types most frequently recorded during timed feeding observations were Sandeel (n = 1250) and clupeids (n = 562). Sandeels were recorded in chick diet from all twelve of the colonies at which feeding data were collected through timed observations (Figure 2.2a). Other named fish species made up less than 1% of the total prey records. The majority of these other fish species were Goby (n = 6) with a small number of flatfish (n = 2) and a single record of an unsuccessful attempt to feed Butterfish *Pholis gunnellus* to a chick.

The dominant prey species identified in camera trap data from Langstone Harbour was Goby (n = 137), with Sandeels (n = 30) and clupeids (n = 82) together making up 25% of prey items. Small numbers of flatfish (n = 8) and European Seabass *Dicentrarchus labrax* (n = 4) were also recorded.

Invertebrates were a minor component of chick diet in data from the LIFE Project and made up 3% of prey items recorded. Despite the overall low number of records (n = 60), invertebrate prey items were reported in nine out of the twelve colonies at which timed

feeding observations took place (Figure 2.3). The majority of these were identified as ‘shrimp’ on recording forms. In addition to the twelve colonies at which timed feeding observations were undertaken, the Langstone Harbour camera trap data contained only two records of invertebrate food items.

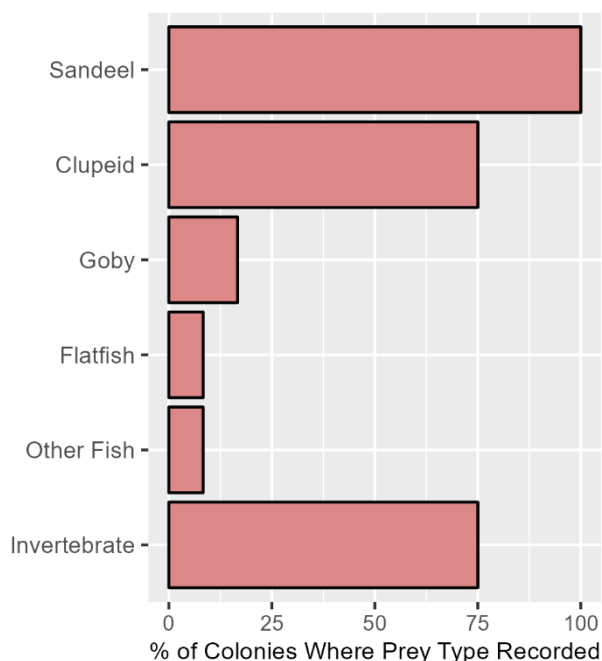
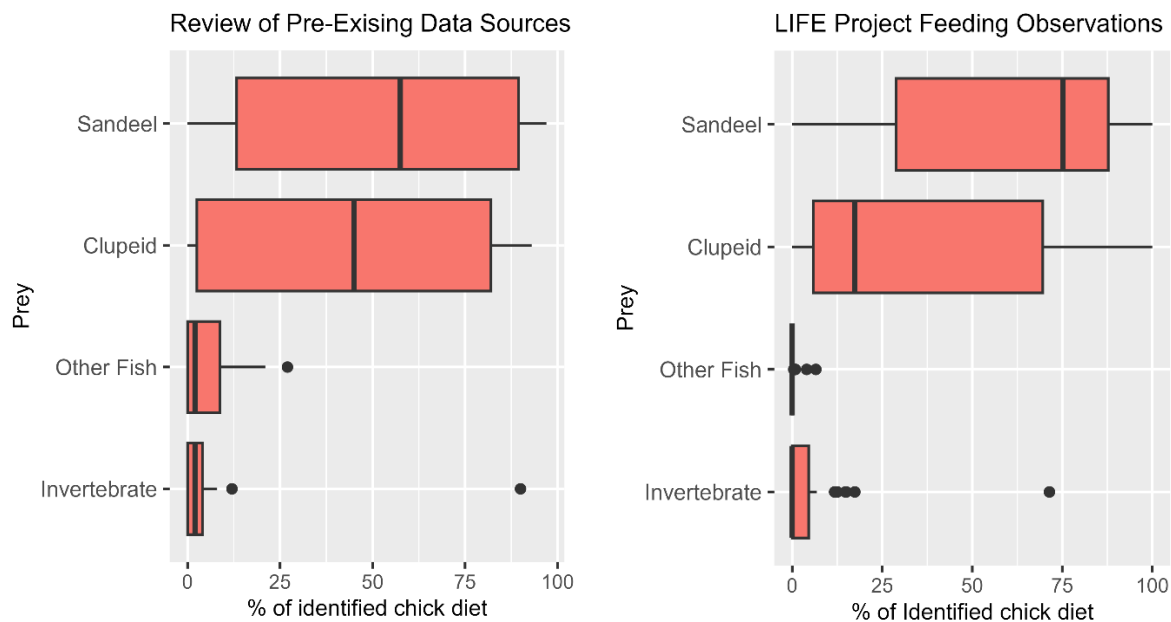


Figure 2.3. Frequency at which prey types were recorded at LIFE project colonies (n=12). Data are for timed observation only and does not include Langstone Harbour camera trap records.

Prey items were classified as being ‘unidentified’ in 12% of records from timed observations and 41% of the records from Langstone Harbour camera trap data.

2.4.3 Comparison of LIFE Project and Pre-existing Sources

The relative abundance of identified prey items recorded through the LIFE Project was broadly similar to that identified in those existing data sources in which numbers or percentage of prey were given (Figure 2.4). The exception to this was prey falling into the category of ‘Other Fish’ which were recorded almost four-times more frequently in the existing studies than in the LIFE Project observations, although it should be noted that 90% of the prey records for this category came from only three out of the fourteen pre-existing surveys used in the production of these figures.



Figures 2.4. The range of contributions which different prey types made to overall chick diet across all colonies and years for which numeric data were available. Calculations of proportions exclude unidentified prey items.

Butterfish ($n = 1$) and Seabass ($n = 4$) were both recorded in LIFE project data (at Long Nanny and in Langstone Harbour camera trap records respectively) and do not appear to have been recorded previously as part in the diet of Little Tern within the UK. However, both of these species were minor components of chick diet. No records of freshwater fish, such as Stickleback featured in the primary data collected as part of the LIFE project but feature in pre-2014 colony reports from Long Nanny and in reports from Easington Lagoon.

The LIFE project brought the number of UK Little Tern colonies for which multi-year numeric data on chick diet was available up to eight from a previous total of three. This included four sites for which no previous information on chick diet has been presented in the available literature.

2.4.4 Variation in diet composition between colonies and years

Chick provisioning data from timed feeding observations were available from multiple years for five locations: Blakeney, Holkham, Gronant, Lindisfarne, and Scolt Head. The composition of chick diet differed significantly between colonies ($\Lambda = 1.755, p = 0.037$) but there was no evidence within individual colonies of a statistically significant difference between years ($\Lambda = 0.499, p = 0.74$). ANOVAs showed that, relative to the 'Other Fish' category, there was a significant difference between colonies in the proportion of Sandeels observed within chick diet ($F_{11,14} = 3.32, p = 0.02$). No significant inter-colony differences were found in the proportion of clupeids ($F_{11,14} = 1.47, p = 0.25$) or Invertebrates ($F_{11,14} = 1.34, p = 0.3$) relative to prey in the 'Other Fish' category.

The proportion of Sandeel observed in chick diet varied between colonies at which timed feeding observations were made. In nine of the twelve colonies, Sandeel made up more than half of total observed chick diet. The mean percentage of Sandeel observed in chick diet from these twelve colonies across all years was 58.7% ($\pm 6.3\%$ se). Only at Blakeney, Chesil Beach, and Holkham was the proportion of Sandeel in observed chick diet less than 50%. Clupeids were the main component of chick diet at these three sites.

2.4.5 Feeding Records from Long Nanny

Data on the observed composition of chick diet were available for seventeen out of the twenty-one Little Tern breeding seasons from 1998 to 2018 (Figure 2.5).

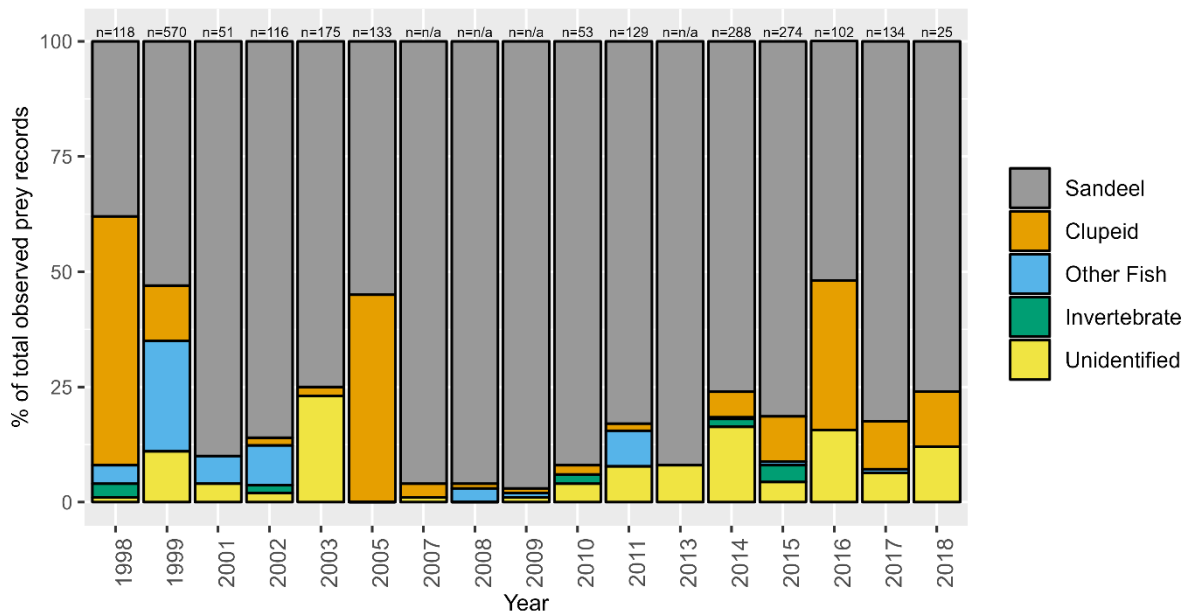


Figure 2.5. Chick diet composition at Long Nanny from 1998 to 2018 based on annual feeding surveys. n= total number of individual prey items recorded. No quantitative data were available in reports from 2000, 2004, 2006, and 2012.

Between two and six categories of identified prey were observed in each year (median = three). Sandeel were the dominant prey item observed in chick diet in all years, with the exception of 1998 (Figure 2.5). Clupeids were recorded in fifteen out of the seventeen years and were the dominant prey species recorded in 1998 (when they accounted for 54% of prey records). Records of Goby, flatfish and Stickleback made up a minor component of observed chick diet (mean = 3% of chick diet). The exception to this was 1999 where together they made up 24% of total observed prey.

Flatfish were identified as Dab *Limanda limanda* in 2008 and 2011 feeding surveys but no detailed taxonomic classification was given in other survey years. Invertebrate prey items (predominantly identified as shrimp) were recorded in five out of the 17 years and made up only a minor proportion of observed prey items (mean of 0.7%).

Data were available on the numbers of individual prey items recorded from 17 years of the period 1998-2018. Comparison of these feeding records showed a significant variation in diet composition between years ($\chi^2_{12} = 66.01, p < 0.001$).

2.5 Discussion

This study brings together the available data on chick diet from feeding surveys carried out by the EU-LIFE funded Little Tern Recovery Project, with data from other UK studies including a long-term monitoring project in Northumberland. While a number of pre-existing sources of information on chick diet were available from the UK these were from a small number of named locations, with limited quantitative multi-year data (Table 1.A1 in section 3.6).

The results gathered here confirm the picture of Little Tern as dietary generalists who make use of a wide range of different prey (across different colonies and years). However, the overall diversity of prey recorded in chick diet during any single breeding season was generally low, suggesting a reliance on a small number of prey species. Both Sandeel and clupeids are lipid-rich food items and considered to be of high nutritional value for chick development (Green 2017, Norman 1992, Wanless *et al.* 2005) and the frequent occurrence of these two prey perhaps suggests that foraging adults may have been preferentially selecting certain prey types with which to provision chicks. However, in the majority of locations, no measure of prey availability was available therefore the results can be interpreted as dietary differences between or within colonies years but any patterns could be a result of either prey selection or availability or a combination of both.

The composition of diet in Little Terns is generally taken to be a reflection of prey abundance within foraging distance of colonies, with both Catry *et al.* (2006) and Perrow *et al.* (2011) having found that the dominant species observed in chick diets reflect those found in fish surveys of adjacent waters. Some limited data on prey resources within foraging areas around LIFE project colonies were available from 2015 and 2016 fish surveys of Langstone Harbour (Maccallum 2015, 2016) and from 2016 of the areas adjacent to Long Nanny (Northumberland Inshore Fisheries and Conservation Authority 2017). Data were insufficient to make a statistical analysis of the relationship between chick diet and available prey but indicated that the dominant species in chick diet coincided with species which are abundant in areas around the colony. However, they also indicated that a range of other potential fish prey appeared to be available to

foraging birds which were not regularly recorded in chick diet. This could suggest that adult terns were not provisioning the full range of potentially available prey species to chicks and were selectively taking Sandeels and clupeids when foraging for food for their young. Further study would be needed to confirm this, although some evidence of prey selection by adult Little Terns has previously been found by Phalan (2000) at Kilcoole in Ireland, where Goby was strongly selected for by breeding adults foraging in brackish water but crustaceans appear to have been largely ignored.

The lack of evidence of inter-annual variation in the composition of chick diet from LIFE project colonies contrasts with the findings of Catry *et al.* (2006) in their paper on the diet of Little Terns in Portugal. This difference may reflect a greater stability in the availability of individual prey species in the foraging areas surrounding at UK colonies, although it is also possible that the small sample sizes from a number of colonies has led to lack of statistical power in the LIFE project data. This latter explanation is given some support from the evidence of interannual variation in the available chick feeding data from Long Nanny for the period between 1998 and 2018.

Starvation was recorded as a major cause of chick mortality at Long Nanny in 1999 (Harvey and Shields 1999), one of the years with a notably different chick diet composition (see Figure 8). During 1999 adult Little Tern appear to have compensated for food shortages by bring a wider variety of fish species to chicks, as might be expected under the Alternative Prey Hypothesis. The high mortality of chicks reported in this year suggests however that this strategy had limited success. There also appears to have been some starvation-related mortality of chicks at Long Nanny in 2004 (RSPB 2004) but unfortunately no detailed breakdown of chick feeding is available for that year so it is not possible to assess how any shortages were reflected in diet composition. Some uncertainty has been expressed in the literature on Little Terns about the relative importance of fish and crustacea in diet (Cabot and Nisbet 2013). In the UK context, the finding by Davies (1981) are often cited as an example of the importance of crustacean in chick diet. However, this current study suggests that while invertebrates are frequently reported as a component of chick diet at UK colonies there is little evidence to conclude that they form a major food source. It was noted by Catry *et al.* (2006) that previous studies in which crustacea were found to be an important component of chick

diet have been at locations where adults foraged over brackish waters. The majority of UK Little Tern colonies, and all of the colonies studied through the LIFE Project, are in locations where adult foraging is likely to have primarily taken place on the open coast. This might explain the lack of abundance of crustacea in chick feeding records and would suggest that Davies results are likely to be unrepresentative of the diet of Little Tern chicks within wider UK colonies, at least during those years where alternative prey is in abundance.

Similarly, freshwater fish can form an important part of chick diet in Little Tern colonies elsewhere in the world (Bogliani *et al.* 1992, 1994) where colonies are adjacent to freshwater lagoons or river systems but data presented here suggest their importance is limited in the UK. This presumably reflects the foraging habitat available around UK colonies and because of the presence of higher quality prey items in the form of marine fish.

2.5.1. Summary of findings and potential impacts of climate change for management

The results presented here confirm the generalist nature of Little Tern diet, with a wide variety of prey recorded, but indicate that chick diet is generally dominated by a small number of food types, principally Sandeel and clupeids. The predicted declines of Sandeel to rising sea temperatures is a matter of concern for UK seabird conservation, with changes in the abundance and nutritional quality likely to be affected by future climate change (Wright *et al.* 2018, Mitchell *et al.* 2020a). The dominance of Sandeel within chick diets found at many of the LIFE project colonies suggests that UK Little Tern colonies are potentially highly vulnerable to any such impacts. The two most likely responses of Little Tern to any reduction in quantity or quality of Sandeel would be a switch in diet to alternative prey, as predicted by the Alternative Prey Hypothesis, or a move in colony location to areas adjacent to better food resources (Perrow *et al.* 2003). The latter scenario would be particularly unpredictable and could see the abandonment of long-established breeding colonies. Any such changes in breeding location would likely require a flexible and rapid response from site wardens or others involved in the protection of nesting colonies especially if attempts are made to breed on busy public beaches outside of current conservation management or on otherwise sub-optimal

habitat. Action to pro-actively manage more areas of the coast to provide suitable locations for nesting shorebirds would be advantageous if there is increased movement of Little Tern colonies in future in response to changes in food availability, as well as being of benefit to a wider range of breeding coastal birds.

The majority of UK studies on Little Tern diet have used observational techniques to record sightings of feeding. This reflects the high levels of legal protection from disturbance given to Little Tern in UK legislation and the subsequent need for survey methods which are non-invasive and which minimise human presence within breeding colonies. However observation of chick feeding is labour intensive technique and carries a risk that prey items will be misidentified (Barrett *et al.* 2007). There is scope to use a range of other techniques, such as photography (Gaglio *et al.* 2018a, Gaglio *et al.* 2017), stable isotope analysis (Ismar *et al.* 2014b), DNA barcoding of faecal material (Jo *et al.* 2022) or examination of scales and otoliths in regurgitated food pellets (Correia *et al.* 2016), to bring new insights patterns of tern diet. Of these, use of photography or video to gather additional information on diet is likely to be the technique that could be incorporated into chick diet studies at UK Little Tern colonies with fewest logistical or resource issues. The camera trap data available from Langstone Harbour indicated that chick diet was dominated by Goby and clupeids in contrast to the dominance of Sandeel and/or clupeids seen at the LIFE project colonies where timed observations were used. Available information of the abundance of small fish at Langstone Harbour (Maccallum 2015, 2016) suggests that this difference was likely a true reflection of local prey availability but additional study at other sites to compare the results obtained from camera trapping and timed observation techniques would be welcome. The LIFE project was notable for producing feeding surveys from a wide geographic spread of English and Welsh Little Tern colonies. However, the recording effort put into gathering data on chick diet varied strongly between colonies with relatively low sample sizes being obtained at some locations. Continued and ongoing data collection on chick diet at colonies would therefore be desirable to help build on our current knowledge and to detect any changing patterns of prey availability.

There is limited monitoring of food resources in the foraging areas used by Little Terns in the UK and with the exception of some previous studies in Norfolk (Perrow *et al.* 2003,

Perrow *et al.* 2011) few attempts to link data on food resources with chick provisioning. This would be a valuable research area and would help address some of uncertainties identified in the paper about the degree to which prey selection influences the composition of chick diet. Such research could also provide an early warning of future problems especially if combined with ongoing surveys of chick diet and monitoring of colony productivity.

2.6 Appendix

Table 2.A1. Results of Literature Review into Little Tern Diet for the period up to 2014 (the commencement of the EU LIFE-funded Little Tern Recovery project). Asterisk against source indicates that it was included by Eglington and Perrow (2014) in their review of tern foraging.

Location	Source	Reference Type	Method of data collection	Adult or chick diet?	Year(s) of data collection	Sandeel (Ammodytes spp.)	Clupeidae	Goby (Gobius spp.)	Flatfish (Pleuronectiformes)	Stickleback (Gasterosteidae)	Other Fish	Invertebrate
Long Nanny, Northumberland	Anthony and Veal (1998)	Colony Report	Observation	Chick	1998	●	●		●			●
				Adult		●	●		●			●
Long Nanny, Northumberland	Harvey and Shields (1999)	Colony Report	Observation	Chick	1999	●	●	●	●	●		●
Long Nanny, Northumberland	Lewis and Butler (2000)	Colony Report	Observation	Chick	2000	●	●	●				
Long Nanny, Northumberland	Bradbury and Cox (2001)	Colony Report	Observation	Chick	2001	●		●				
Long Nanny, Northumberland	Cottam and Wakefield (2002)	Colony Report	Observation	Chick	2002	●	●	●	●			●
Long Nanny, Northumberland	Dalrymple and Riddell (2003)	Colony Report	Observation	Chick	2003	●	●		●			

Location	Source	Reference Type	Method of data collection	Adult or chick diet?	Year(s) of data collection	Sandeel (<i>Ammodytes</i> spp.)	Clupeidae	Goby (<i>Gobius</i> spp.)	Flatfish (<i>Pleuronectiformes</i>)	Stickleback (<i>Gasterodeidae</i>)	Other Fish	Invertebrate
Long Nanny, Northumberland	Lane and Taylor (2004)	Colony Report	Observation	Chick	2004	●	●			●	●	●
Long Nanny, Northumberland	Veal <i>et al.</i> (2005)	Colony Report	Observation	Chick	2005	●	●		●			
				Adult		●	●			●	●	●
Long Nanny, Northumberland	The National Trust (2006)	Colony Report	Observation	Chick	2006	●	●	●	●		●	●
Long Nanny, Northumberland	Rogerson and Townsend (2007)	Colony Report	Observation	Chick	2007	●	●					
Long Nanny, Northumberland	Mackey and Owen (2008)	Colony Report	Observation	Chick	2008	●	●		●			

Location	Source	Reference Type	Method of data collection	Adult or chick diet?	Year(s) of data collection	Sandeel (<i>Ammodytes</i> spp.)	Clupeidae	Goby (<i>Gobius</i> spp.)	Flatfish (<i>Pleuronectiformes</i>)	Stickleback (<i>Gasterosteidae</i>)	Other Fish	Invertebrate
Long Nanny, Northumberland	Bruce-White <i>et al.</i> (2009)	Colony Report	Observation	Chick	2009	●	●	●				
Long Nanny, Northumberland	Brockless <i>et al.</i> (2010)*	Colony Report	Observation	Chick	2010	●	●					●
Long Nanny, Northumberland	Bannister <i>et al.</i> (2011)	Colony Report	Observation	Chick	2011	●	●	●	●	●		●
Long Nanny, Northumberland	Cartwright <i>et al.</i> (2012)	Colony Report	Observation	Chick	2012	●	●					
Long Nanny, Northumberland	Gallagher <i>et al.</i> (2013)*	Colony Report	Observation	Chick	2013	●	●					●
North Denes and Yarmouth SPA, Norfolk	Perrow <i>et al.</i> (2003)*	Conference Paper	Observation	Chick	2002-2003	●	●					●
North Denes and Yarmouth SPA, Norfolk	Perrow <i>et al.</i> (2011)*	Paper	Observation	Chick	2002-2006	●	●					●
North Denes and Yarmouth SPA, Norfolk	Perrow and Eglington (2014)	Paper	Observation	Chick	2002-2006	●	●					●

Location	Source	Reference Type	Method of data collection	Adult or chick diet?	Year(s) of data collection	Sandeel (<i>Ammodytes</i> spp.)	Clupeidae	Goby (<i>Gobius</i> spp.)	Flatfish (Pleuronectiformes)	Stickleback (Gasterosteidae)	Other Fish	Invertebrate
North Denes and Yarmouth SPA, Norfolk	Perrow <i>et al.</i> (2008)* <i>op. cit.</i> Eglington and Perrow (2014)	Unpublished Monitoring Report	Not Known	Chick	2002-2006	●	●					●
Easington, Lincolnshire	Davies (2011)	Dissertation	Observation	Chick	2011	●	●	●	●	●		●
Easington, Lincolnshire	Mercer (2013)	Dissertation	Observation	Chick	2013	●	●		●	●		●
Easington, Lincolnshire	Parry (2012)	Dissertation	Observation	Chick	2012	●	●		●	●		
Easington, Lincolnshire	Colver (2014)	Dissertation	Observation	Chick	2014	●	●	●	●	●		●
Gibraltar Point, Lincolnshire	Davies (1981)*	Paper	Observation	Chick	1980	●						●
Scotland	BirdLife International (2000) <i>op. cit.</i> Eglington and Perrow (2014)*	Report	Observation	Chick	Unknown	●	●					●

Location	Source	Reference Type	Method of data collection	Adult or chick diet?	Year(s) of data collection	Sandeel (<i>Ammodytes</i> spp.)	Clupeidae	Goby (<i>Gobius</i> spp.)	Flatfish (Pleuronectiformes)	Stickleback (Gasterodeidae)	Other Fish	Invertebrate
St Cyrus, Scotland	N K Atkinson <i>op cit</i> Fasola <i>et al.</i> (2002)*	Paper	Unknown	Chick	Unknown	●	●					
Ythan Estuary, Scotland	Taylor (1975)*	Thesis	Observation	Adult	1972-1973							●
Unknown	Witherby (1941)*	Book	Stomach content analysis	Adult	Unknow (pre-1941)	●						●
Gronant, North Wales	Norman (1992)	Paper	Observation (incidental records)	Chick	1989 and 1991	●	●		●			

Chapter 3. Chick Provisioning in UK Little Tern

3.1 Abstract

For many seabird species a link has been established between availability of food during the breeding period and eventual breeding success and productivity. Here I use data on chick feeding collected by the EU LIFE-funded Little Tern Recovery Project from 12 English and Welsh Little Tern colonies during the period 2014-2018 to examine the factors driving observed patterns of chick provisioning and attempt to establish the relationship between chick feeding and colony productivity. I looked at three separate measures of chick provisioning: food delivery rates (feeds/chick/hour), estimated energy delivery rates (kJ/chick/hour), and prey size. All measures of provisioning were strongly linked to chick age with older chicks being fed at higher rates and with larger prey than younger chicks. Some evidence was found of differences in chick provisioning between locations and years although analysis was frequently lacking statistical power due to low sample sizes from some colonies and years. No significant evidence was found of a relationship between food delivery rates and eventual colony productivity but the relationship was positive from the eight years in which data were available. This low sample size to test the effects of provisioning on colony productivity was a consequence of the major role of predation, tidal flooding and/or bad weather in causing substantial chick losses within a colony in 21 out of 30 years (70%). While no significant evidence was found to suggest poor chick feeding was a regular or frequent cause of poor productivity, the LIFE project data were insufficient to draw any clear conclusions about whether higher levels of chick provisioning are linked to higher productivity in the absence of other sources of mortality.

3.2 Introduction

3.2.1 Food provisioning and Seabird Breeding Success

Variation in food supply has a strong influence on productivity and breeding success in seabirds (Cury *et al.* 2011, Durant *et al.* 2003, Paiva *et al.* 2006a, Petersen *et al.* 2020). Optimum foraging theory suggests that, during the breeding season, adult birds would

optimally allocate food resources to sustaining both themselves and their chicks, which will influence foraging choices and prey selection and all other things being equal prey will be selected closer to the nest when feeding chicks (Bugge *et al.* 2010). A link between poor breeding success and poor feeding has been identified in several species of seabird, including various species of tern (e.g. Monaghan *et al.* 1989; Uttley *et al.* 1989). Terns are reported to spend a relatively greater proportion of their time foraging than do larger seabird species (Pearson 1968). As a result their reproductive success is more likely to be more sensitive to low food availability than for larger species of seabird (Monaghan 1996). Prior to fledging, tern chicks are wholly reliant on their parents for food (Cabot and Nisbet 2013) and their survival is therefore linked to the ability of their parents to provide them with food. Low availability of prey at the chick rearing stage, whether due to lack of prey in foraging habitats or to a practical inability to access prey, for example due to adverse weather conditions, may result in starvation or inadequate growth rates in chicks. Lack of prey can affect the performance of tern colonies in a variety of other ways. At its most extreme, food shortage can lead to reduced reproductive output and desertion of nests by adults (Monaghan 1992) or to catastrophic colony failures, such as those recorded for Arctic Terns *Sterna paradisaea* in the Shetland Islands during the 1980s (Uttley *et al.* 1989). More subtle impacts of food shortage can include reductions in the breeding condition of adult birds leading to deferred breeding (Fayet *et al.* 2021), delayed egg laying and reductions in clutch size (Regehr and Montevecchi 1997), and increases in chick mortality from predation and exposure resulting from the increased lengths of times that adults had to spend away from the nest foraging (RSPB 2015b). For migratory species, fledged birds may not survive migration if their nutrition is poor (Afán *et al.* 2019). However, it has been suggested that for many species of seabirds, demographic parameters such as breeding performance can be relatively insensitive to changes in food availability due to their long life-span and ability to switch between different types of prey (Votier *et al.* 2004, Church *et al.* 2019).

As chicks grow their energy demands increase (Klaassen *et al.* 1992). Their parents can meet these through increasing the rate at which food is brought to chicks or by increasing the energetic value of the food which is delivered, for example by bringing larger items or selecting prey species which are more energy-rich (Robertson *et al.*

2016). The greater the number of chicks within a brood, the greater will be the energy requirements of that brood, resulting in broods of larger size having a greater food requirement than broods of smaller size. In some species such as Common Terns *Sterna hirundo* and Arctic Terns *Sterna paradisaea* this has been observed to result in lower energy supply per chick and lower growth rates compared to chicks from smaller broods (Robinson and Hamer 2000).

3.2.2 Factors Influencing Seabird Foraging and Food Provisioning

A link between poor foraging conditions and poor food provisioning of chicks has been reported for a range of coastal bird species (Frank 1992, Furness 2007, Wanless *et al.* 2005). Diurnal foraging conditions for seabirds, and their success in finding and capturing prey are influenced by a range of environmental factors (Eglington and Perrow 2014) and patterns in foraging have been observed in many seabirds, including Arctic and Common terns (Morris 2013), Sandwich Tern *Sterna sandvicensis* (Stienen *et al.* 2000) and Roseate Tern *Sterna dougallii* (Ramos *et al.* 1998). Weather conditions can also play a major role in the ability of seabirds to forage for food, both by affecting the ability of birds to access food resources and by increasing the amount of time required to brood eggs or chicks to protect them against adverse conditions (Anderson *et al.* 2005, Dunn 1975). Adverse weather conditions can also make it more difficult for chicks to maintain a steady body temperature which when combined with lower feeding rates may result in lower growth rates and additional chick mortality (Dunn 1975, Klaassen *et al.* 1989, Ritz *et al.* 2005). Sea Surface Temperature (SST) and large-scale climatic phenomena such as the North Atlantic Oscillation (NAO) have been shown to influence both prey availability and quality (Marine Climate Change Impacts Partnership 2018, Mitchell *et al.* 2020b, Wanless *et al.* 2004), with an associated impact on reproductive success (Frederiksen *et al.* 2004).

3.2.3 Food Provisioning in Little Tern

Little Tern chicks develop rapidly and reach close to their full weight by around 10 days of age (Norman 1992). The main factors influencing growth rate in Little Tern chicks is thought to be the type and size of available food and the rate at which it is delivered (Norman 1992, Paiva *et al.* 2006a, Paiva *et al.* 2006b).

Productivity in Little Terns varies between colonies and between years (Brown and Grice 2005) but there has been relatively little investigation into the relationship between this and chick provisioning. A range of food delivery rates to Little Tern chicks have been reported in the available literature (Fasola *et al.* 2002) although it is often difficult to make direct comparisons between studies due to differences in reporting and because of lack of important contextual information, particularly on chick age. Differences in rates of food delivery have been observed between older and younger chicks, with older chicks being fed more frequently (Fasola *et al.*, 2002, Davies 2011). In contrast Paiva *et al.* (2006a) found that the rate at which chicks ingested food did not vary with age but that older chicks were fed larger items than younger chicks. Differences in prey size with chick age were also noted by Bogliani *et al.* (1994), with younger chicks receiving smaller food items and fewer crustacea than were observed with older chicks. However, Fasola *et al.* (2002) have noted that any differences in diet may be as a result of younger chicks rejecting food items which they find difficult to swallow.

Paiva *et al.* (2006a) reported that in broods of two or more, chicks may grow at different rates depending on their hatching order, with the first to hatch developing more rapidly than second and third to hatch). However, all chicks eventually reach similar weight and wing length. Davies (1981) noted that, at times of food scarcity, the oldest chick in a brood is fed at the expense of the younger ones, sometimes leading to starvation or retarded growth in the younger chicks.

Changing patterns in chick provisioning throughout the day have been noted in some studies with feeding being most frequently in the morning and evening (Bogliani *et al.* 1992, Davies 1981, Norman 1992) while other authors have found no evidence of a diurnal pattern of chick feeding (Davies, 2011, Howe, 1982 *op. cit.* Eglington and Perrow 2014). Variation in patterns of chick feeding with tide have also been reported (Davies 1981, Taylor and Roe 2004) although, as with diurnal differences, other studies have detected no influence (Davies, 2011).

3.2.4 Aim of this study

There have been fewer studies into chick provisioning in Little Tern than for related species such as Arctic Tern and Common Tern, probably as a result of the many practical difficulties involved in undertaking research on Little Tern in the field (Cabot and Nisbet 2013). The existing literature on Little Tern suggest that chick age, brood size, time of day, tide, weather, and foraging conditions may all influence rates of chick provisioning, but the available evidence is often contradictory with some studies detecting an effect while others fail to detect a significant impact.

I used data on chick provisioning from the EU LIFE-funded Little Tern Recovery Project (“The LIFE project”) to investigate differing patterns of food provisioning to chicks between colonies and across years and to identify any links between chick provisioning and colony success. My research questions were:

- *What factors have the greatest influence on the observed patterns of chick provisioning?*

I predicted that chick age, brood size, location, year, time of day and tidal stage would all influence the provisioning of chicks.

- *What is the relationship between the energetic content of food items and the rate at which food items are delivered to chicks?*

I predicted that food delivery rates to chicks would be higher where prey was of lower energetic or nutritional content.

- *What is the relationship between measures of chick provisioning rates and colony productivity?*

I predicted that chick provisioning would be positively correlated with fledging success in chicks.

3.3 Methods

3.3.1 Data collection

Data on chick provisioning were obtained through timed feeding observations of chicks. The majority of data used in this Chapter were collected through EU LIFE-funded Little Tern Recovery Project (henceforth “the LIFE project”). Details of the project, and of the methodology used to make timed feeding observations, are given in Chapter 1, section 1.4.3.

These data provided three separate measures of chick provisioning:

- **Food Delivery Rates:** the number of individual prey items presented to an individual chick within a sixty-minute period (whether accepted or rejected by the chicks).
- **Estimated Energy Delivery Rates:** energy values for individual prey items were combined where possible to derive an estimated energy delivery rate per chick (kJ per chick per hour). The energy value of individual prey items (in kJ) was estimated from their length using the equation published by Wanless *et al.* (2005) for Sandeel *Ammodytes* spp. and for fish from the Family Clupidae (hereafter called “clupeids”) :

$$\text{kJ Sandeel} = 0.0081 \times \text{Length (cm)}^{3.427}$$

$$\text{kJ Clupeid (Sprat)} = 0.0096 \times \text{Length (cm)}^{3.845}$$

Estimated energy delivery rates were not calculated from timed feeding observations that included unidentified prey items or prey other than Sandeel or clupeids. As a result, the number of timed feeding observations from which estimated energy delivery rates were calculated (n=254) is smaller than the number of observations from which food delivery rates could be calculated (n=429).

- **Prey size:** As part of the timed observations of chick feeding, the size of prey items was estimated in relation to the length of the bill of an adult Little Tern. The length of an adult bill was taken as 3.05cm (RSPB 2015b)

3.3.2 Modelling Provisioning of Chicks

Generalized Linear Mixed Models (GLMMs) were used to investigate the factors influencing observed patterns of chick provisioning. Data came from timed observations of chick feeding carried out as part of the EU LIFE project (see Chapter 1, section 1.3.3). The models were run using the “lme4” package in R (Bates *et al.* 2015) with explanatory variables tested for significance using the Wald test in the “car” package (Fox *et al.* 2019).

3.3.2.1 Food delivery to chicks

A GLMM with a Poisson offset was used investigate the factors influencing the observed counts of the numbers of prey items presented to chicks. The predictors included within the model were brood size, chick age, time of day, tidal stage, location and year (see Table 3.A1 in Appendix for description of how each predictor was included in the model). Brood identity was used as a random factor to account for individual variation, with a unique code given to each brood. Broods which were recorded without an identifier were assigned to a single code for the purposes of the model. Observation length was used as an offset in the model. Available data on wind speed and sea state were not included in the model due to the high number of missing values.

LIFE project data were of an unbalanced design with unequal recording effect between individual colonies and different age of chicks. In particular, five colonies only provided chick feeding observations for a single year. However, running the model on data which omitted those colonies for which only a single year of observations were available did not affect the main conclusions, with the exception of ‘Year’ which showed a non-significant result with the reduced dataset. For this reason, additional analysis of inter-annual differences in food delivery rates was focused solely on chick feeding observations from the Long Nanny colony in Northumberland, as this location consistently provided large numbers of feeding observations to the LIFE Project across all years.

3.3.2.2 Estimated Energy Delivery Rate to Chicks

The factors influencing the estimated energy delivery rate observed during chick provisioning was investigated using a GLMM with a Gaussian error structure. The method for calculating estimated energy delivery rates is described in section 3.3.1 and was based on the estimated length of Sandeel and clupeid prey items. The same fixed effects, random effects and offsets were used as in the previous GLMM (Table 3.A1, in Appendix). Available data on wind speed and sea state was again omitted from the model due to the high number of missing values with the LIFE project data.

The model was run using both the full available data set and with reduced data which removed outlier values. The conclusions drawn from both approaches were identical. The results section shows the analysis based on the full data set.

3.3.2.3 Additional Statistical Analysis

Predictors with significant p -values were analysed further using Welch's ANOVA and Welch's t-test as the data were found to be heteroscedastic. These tests make no assumption about homoscedasticity of data and are considered robust to deviations from normality (Mcdonald 2014).

Post-hoc tests on any significant results from Welch's ANOVA were carried out using the Games-Howell Simultaneous Test due to homogeneity of variances and unequal sample sizes. A post-hoc analysis of statistical power was carried out on data for food deliver rates to individual chicks within different sizes of brood using GPower 3.1.9.7 (Faul *et al.*, 2007).

The relationship between Food Delivery Rate and Estimated Energy Delivery Rate was investigated using a Spearman's Rank Correlation test.

3.3.2.4 Sea Surface Temperature (SST)

An investigation into the impacts of climatic variables such as Sea Surface Temperature (SST) was largely outside the scope of this study but because of their importance to seabird feeding and reproduction a limited analysis was carried out using monthly Sea

Surface Temperature Anomaly data for the Northern Hemisphere (HadSST.4.0.1.0 data set) from the UK Met Office (Rayner *et al.* 2003).

To investigate the potential impact of Sea Surface Temperature on food delivery rates (feeds/chick/hour), monthly Sea Surface Temperature Anomaly and the square of monthly Sea Surface Temperature Anomaly were included as a fixed effect in the GLMM described in Section 3.3.2.1. The square of SST was included to take account of possible non-linearity of the SST data. The results of this amended model were compared with those of the original model (3.3.2.1) using the ANOVA function in R to assess whether the more complex model (incorporating SST) was significantly better at capturing the data than the simpler model.

A Spearman's Rank Correlation Test was carried out on to investigate any relationship Sea Surface Temperature the estimate size of Sandeel prey delivered to chicks. For this analysis an average of the winter SST Anomaly was derived using data from the months October to March for the months prior to the breeding season. Data from this period were used because Sandeel spawns in mid-winter with the larvae hatching near to the onset of the spring (Régnier *et al.* 2019).

3.3.3 Relationship between chick provisioning and colony success

A Spearman's Rank Correlation Test was used to investigate the relationship between mean food delivery rates to chicks and reported colony productivity. Figures for productivity were obtained from the LIFE Project from the RSPB's Annual Little Terns Newsletter (RSPB 2015a, 2014, 2016, 2017, 2018). Details of productivity were only available at the colony level and not for individual broods as the high mobility of Little Tern chicks makes it difficult to assign them to individual nests.

3.4 Results

The observed food delivery rates (feeds/chick/hour) in LIFE project observations ranged from zero to 16 items an hour with a median of 2 (n=429).

Estimated energy delivery rates in LIFE project observations ranged from zero to 124 kJ/chick/hour with a median of 1.66kJ/chick/hour (n=254).

Prey items recorded by the LIFE project were predominately either Clupeidae or Sandeel (see Chapter 2). Size estimates were made for Sandeel and clupeid prey items ($n=1250$ and $n=562$ respectively). Estimated Sandeel size ranged from 0.3 to 4 adult bill lengths in size, with a median of 1.2 bill lengths (0.9 to 12.2 cm with a median of 3.7cm). Estimated clupeid size ranged from 0.2 to 3 adult bill lengths, with a median of 1 bill length (0.6 to 9.1cm with a median of 3cm).

A further breakdown of the various measures of chick provisioning is shown in the Appendix (section 3.6).

3.4.1 Food Delivery Rates

Counts of the number of chick feeds varied significantly with chick age ($\chi^2_2 = 52.85, p < 0.001$), colony location ($\chi^2_{10} = 67.23, p < 0.001$), year ($\chi^2_4 = 10.88, p = 0.03$), and brood size ($\chi^2_1 = 28.84, p < 0.001$). The observed number of chick feeds was not found to vary significantly with time of day ($\chi^2_5 = 5.18, p = 0.39$) or tidal stage ($\chi^2_3 = 5.06, p = 0.17$). Food delivery rates recorded through the LIFE project ranged from a mean of 1.91 ± 0.08 feeds/chick/hour for chicks aged less than seven days to a mean of 3.19 ± 0.15 feeds/chick/hour for chicks aged over seven days.

3.4.1.1 The influence of chick age

Increased food delivery rates (feeds/chick/hour) were associated with increasing chick age (Figure 3.1). Welch's ANOVA confirmed that these observed differences were statistically significant ($F_2=30.55, p < 0.001$). A Games-Howell Pairwise post-hoc test showed significant pairwise differences in mean food delivery rate between chicks aged less than seven days and chicks aged seven to 14 days, and with chicks older than 14 days of age ($p < 0.001$ in both instances). No significant difference in mean food delivery rate was detected between chicks aged seven to 14 days and chicks older than 14 days of age ($p = 0.12$) and in subsequent analysis data for the two age bands have been combined.

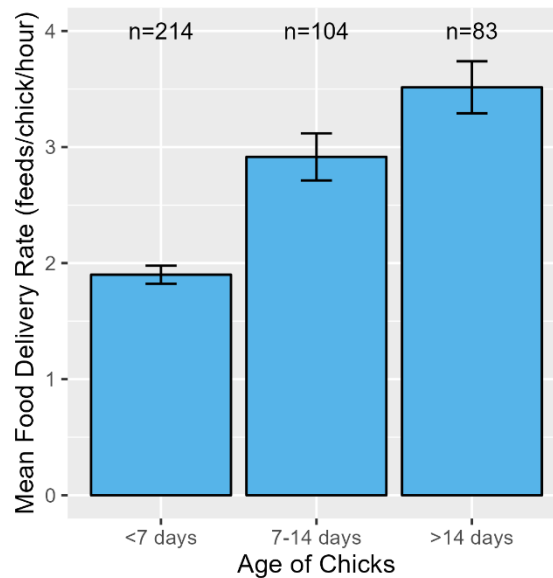


Figure 3.1. Variation in observed food delivery rates (feeds per chick per hour) with chick age (controlling for differences in brood size). N = number of timed observations. Bars indicate standard error of means. Only food delivery rates which come from observation of chicks of known age are included within the graph.

3.4.1.2 The influence of brood size

The number of food items observed being delivered to individual broods increased with the number of chicks within the brood. This was observed across all ages of chick (Figure 3.2).

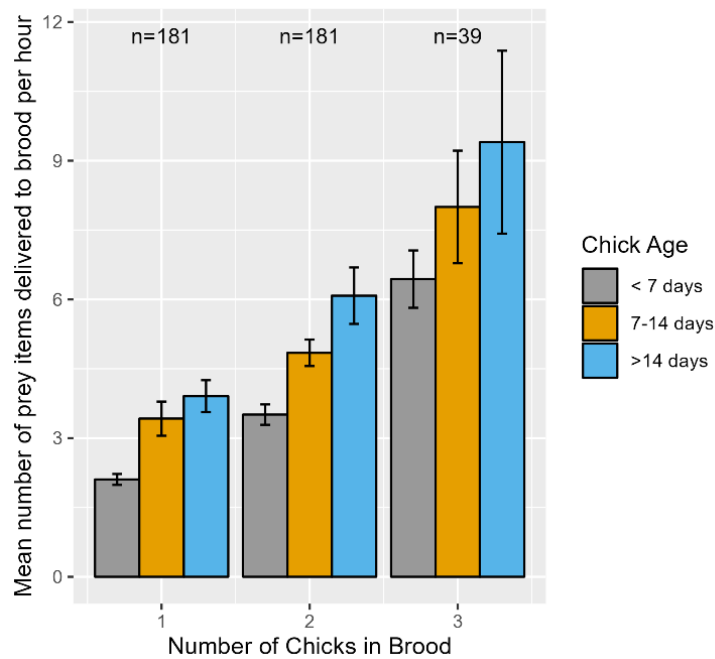


Figure 3.2. Variation in observed brood delivery rates (feeds/brood/hour) with brood size. Please note n refers to the overall number of feeding observation for broods of 1, 2, or 3 chicks and is not subdivided by chick age. Bars indicate standard error of means.

Further analysis using Welch's ANOVA found no evidence that brood size significantly affected the rate of food delivery to individual chicks once differences in chick age had been taken into account (Chicks aged less than seven days: $F_2=1.76$, $n = 214$, $p = 0.18$; Chicks aged over seven days: $F_2= 2.9$, $n = 187$, $p = 0.06$). Power analysis indicated that the effect sizes (f) of data from chicks aged less than seven days and for data from chicks aged over seven days were 0.07 and 0.175 respectively. For these values of f and $\alpha = 0.05$ the sample sizes required for a statistical power of 0.80 would have been approximately 2016 for chicks aged less than seven days and 318 for chicks aged over seven days. It therefore appears that the sample sizes obtained in this study had a very low probability of detecting a significant variation in food delivery rates (based on the observed mean differences) to individual chicks with increasing brood size. There is much variation in these rates (both intra and inter-specific) and so large sample sizes are needed.

3.4.1.3 Variation between years and between colonies

The use of a GLMM indicated that counts of food items varied between years and between colonies. However, due to the lack of a balanced design in data collection by the LIFE project, additional analysis of interannual differences in food delivery rates was focused solely on chick feeding observations from the Long Nanny colony in Northumberland, as this location consistently provided large numbers of feeding observations to the LIFE project across all years.

Figure 3.3 shows food delivery rates (feeds/chick/hour) at Long Nanny in the years between 2014 and 2018. Chicks aged less than seven days showed a significant difference in food delivery rates between years (Welch's ANOVA: $F_4 = 3.96$, $p = 0.007$). No inter-annual difference was found for chicks in chicks of age greater than seven days (Welch's ANOVA: $F_3 = 0.93$, $p = 0.44$). A post hoc Games-Howell test for chicks aged less than seven days showed that there was a significant difference in food delivery rates between 2014 and 2016 ($p = 0.025$) and between 2014 and 2018 ($p = 0.021$).

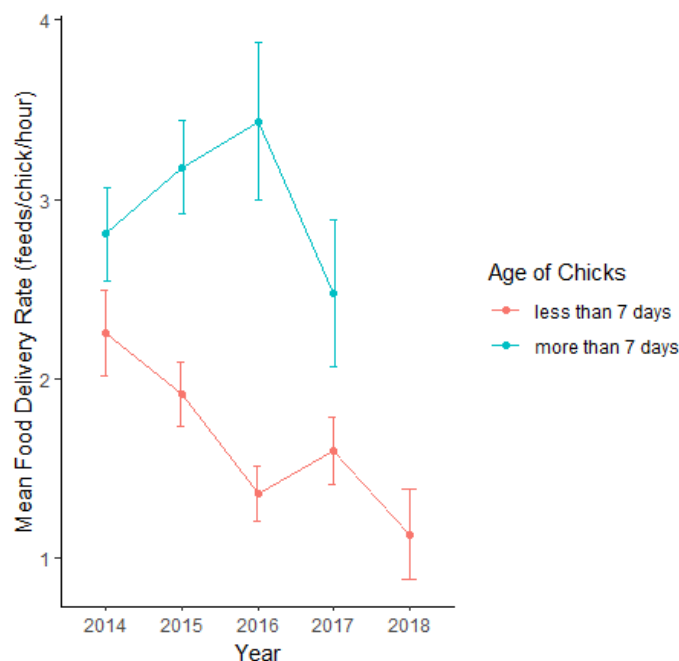


Figure 3.3. Inter-annual variation in observed food delivery rates (feeds/chick/hour) at the Long Nanny colony in Northumberland for chicks of less than seven days of age (number of observations: $n_{2014} = 25$; $n_{2015} = 41$; $n_{2016} = 13$; $n_{2017} = 31$; $n_{2018} = 15$) and chicks of greater than seven days (number of observations: $n_{2014} = 33$; $n_{2015} = 28$; $n_{2016} = 6$; $n_{2017} = 23$; $n_{2018} = 0$). Bars indicate standard error of means.

The unequal design of data collection by the LIFE project also provided challenges to further examination of inter-colony differences in food delivery rates. Evidence of differences was found for chicks aged less than seven days at Long Nanny, Scolt Head and Gronant, in 2016, with a marginally significant difference also found between Long Nanny and Crimdon in 2017. In contrast, no evidence was found of any significant difference in food delivery rates between Long Nanny and Scolt Head in 2015. These are summarised in Table 3.A2 (section 3.6). Attention is drawn to the low sample sizes used in the analysis. A post hoc Games-Howell test for 2016 data showed that there was a significant difference in provisioning rates between the Scolt Head and Long Nanny colonies ($p = 0.001$).

Overall, there is some evidence for differences in food delivery rates between years. Note these differences might be explained by differences in provisioning of the same prey between year or by prey switching between years where the same energy is provided to chicks but via a combination of different prey types (or a combination of both of these effects).

3.4.1.4 Food Delivery Rates and Sea Surface Temperature

No evidence was found that a GLMM incorporating monthly SST provided a better fit to data than a GLMM which did not incorporate monthly SST ($\chi^2_2 = 5.9$, $p = 0.052$).

3.4.2 Estimated Energy Delivery Rates

The GLMM indicated that estimated energy delivery rates (kJ/chick/hour) varied significantly with chick age ($\chi^2_2 = 31.9$, $p < 0.001$) and colony location ($\chi^2_8 = 62.05$, $p < 0.001$). No significant impacts were detected from year ($\chi^2_4 = 5.59$, $p = 0.23$), and brood size ($\chi^2_1 = 0.87$, $p = 0.35$), tidal stage ($\chi^2_3 = 0.26$, $p = 0.97$) or time of day ($\chi^2_5 = 10.22$, $p = 0.07$).

3.4.2.1 The influence of chick age

Increased energy delivery rates were associated with increasing chick age (Figure 3.4).

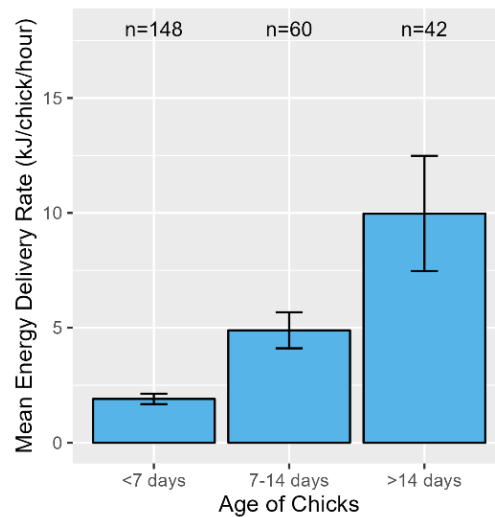


Figure 3.4. Variation in estimated energy delivery rates (kJ/chick/hour) with chick age. n = number of observations. Bars indicate standard error of means. Only estimated energy delivery rates from chicks of known age are shown.

Welch's ANOVA confirmed that these observed differences were statistically significant after controlling for brood size ($F_2 = 11.54$, $p < 0.001$). A post-hoc Games-Howell Test indicated that there was a significant difference in mean estimated delivery rate between chicks of less than seven days and between those of seven to 14 days of age ($p = 0.001$), and those of greater than fourteen days of age ($p = 0.008$). No significant difference was detected between chicks seven to 14 days of age and those of greater than 14 days of age ($p = 0.065$) and in subsequent analysis data from these two age categories have been combined.

3.4.2.2 Impact of location

Welch's ANOVA showed that estimated energy delivery rates chicks of less than seven days age varied significantly between colony locations ($F_6 = 4.52$, $p = 0.009$) after controlling for other predictors in the model. Observations from different years were pooled during analysis as no influence of year on energy delivery rates was detected by the GLMM (section 3.4.2). A post-hoc Games-Howell Test indicated that there was a significant difference in estimated energy delivery rates between Long Nanny and Blakeney ($p < 0.001$) and Long Nanny and Scolt Head ($p = 0.033$). The mean energy delivery rates for these three colonies are summarised in Figure 3.5. Attention is drawn towards the unbalanced number of observations between colonies and to the small sample size for the Blakeney colony.

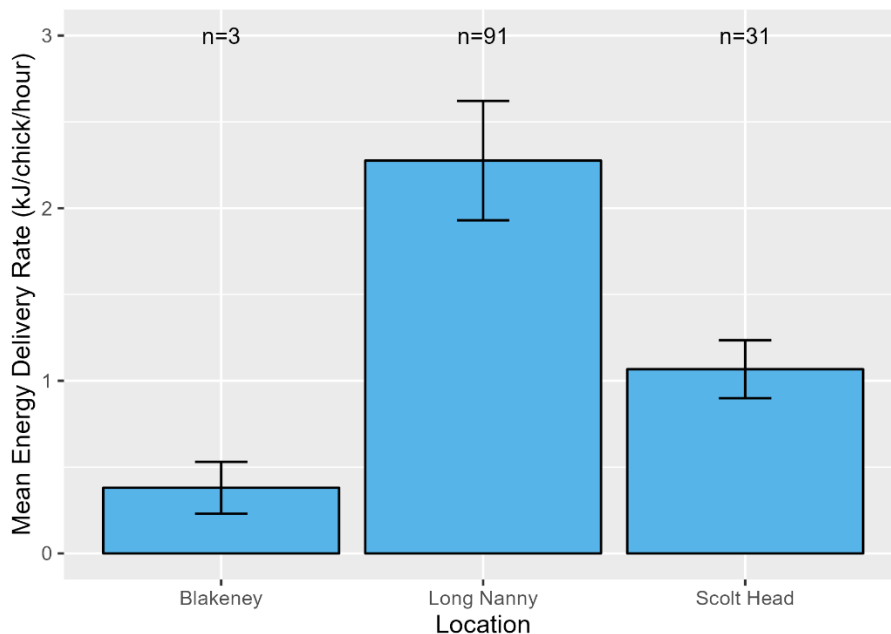


Figure 3.5. Mean estimated energy delivery rates (kJ/chick/hour) at the Blakeney, Long Nanny and Scolt Head colonies. Games-Howell Simultaneous Test indicated that a statistically significant difference in estimated food energy delivery rates existed between these locations. Observations have been pooled from multiple years. Bars indicate standard error of means. n = number of observations.

There was also weak evidence that estimated energy delivery rates varied with location in chicks aged greater than seven days ($F_6 = 3.02$, $p = 0.047$) although post-hoc testing did not identify any significant differences between individual colonies.

3.4.3 Prey Size

3.4.3.1 Influence of chick age

The mean size of Sandeel delivered to chicks increased significantly with chick age ($F_2 = 61.4$, $p < 0.001$). Post-hoc Games-Howell Simultaneous Tests showed that there were statistically significant differences in prey size between all three age categories of chick ($p < 0.001$ in all comparisons).

The mean size of clupeids also increased with chick age ($F_2 = 8.60, p < 0.001$). Post-hoc Games-Howell Simultaneous Tests showed that there were statistically significant differences in prey size between chicks aged less than seven days and chicks aged seven to 14 days ($p = 0.008$), between chicks aged less than seven days and chicks aged over 14 days ($p = 0.003$). No significant difference in mean prey size was detected between chicks aged seven to 14 days and chicks aged over 14 days ($p = 0.92$). A further breakdown of variation in prey size with chick age is given in Figure 3.A1 (in Appendix).

3.4.3.2 Influence of Sea Surface Temperature on prey size

A Spearman's test showed a negative correlation between the estimated size of Sandeel prey items and average winter Sea Surface Temperature (SST) anomaly for chicks aged seven days or less ($\rho = -.105, p = 0.023, n = 470$).

No correlation was found between estimated Sandeel prey size and average winter Sea Surface Temperature (SST) anomaly for chicks aged seven to 14 days of age ($\rho = .083, p = 0.15, n = 305$) or for chicks aged 14 days or older ($\rho = -.005, p = 0.45, n = 226$).

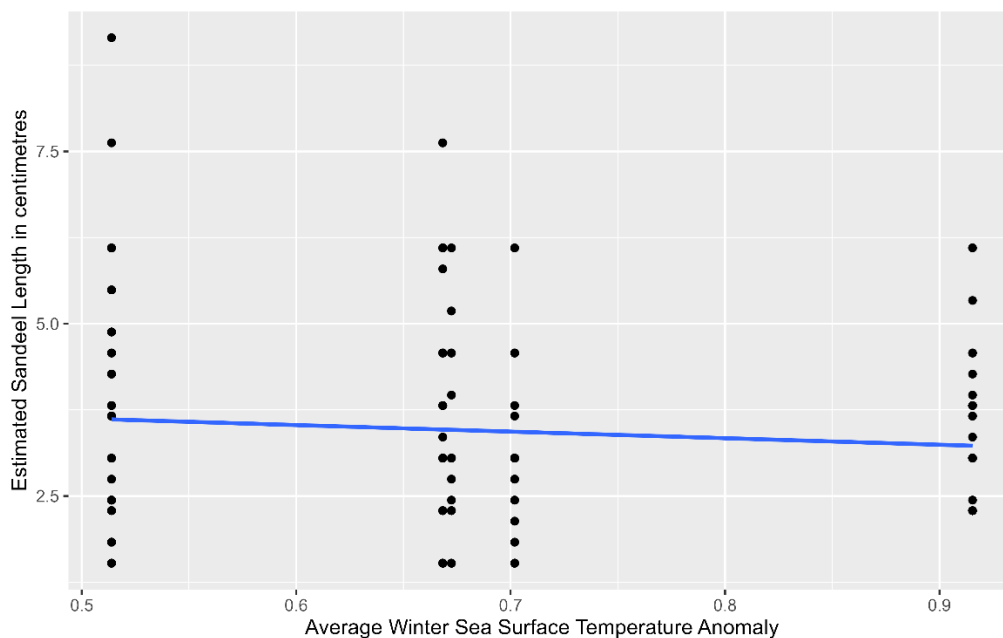


Figure 3.6. Estimated length of Sandeel prey items delivered to chicks of age less than seven days against mean Sea Surface temperature anomaly for the previous winter period (October-March)

3.4.4 Relationship between Food Delivery Rate and Estimated Energy Delivery Rate

A positive relationship was found between the food delivery rate and estimated energy delivery rate (Spearman's Correlation: $\rho = .59$, $p < 0.001$, $n = 254$) (Figure 3.7).

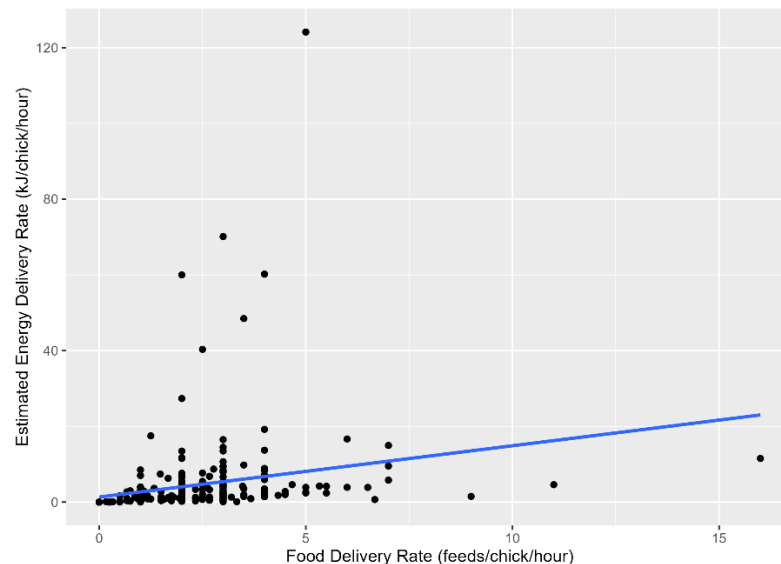


Figure 3.7. Observed food delivery rates (feeds/chick/hour) against estimated energy delivery rate (kJ/chick/hour) to chicks.

3.3.5 Relationship between chick provisioning and colony success

No correlation was detected between colony productivity and observed mean food delivery rates of chicks aged less than seven days (Spearman's Correlation: $\rho = .137$, $p = 0.54$, $n = 22$) or between colony productivity and mean provision rates of chicks aged over seven days (Spearman's Correlation: $\rho = -0.03$, $p = 0.91$, $n = 15$), or between overall mean food delivery rates for all ages of chick (Spearman's Correlation: $\rho = .16$, $p = 0.418$, $n = 26$). A summary of colony size/productivity against observed food delivery rates from LIFE project data is given in Table 3.1. This table also provides additional information about any significant sources of chick or egg mortality (predation, high tides, or bad weather) at each colony.

Table 3.1. Summary of productivity and food delivery rates for LIFE project colonies for which chick feeding data are available. Asterisk denotes any substantial causes of chick or egg mortality reported in the annual Little Tern Newsletter published by the RSPB (RSPB 2014, 2015, 2016, 2017, 2018). Food shortages were also reported early in the season in 2015 at Blakeney but these appeared to affect initial egg laying dates and not subsequent chick mortality (RSPB 2015).

Year	Location	Breeding pairs	Productivity	Number of food delivery rates calculated	Mean food delivery rate (feeds/chick/hour) \pm se			Substantial impacts on productivity from food shortage identified	Substantial impacts on productivity from predation/weather /tide identified
					All ages	< 7 days old	≥ 7 days old		
2014	Blakeney	110	0.06	11	1.88 \pm 0.2	1.84 \pm 0.1	2.14 \pm 0.4		*
	Holkham	108	0.11	3	1.39 \pm 0.3	1.39 \pm 0.3	n/a		*
	Kessingland	12	1.25	3	5.02 \pm 3.2	2.33 \pm n/a	6.36 \pm 5.0		*
	Lindisfarne	27	1.59	6	3.39 \pm 0.5	n/a	3.75 \pm 1.8		
	Long Nanny	30	1.5	58	2.56 \pm 1.4	2.26 \pm 0.2	2.8 \pm 1.5		
	Scolt Head	128	0.21	12	1.67 \pm 0.2	1.26 \pm 0.2	2.25 \pm 0.2		*
2015	Benacre	116	1.04	3	3.34 \pm 1.2	n/a	3.34 \pm 1.2		
	Blakeney	52	0.63	7	1.65 \pm 0.5	1.6 \pm 0.3	n/a		*
	Gronant	123	0.8	1	3.33 \pm n/a	3.33 \pm n/a	n/a		*
	Holkham	62	0	4	2.4 \pm 0.3	2.54 \pm 0.4	2.0 \pm n/a	*	*
	Lindisfarne	17	2.24	23	3.83 \pm 0.4	2.40 \pm 0.4	4.22 \pm 0.4		
	Long Nanny	27	0.52	71	2.47 \pm 0.2	1.94 \pm 0.2	2.76 \pm 0.2		*
	Scolt Head	88	0.13	16	1.73 \pm 0.2	1.54 \pm 0.3	2.29 \pm 0.2	*	*

Year	Location	Breeding pairs	Productivity	Number of food delivery rates calculated	Mean food delivery rate (feeds/chick/hour) ± se			Substantial impacts on productivity from food shortage identified	Substantial impacts on productivity from predation/weather /tide identified
					All ages	< 7 days old	≥7 days old		
2016	Eccles Beach	168	1.80	5	4.28 ± 3.8	2.17 ± n/a	4.80 ± 2.1		
	Gronant	141	1.21	15	2.23 ± 0.3	2.3 ± 0.4	2.0 ± n/a		
	Lindisfarne	37	1.14	11	1.17 ± 0.3	n/a	2.0 ± 1.4		
	Long Nanny	17	0.29	29	2.56 ± 0.3	1.36 ± 0.2	3.44 ± 0.4		*
	Scolt Head	173	0.31	22	3.25 ± 0.3	2.82 ± 0.3	3.86 ± 0.3		*
2017	Chesil Beach	38	1.92	0	n/a	n/a	n/a		
	Crimdon	79	0.1	28	2.96 ± 0.3	2.8 ± 0.5	3.05 ± 0.4		*
	Gronant	161	1.25	4	5.13 ± 3.7	0.75 ± 0.4	9.5 ± 6.5		*
	Holkham	45	0.02	4	3.38 ± 1.1	3.0 ± 0.0	3.75 ± 2.8		*
	Long Nanny	38	0.11	56	2.04 ± 0.2	1.63 ± 0.2	2.61 ± 0.4		*
	Scolt Head	135	0	1	n/a	1.17 ± n/a	n/a		*
2018	Gronant	171	1.12	1	n/a	4.5 ± n/a	n/a		*
	Hodbarrow	11	0.91	11	3.64 ± 0.6	n/a	3.3 ± 0.7		
	Holkham	56	0.02	4	1.39 ± 0.2	1.19 ± 0.1	2.0 ± n/a		*
	Lindisfarne	50	0.36	9	2.41 ± 0.9	n/a	2.41 ± 0.9		*
	Long Nanny	40	0	15	1.13 ± 0.3	1.13 ± 0.3	n/a		*
	Scolt Head	83	0.19	3	2.11 ± 0.1	2.11 ± 0.1	n/a		*

The analysis was run again omitting data from colonies which reported losses due to non-food related issues (21 out of 30 colony/years). Although there appeared to be some evidence of a positive relationship between provisioning rates and overall colony productivity (Figure 3.9) these were not statistically significant but note the small sample sizes with a maximum of eight (a summary of test results is provided in Table 3.A3 in the Appendix – section 3.6).

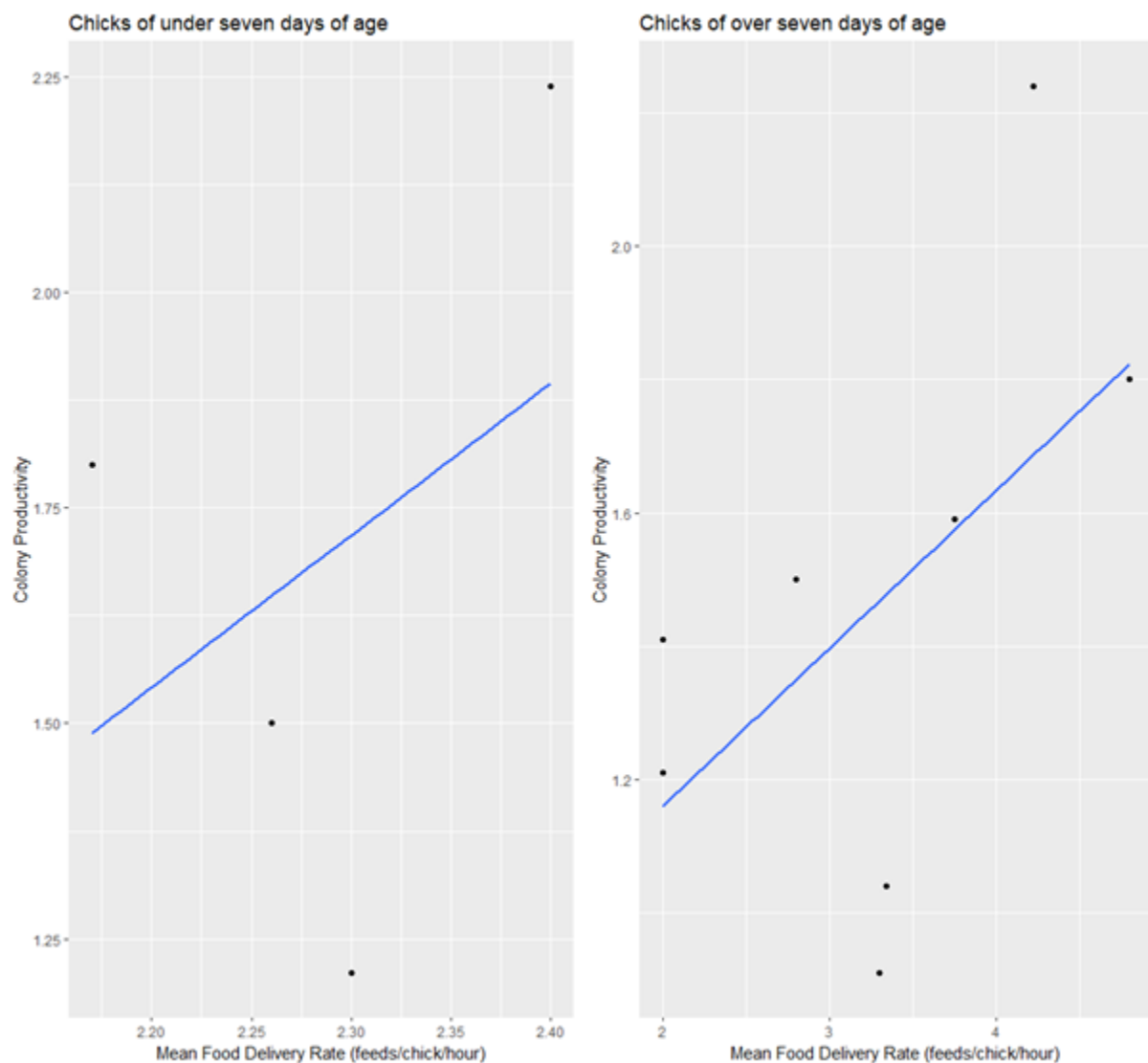


Figure 3.8. Observed mean food delivery rates (feeds/chick/hour) against overall colony productivity. Only colonies which did not report losses of chicks and eggs due to predation, high tides or weather are included (see Table 3.1 for summary). Results are separated by chick age. No statistically significant correlation was found between food delivery rates and colony productivity (Table 3.A3 in chapter appendix).

3.5 Discussion

The LIFE project is the first attempt in the UK to collect data on chick provisioning in Little Tern from multiple colonies across multiple years using a common methodology. The variation in observational effort at the participating colonies has resulted in issues of low statistical power in some of these data (see Chapter 2, Table 2.1 for summary of differing recording effort by colony) but nevertheless has shown evidence that differences in the food provisioning of chicks of similar age exists between colonies and between years. While this result is perhaps not surprising given the likely variation between food availability and prey types between UK colonies and between years, it is the first time that this has been demonstrated. Inter-annual and inter-colony differences were in food delivery rates and in prey size (and by extension in energy delivery rates which were strongly positively correlated with the former).

Due to high levels of chick mortality, it was not possible to link differences in chick provisioning with differences in productivity or other measures of colony success. Early season food shortages were reported in 2015 at some colonies including Crimdon, Holkham and Scolt Head and were noted as contributing towards chick mortality at some locations (RSPB 2015a). Unfortunately, these were not reflected in the chick feeding observations collected by the LIFE project, probably because of the majority of observations at the effected colonies seem to have taken place in July once prey availability had increased. However, mortality of Little Tern chicks due to starvation appears to be relatively uncommon, as previously reported by Wilson *et al.* (2020) and reflected in Table 3.1, with the most frequently reported causes of the loss of eggs or chicks at project colonies being predation, tidal flooding, disturbance and extreme weather. Participation in chick feed studies came to a total of 30 colony/years across the period of the project. Out of these 30 colony/years, 21 reported losses of chicks or eggs due to predation, tidal flooding or bad weather. In itself, chick provisioning does not appear to be a good predictor of likely fledging success in Little Tern based on the evidence available from the LIFE project. This contrasts with some other seabird species such as Puffin *Fratercula arctica* and Arctic Tern where a more direct association between provisioning of chicks and fledging success can be drawn (Barrett

et al. 1987, Morris 2013, Vigfusdottir *et al.* 2013). Given the wide range of causes of chick mortality (and the key role of chick predation noted for this species) it is likely that the main influence of low food availability on productivity and breeding success in Little Tern will manifest itself through impacts on adult breeding condition or through survival rates of new fledglings, both of which were outside of the scope of this study. However, while no evidence was found to suggest the poor chick feeding was a regular or frequent cause of poor productivity, the data were insufficient to draw any clear conclusions about whether higher levels of chick provisioning are linked to higher productivity in the absence of other mortality factors.

Sea Surface Temperature (SST) and wider climatic phenomena such as from the North Atlantic Oscillation, are widely reported as influences on the productivity of seabirds, probably via effects on the availability and quality of various prey species (Durant *et al.* 2005, Ramos *et al.* 2013). Some contradictory evidence of the possible impacts SST on chick provisioning was derived from the data. While no indication of impacts on food delivery rates was determined, the size of Sandeel fed to chicks aged one week or less appeared to be linked to sea temperatures in the winter period before breeding. Sea temperature has been linked to Sandeel development and to declines in Sandeel populations in the North Sea (Macdonald *et al.* 2019, Macdonald *et al.* 2018) but it is not clear why the apparent influence on prey size was only observed in younger chicks. The interactions between climatic conditions and the food webs on which Little Tern rely is a complex subject and outside of the scope of this current study. However, data from the LIFE project does offer some limited evidence of possible impacts.

Feeding observations of Little Tern chicks made by the LIFE project showed a wide variation across all measures of food provisioning. The apparent lack of any statistically significant variation in food delivery rates to individual chicks with increasing brood size contrasts with evidence from other tern species (e.g. Robertson *et al.*, 2016) and from Davies (1981) who observed the eldest chick in broods of Little Tern being fed at the expense of younger chicks at time of food scarcity. However post-hoc power analysis indicates that the sample sizes obtained in this study had a very low probability of detecting a significant variation in food delivery rates of broods of different sizes.

The greatest single predictor of chick provisioning rates was found to be chick age. Older chicks were fed more frequently and with larger prey items than younger chicks due to the increasing energy requirements of growing birds. Growth in Little Tern chicks follows an S-shaped 'logistic' curve with weight gained slowly at first, then accelerates through the middle part of their growth before levelling off after about 10 days (Norman 1992). The observed patterns of food provision in chicks would appear to reflect this pattern with a statistically significant difference seen between chicks of less than seven days of age and those aged more than seven days. This result highlights the importance of specifying chick age when reporting on feeding studies of Little Tern or when making comparisons between studies.

The size of prey items also increased significantly with chick age. Differences in the size of prey provisioned to chicks of different ages has sometimes been attributed to an inability of young chicks to physically consume larger prey items (Bogliani *et al.* 1994, Fasola *et al.* 2002). However, the statistically significant increases seen in the size of Sandeel brought to chicks across all ages suggests that parents are meeting the increasing energy demands of growing chicks by a combination of increased food delivery rates and by increasing the prey size/energy content of food delivered to chicks. This finding differs from that of Paiva *et al.* (2006b) who suggested that parents of Little Terns in Southern Portugal do not alter provisioning rates of chicks but instead meet increasing food demands solely by increasing the size of prey fed to chicks. The reason for this difference is not clear but Little Terns at the Southern Portuguese colonies appear to utilise a much wider range of different prey species than their UK counterparts (Chapter 2; Paiva *et al.* 2006a, Paiva *et al.* 2006b) and forage over a wider range of coastal and estuarine habitats than at the colonies which were part of the LIFE project.

Food delivery rates recorded through the LIFE project were generally lower than those reported by Davies (1981), Bogliani *et al.* (1992) and Fasola *et al.* (2002). This difference may relate to the differences in prey types between locations, with LIFE project feeding records being dominated by lipid-rich marine fish whereas chick diet was dominated by

crustacea in Davies' study and by freshwater fish at Bogliani's study site. In contrast, the food delivery rates identified through the LIFE project are much closer to those reported by Norman (1992) and Davies (2011) from locations where marine fish dominated observed chick diet. This suggests that a negative correlation should exist between food delivery rates and prey quality, and with delivery rates being higher when the energetic content of prey was lower. However, data from the LIFE project confounded this expectation by showing a positive relationship between food delivery and energy delivery to chicks. Over 80% of identified prey in the LIFE project feeding records were made up of high-quality prey items (Sandeel and clupeid species - see Chapter 2) and the generally high nutritional value of the food on offer to chicks may explain the lack of any detectable correlation between diet quality and food delivery rates in this study.

It has been widely reported that terns and other seabirds show clear diurnal patterns in food provisioning, usually increased foraging rates in the early morning and late evening (Stienen *et al.* 2000). Dunn (1972) attributed this foraging behaviour in turn to the hunger of the chicks on waking and to their need to take a final opportunity to feed before nightfall. In contrast to this, no statistically significant diurnal patterns in food provisioning could be detected in the LIFE project data. The evidence for diurnal provisioning patterns in Little Tern is mixed with some studies failing to detect a diurnal influence (Davies, 2011, Howe, 1982 *op. cit.* Eglington and Perrow 2014), while others have reported strong diurnal patterns in feeding rates (Bogliani *et al.* 1992, Davies 1981). The reasons for this are unclear but may relate to differences in diurnal pattern of food availability between study sites. The diurnal pattern in feeding rates found by Bogliani *et al.* (1992) in their study of Adriatic wetlands was partly attributed to a greater availability of crustaceans and freshwater fish during the mornings while the feeding peaks observed by Davies (1981) also coincided with potential tidal influences on prey availability.

Changing patterns of foraging and feeding with tidal stage have been detected by previous authors such as Davies (1981) and Taylor and Roe (2004). These observed patterns usually relate to a specific interaction between local site features and tide which result in food becoming more available at some tidal stages. One explanation of

the absence of any statistically significant pattern of foraging rates with tide in the LIFE Project data may be that any influence is too site specific to be identified in data collected from a widely disparate number of sites. It is also possible that such interactions are relatively fine-grained and that the classification of tidal stage used in the analysis is too coarse to have detected any changes in provisioning rates.

3.5.1 Conclusions

Measures of chick provisioning in Little Tern show a high degree of variability both within and between colonies. Chick age appears to be the main predictor of food delivery rates and prey. No evidence was found of diurnal or tidal patterns of food delivery in chicks. This result contrast with some previous studies and may suggest that Little Tern foraging behaviour is strongly influenced by local site conditions. It may however be an artifact of low statistical power of the data used, and this should be verified with further study.

Little Tern chicks suffer high mortality, mostly due to causes unrelated to food availability (Cabot and Nisbet 2013, Wilson *et al.* 2020). This may have masked any link between chick provisioning rates and colony success across the UK, although it is clear from reports from individual colonies that food shortages can and do have an impact on chick survival in some years. However, while no evidence was found to suggest the poor chick feeding was a regular or frequent cause of poor productivity the data obtained through the LIFE project were insufficient to draw any conclusions about whether higher levels of chick provisioning are linked to higher productivity in the absence of other mortality factors. This is an area that still requires further research.

Impacts of food available on breeding success in Little Tern are mostly likely to occur through impacts on the condition of birds and through reproductive choices such as date of egg lay and clutch size. This is an area for further study and is given additional urgency by the likely impacts of climate change on the quality and availability of prey.

3.6 Appendices

Table 3.A1. Summary of variables used in Generalized Mixed Effect Models.

Variable	Type of Variable	Role in GLMMs	Description
Number of chick feeds	Numeric	Response variable in food delivery GLMM	Count of total number of feeds of chicks within brood during the observation period. Includes both successful and unsuccessful chick feeds
Estimated Energy Delivery Rate	Numeric	Response variable in Energy Delivery Rate GLMM	The estimated energetic value of prey delivered to each chick within a 60-minute period, expressed as kJ/chick/hour.
Length of observation	Numeric	Offset	Length of timed observation of chick feeding in minutes
Chick Age	Categorical	Fixed effect	Chicks were assigned to one of three age bands: Age Band 1 (less than seven days of age), Age Band 2 (seven to 14 days of age), Age Band 3 (greater than 14 days of age)
Brood Size	Numeric	Fixed effect	Number of chicks within the brood being observed
Location	Categorical	Fixed effect	Name of colony
Brood Identity	Categorical	Random	A unique code given to each brood. Broods with were recorded without an identifier were assigned to a single code for the purposes of the model
Year	Categorical	Fixed effect	Year in which observations were made
Time of Day	Categorical	Fixed effect	Feeding records were assigned to one of six categories consisting of three-hour blocks spread between 4am and 10pm.
Tidal Stage	Categorical	Fixed effect	Tidal stage was classified as either “High”, “Low”, “Rising” or “Falling” based on reference to published Tide Tables for the closest port or harbour to the colony.

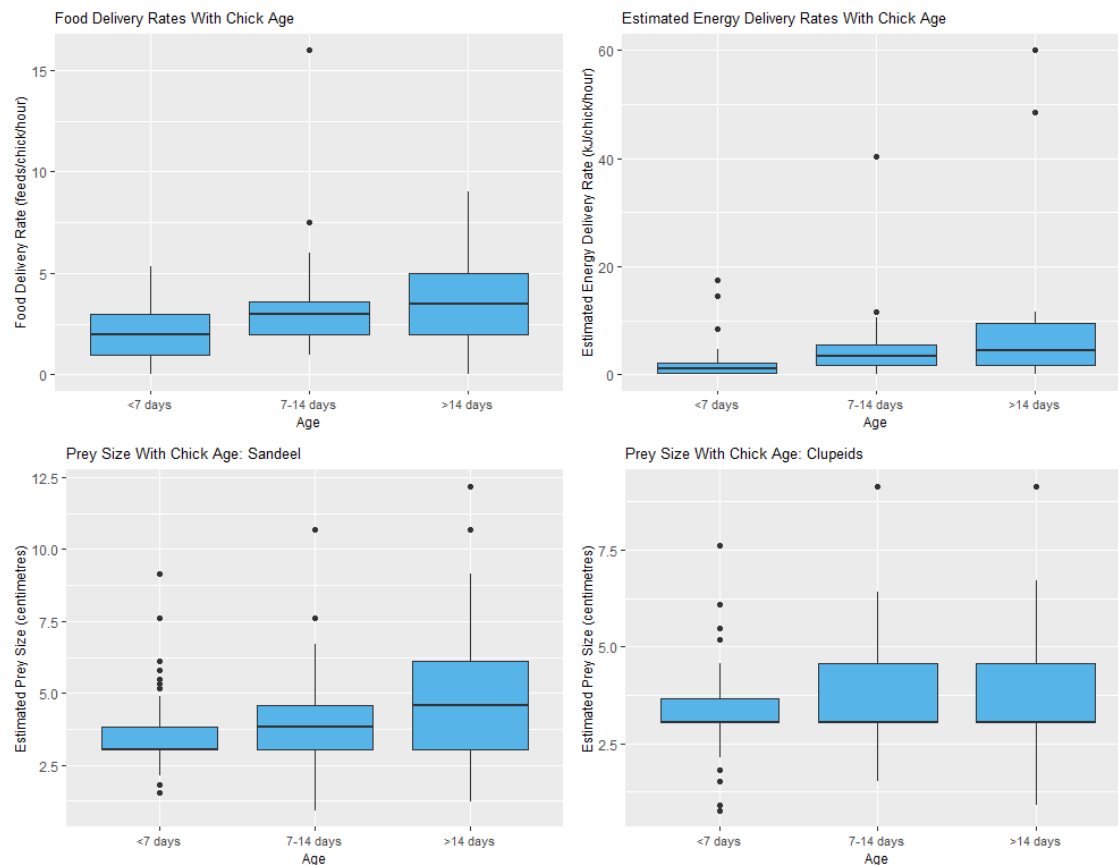


Figure 3.A1. Summaries of chick provisioning observations by chick age from the LIFE project. Four different measures of chick provisioning are shown: Food Delivery Rates, Estimated Energy Delivery Rates, Prey Size (Sandeel), and Prey Size (clupeids). All measures showed a statistically significant difference with increasing chick age. Variation in Food Delivery Rate and Estimated Energy Delivery Rate are covered in sections 3.4.1.2 and 3.4.2.1. Welch's ANOVA also showed significant difference with chick age for both Sandeel prey ($F_2 = 60.98$, $p < 0.001$) and clupeid prey ($F_2 = 8.60$, $p < 0.001$).

Table 3.A2. Results of Welch's ANOVA looking at inter-colony variations in food delivery rates to chicks. All chicks were of less than seven days age. Insufficient sample sizes existed to analyse inter-colony variation among older chicks.

Year	Sites from which provisioning records compared	Mean food delivery rate (\pm se)	F-value _{df}	p-value
2015	Long Nanny (n=41)	1.9 \pm 0.2	1.13 ₁	0.301
	Scolt Head (n=12)	1.54 \pm 0.30		
2016	Long Nanny (n=13)	1.36 \pm 0.15	11.34 ₂	<0.001
	Scolt Head (n=10)	2.82 \pm 0.3		
	Gronant (n=13)	2.3 \pm 0.4		
2017	Long Nanny (n=31)	1.63 \pm 0.2	4.66 ₁	0.052
	Crimdon (n=10)	2.8 \pm 0.5		

Table 3.A3. Results of Spearman's Correlation test looking at relationship between colony productivity and observed food delivery rates. These tests remove data from colonies which were reported to have suffered substantial problems with loss of chicks or eggs from predation, tides or bad weather. Results of correlation tests for full data set are given in section 3.3.5. N = sample size. Note the small sample sizes and positive direction of effect sizes.

Age of chicks	ρ	p-value	n
All ages	.48	0.23	8
< 7 days	.2	0.8	4
\geq 7 days	.61	0.1	8

Chapter 4. The Use of Video Imagery in Little Tern

Chick Feeding Studies

4.1 Abstract

The use of video is an increasing popular technique in bird feeding studies as a means of collecting data on bird diet and feeding rates and for validating prey identifications and size estimates in the field. For Little Tern, which are challenging to study in the field, video capture offers an alternative to timed feeding studies undertaken by an observer. I investigated the use of video capture in Little Tern chick feeding studies using two different approaches: camera traps set to record clips of 30-60 seconds duration when triggered by motion, and an “action cameras” (GoPro) in a digi-scope arrangement (i.e. attached to the eyepiece of an optical telescope) to capture continuous footage of chick broods.

Due to technical and practical difficulties, including battery failure and the movement of chicks to new locations within the colony, only a small number ($n = 34$) of direct comparisons could be made between prey type and prey size captured on video and recorded contemporaneously through field observation. However, there was good agreement between contemporaneous records made using the different techniques: (i) only in 5% of records were prey items identified differently depending on the method of data collection used; (ii) prey size estimates obtained from direct observation and by review of video footage were identical in 39% of recorded chick feeds; (iii) both methods produced a high rate of records of unidentified prey items (50%) and prey size estimates. I conclude that: (i) digi-scoped video footage offers a potential additional means of capturing feeding rate information for younger chicks but is less useful for determining diet composition; (ii) the issues of triggering of camera traps make them unsuitable as a substitute for field observations for studies where the aim is to derive chick feeding rates but they may be of use where the aim is to sample the types and size of prey brought to chicks, however, they may be a useful method of passively

sampling chick diet at locations where direct field observations are not possible and for younger chicks which are less mobile.

4.2 Introduction

Understanding the prey of a species is important for a range of reasons including to understand potential drivers of population dynamics and to construct food webs. Direct observation of feeding is a widely used method in diet studies, particularly for bird species returning to the nest to feed their young. The method can avoid disturbance to the focal species and enable relatively large amounts of data to be collected over a short period of time (Barrett *et al.* 2007). However, previous studies, such as those of Cezilly and Wallace (1988) have indicated that incorrect identification of prey can be common during direct observations while Goss-Custard *et al.* (1987) and Lee and Hockey (2001) have reported individual bias in estimates of prey size.

Some of these issues can be mitigated through the collection of prey specimens to supplement data collected from direct observation. However, physical collection of specimens may not be appropriate at all locations or with all species due to issues of disturbance and/or welfare. This has led to investigations into the use of digital imagery as an alternative means of collecting voucher specimens (Larson and Craig 2006) or as a means of primary data collection (Gaglio *et al.* 2017, Gaglio *et al.* 2018b). Recent years have also seen the use of video imagery in bird feeding studies. A number of video surveillance systems of varying degrees of technical complexity have been used (for example Au - Wall *et al.* 2018, Kross and Nelson 2011, Shin and Han 2019 but as with many other aspects of ecology, the use of camera traps is becoming more common. Camera traps offer a non-invasive and relatively inexpensive means of collecting large data samples but their effectiveness as a research tool may vary with the species being studied and the research questions being posed (García-Salgado *et al.* 2015, Wearn and Glover-Kapfer 2019).

In this chapter I investigate the use of video imagery in Little Terns feeding studies. There were two specific drivers for this. The first is to validate the results of direct feeding observations of chicks and to use video footage as a point of comparison for prey

identification and size estimates. The second driver was to investigate whether video capture could be reliably used as an additional research tool for use in dietary studies and provisioning rate studies on Little Tern. Camera traps were used as the primary means of capturing video imagery. I also investigated the potential use of digi-scoping (digital imagery capture through a camera attached to the eyepiece of an optical telescope) as a video capture technique using an ‘action camera’ (GoPro Hero 7). My aims were:

- To determine whether video footage could be used to validate chick feeding records obtained by field observations.
- To investigate if the results of video capture produced similar diet composition and prey size distribution to direct observations of chick feeding.
- To assess whether use of camera traps, or other video capture methods, could be used as an alternative to timed feeding observation in the study of chick diet in Little Terns.

4.3 Methods

4.3.1 Evaluating the potential use of camera traps in chick provisioning studies

4.3.1.1 Collection of camera trap imagery

Camera traps were deployed at the Long Nanny tern colony during 2017, 2018, and 2019 to capture video footage of chick feeding in Little Terns. The colony is part of the Newton Links Site of Special Scientific Interest (SSSI). Consent from Natural England under Section 28E of the Wildlife and Countryside Act 1981 (as amended) was obtained for the use of camera traps on the site. Placement of the traps was covered by a licence to disturb Schedule 1 Birds obtained from Natural England by the LIFE project (Ref: 2017-28158-SCI-SCI).

The number of camera traps deployed varied between years across individual seasons, with the locations of individual traps being changed as chicks became mobile and left nest scrapes. A maximum 12 camera traps were deployed at any one time. Camera traps were set to record video footage of between 30 seconds and one minute when triggered by movement. Video footage was date and time stamped. The camera traps

used were Acorn LT-6310 with a single device of Bushnell manufacture was also deployed during 2017. The camera traps were equipped with 32 GB memory cards to store images and powered with AA lithium batteries.

At Long Nanny the majority of active nest scrapes were raised (with human intervention under licence) on to fishing crates prior to egg hatching to provide protection from high tides (see Chapter 1). To provide the necessary height needed to view active scrapes, the camera traps were attached to metal fencing posts using bailing twine and tape (Figure 4.1). This was done prior to the camera traps being placed within the colony. Entry to the active area of the colony was restricted to periods when the National Trust Wardens for the site needed access for essential maintenance or to conduct counts of active scrapes. These visits were strictly limited to a period of no longer than 20 minutes to minimise risks to chicks and eggs. The camera traps were placed approximately one to two metres from active nest scrapes or, in later stages when chicks were mobile within the colony, close to areas where chicks were observed to gather. Memory cards were replaced by the wardens on an opportunistic basis on any subsequent visits into the colony and batteries replaced as required. The single Bushnell trap deployed during 2017 was used to obtain footage of chicks which had left the fishing crates. It was placed directly on to the sand in localities where chicks were observed to gather.



Figure 4.1. Examples of camera trap attachment to fencing pins. The use of fencing pins was necessary as scrapes at Long Nanny are raised on to fishing crates and pallets to provide protection from high tides. The first two images (left and centre) show cameras and fencing pins in place within the colony. Photographs and Placement of the traps was covered by a licence to disturb Schedule 1 Birds obtained from Natural England by (Ref: 2017-28158-SCI-SCI).

The cameras were active in the periods from the 13th June to the 18th July 2017, the 17th July to the 19th July 2018, and the 10th June to the 18th July 2019. Video images were later downloaded and viewed on a VLC media player, zooming, slowing and pausing footage as necessary to make prey identification and size estimates. Details of prey size and prey type captured on an Excel spreadsheet. Records of other food related activity (adult feeds, displaying males with food items, and uncategorisable records of adults with food) were also noted.



Figure 4.2. Examples of prey capture through camera trap imagery. Image on the left shows a Sandeel. The figure on the right shows a clupeid. Photographs and Placement of the traps was covered by a licence to disturb Schedule 1 Birds obtained from Natural England by (Ref: 2017-28158-SCI-SCI).

4.3.1.2 Timed Feeding Observations of Chicks

Timed feeding observations of scrapes or individual chicks were made during 2017, 2018, and 2019 using the methodology followed by the Little Tern Recovery EU LIFE Project (RSPB 2015). This methodology included a record of prey type and an estimate of prey size based on a proportion of adult bill length and described in Chapter 3. A total of 90 timed observations were made in 2017 (between the 14th June and 28th July), while 48 timed observations of individual broods were made in 2018 (between the 13th June and the 26th July) and 165 were made in 2019 (between the 10th June and 25th July).

During 2017, all but three chick feeding observations were made using scan surveys of the entire colony. Scan surveys were adopted as a method of data collection in an attempt to gather data on feeding activity in the colony as a whole and to assess how this changed throughout the breeding season. The methodology was abandoned after 2017 as it was felt that timed observations of a single or a small number of chicks was a more reliable means of data collection and better allowed for chick age to be taken into account when analysing the factors influencing food delivery rates.

The colony was constantly scanned for periods of an hour using a Swarovski spotting scope or binoculars. The time of all observations of little terns with food items were recorded together with a note of the prey type, prey size, the type of event, and any other notes of interest. Where either prey type or prey size could not be determined this was recorded as 'unidentified'. The times and durations of any dreads (taking flight by adult birds usually not associated with a particular disturbance) were also noted. Notes were also made of wind speed using the Beaufort Scale, sea state using the Douglas Sea Scale, Cloud cover (expressed as oktas), tidal stage, and precipitation. Observations were recorded into a hand-held voice recorder and later transcribed on to spreadsheet.

4.3.2 Analysis of results

4.3.2.1 Direct comparison of individual feeding events by data collection methods

Chick feeding records extracted from camera trap footage were cross-checked against feeding records from timed feeding observations to identify instances where the same chick feed had been recorded using both methods. When such instances occurred a comparison of prey identification and estimated prey size was made, and a note made of any differences. It should be noted that no independent verification of prey type or prey size was available (e.g. through the recovery of individual specimens) to validate the records obtained by either method.

4.3.2.2 General comparison of diet composition and mean prey size by method

The percentage contribution of each prey type was calculated for each of the three years 2017-2019. Separate calculations were made for each data obtained through timed observations of chick feeding and through examination of camera trap footage. The three categories of prey used were Sandeel, clupeid and “unidentified”.

Since relative proportions of different prey types found within samples are not independent of each other it was not possible to use chi-square tests to examine how diet composition of prey differed with method. It was also not possible to use a compositional analysis approach (as in Chapter 2) as there were only two categories of prey which could be used, one of which would act as the denominator in log-ratio calculations. As an alternative, two sample t-test was used to test for any difference in the mean proportion of each prey type to chick diet across the three years of observation. Proportions were arcsine square transformed prior to test. Levene’s test indicated equal variance in the arcsine square transformed proportions ($F = 2.6$, $p = 0.13$).

Estimated prey size in centimetres was calculated for records of Sandeel and clupeids using the assumption that one adult bill length equated to 3.05cm (RSPB 2015b). Two sample t-test to compare the mean prey size of Sandeel and clupeids identified using both of the methodologies. Welch's t-test was used on Sandeel from 2017 as Levene's test indicated unequal variances ($F = 8.3$, $p = 0.007$). Prey size varies significantly with chick age (see Chapter 3) so only data on chicks aged one week or less was used. Data from 2017 were only taken from observation which took place before the 1st July as after this date some of the chicks under observation during whole colony scans were aged over seven days.

4.3.3 Use of Digi-scoped GoPro footage in chick provisioning studies

During 2022 recordings of chick feeding were made on a GoPro Hero 7 in the period between the 13th June and 4th July. The GoPro was attached to a Swarovski spotting scope using a commercially available digi-scope attachment. To extend the battery life of the GoPro it was attached to a power bank (Figure 4.3). Video footage was recorded at distances from chicks that ranged from approximately 70 to 180 metres and at scope magnifications of between x40 and x60. Initial contact was made with Natural England to confirm that the use of a digi-scoped action camera did not specifically require a licence if no birds were being disturbed and undertaken at a distance outside of the colony. All observations were undertaken from outside of the fenced perimeter of the colony, typically in excess of 150 metres from the fence and in liaison with the site wardens, all of whom were all holders of a Schedule 1 bird licence.

Simultaneous timed observations of chick feeding totally 835 minutes were made from a second Swarovski scope placed immediately next to the digi-scope array.

GoPro footage was reviewed after the end of the nesting season viewed on a VLC media player, zooming, slowing and pausing footage as necessary to make prey identification and size estimates. Feeding observations noted for comparison with the results of timed feeding observations.



Figure 4.3. Illustration of digi-scope arrangement. A GoPro Hero 7 is attached to a Swarovski scope using a commercially available digi-scope attachment. To increase the battery life of the GoPro it was attached to a power bank using a USB cable. The power bank was held in a dry bag attached to the arm of the tripod mount.

4.4 Results

4.4.1 Capture of Camera Trap Footage

A typical camera trap was found to capture around 760 clips of one minute duration before the memory card was full. Out of all the footage available across a three-year period a total of 656 food items were identified from video clips, 60% of which were captured in 2017. Of these 376 were related to chick feeding events (successful and unsuccessful) the remainder being either adult feeds (themselves or to their mate), displaying birds, or sightings of adult birds with food that could not be confidently attributed to chick feeding. The most common reasons for failure to collect footage of feeding events were that chicks had moved their location within the colony, that camera traps were incorrectly placed or had moved in the wind and so were not pointed at chicks, or that batteries had become flat, or memory cards had become full in the period before chicks had hatched.

Examination of video footage showed that identified prey items were either Sandeel *Ammodytes* spp. or clupeids, with Sandeel being the most numerous prey species observed during each year. Scan surveys of the colony during 2017 identified two records of Goby *Gobius* spp. and a single record of Flatfish (Pleuronectiformes) but neither of these prey types were recorded within camera trap footage.

4.4.2 Comparison of results of camera traps with results of timed feeding observations

4.4.2.1 Success in capturing chick feeding events

Footage from camera traps was available for four separate broods or chicks during 2018 and 11 separate broods or chicks in 2019. These yielded images of 73 chick feeds in 2018 and 155 chick feeds in 2019. Due to low camera trap capture rates, only 12 periods of chick feeding observations were contemporaneous with active captures from video footage. A total of 41 chick feeds were recorded during these timed feeding observations (total duration 736 minutes), 16 of which were captured on camera trap images, and 25 of which were not captured. In addition to these chick feeds, four adult-to-adult feeds or adult self feeds were caught on video footage and also noted as part of timed observations.

There was some evidence of an influence of chick age on the success of camera trap capture, although attention should be drawn to the small sample sizes on which this is based. For chicks aged under seven days (13 of the timed observation periods), 72% of the sixteen chick feeds recorded were captured on camera trap images. In contrast, for chicks aged over 14 days (three of the timed observation periods) only 13% of the 23 chick feeds recorded were captured on camera trap images.

During 2017 none of the timed observations of chick feeding within individual broods were undertaken while camera traps were actively recording scrapes. However, during whole colony scans a total of 89 individual chick feeds were recorded which were within the potential viewshed of active camera traps. Of these only 17 of the chick feeds (19%)

were captured on camera trap imagery and an additional 16 chick feeds were recorded by camera traps but missed during timed scan surveys.

4.4.2.2 Identification of prey items

A direct comparison of prey item identification collected through field observation and examination of video imagery was available for 34 feeding events during 2017 to 2019. In 82% of instances there was agreement in prey identification between camera trap footage and identifications made in the field, while in 9% of instances the prey species identified through camera trapping was different to that recorded in the field, with examples of both prey being recorded as Sandeel in field observations but clupeids during analysis of camera trap footage (n=2), and as a clupeid while analysis of camera trap footage recorded a Sandeel (n=1). In the remaining instances only one of the two methods used produced a positive identification of prey type (Figure 4.4).

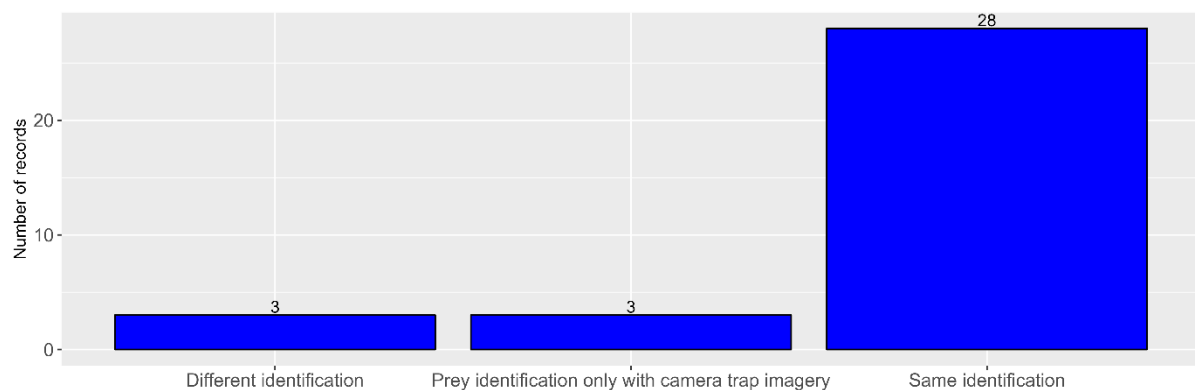


Figure 4.4. A comparison of the results of prey identification made using contemporaneous field observation and camera trap image capture (number of feeding events compared = 34). Numbers of feeds in each category shown above the bar.

4.4.2.3 Estimation of Prey Size

A direct comparison of prey size estimates collected through field observation and examination of video imagery was available for 34 feeding events during 2017 to 2019.

Identical size estimates were obtained in 44% of these feeding events, with differing size estimates being obtained in 53% of instances. During one feeding event, a size estimate was only available from camera trap footage with no size estimate obtained during timed feeding observations (Figure 4.5). The median difference in size estimates obtained using the two methods was 0.5 cm (range = 0 to 2.3 cm).

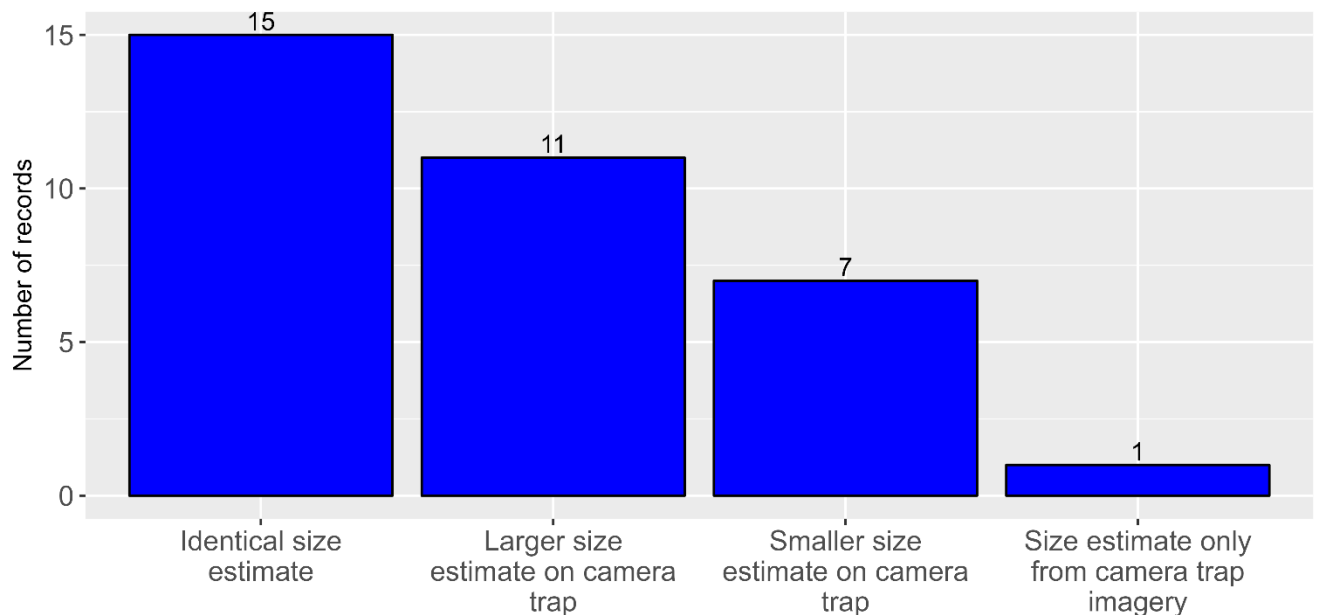


Figure 4.5. A comparison of prey size estimates made using contemporaneous field observation and camera trap image capture (number of feeding events compared = 34).

4.4.3 Use of camera traps to sample composition of chick diet and prey size

4.4.3.1 Diet composition

The proportion of Sandeel and clupeids in chick diet in data from camera trap footage was broadly comparable with data obtained through timed feeding counts (Figure 4.6). No significant difference in the mean proportions of total diet across the three years was attributable to data collection method for either Sandeel ($t_4 = 1.23$, $p = 0.29$) or clupeids ($t_4 = 2.02$, $p = 0.11$).

In contrast the proportion of unidentified prey items was lower in camera trap data when compared to data from timed feeding counts ($t_{44} = -6.3, p = 0.003$) suggesting the greater time for observing the events reduced the numbers in this category.

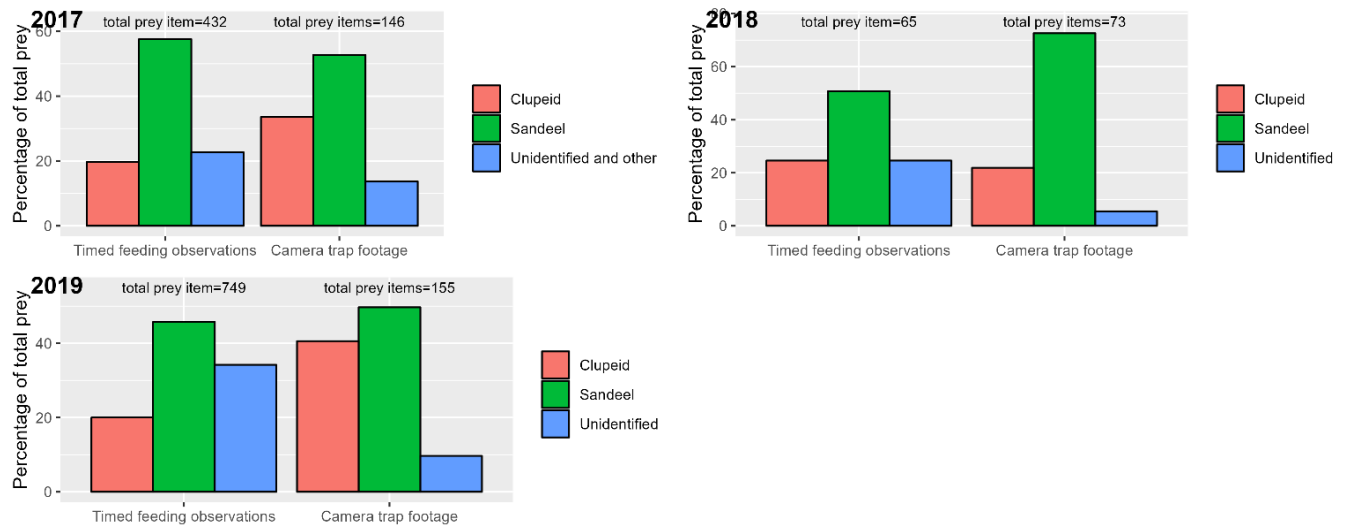


Figure 4.6. Comparisons of chick diet composition identified through timed feeding observations and analysis of camera trap imagery from Long Nanny during 2017, 2018 and 2019. Timed feeding observations in 2017 included two records of Goby and a single record of a Flatfish. For simplicity of display these have been included with the Unidentified category in the 2017 graph.

4.4.3.2 Prey Size

The length of Sandeel and Clupeid prey items estimated from timed field observations and examination of camera trap footage is summarised in Table 4.1. Size estimates obtained from the two methods of data collection were generally in agreement with each other, with the exception of clupeid prey items in 2019, where mean size estimates from field observations were significantly larger than size estimates obtained via examination of camera trap footage. However, attention is drawn to the small size of the difference between the respective means (0.3 cm).

Table 4.1. Comparison of estimated prey size obtained through camera trap imagery and direct feeding observations. Data are for chicks aged under seven days. Levene's test indicated that all data had equal variance apart from Sandeel data from 2017. Welch's t-test was used on data with unequal variances.

Year	Prey	Timed feeding observation (mean length in cm \pm se)	Camera trap imagery (mean length in cm \pm se)	t-value _{df}	p-value
2017	Sandeel	3.4 \pm 0.3 (n=17)	3.5 \pm 0.13 (n=12)	0.34 _{20.6}	0.73
	Clupeid	1.76 \pm 0.1 (n=13)	2.2 \pm 0.2 (n=8)	1.95 _{13.0}	0.073
2018	Sandeel	2.8 \pm 0.1 (n=31)	3.0 \pm 0.06 (n=45)	1.87 _{49.8}	0.067
	Clupeid	2.1 \pm 0.15 (n=16)	2.2 \pm 0.2 (n=15)	0.35 _{25.5}	0.73
2019	Sandeel	2.8 \pm 0.06 (n=54)	3.0 \pm 0.07 (n=68)	1.76 _{119.9}	0.08
	Clupeid	2.06 \pm 0.07 (n=42)	1.79 \pm 0.06 (n=62)	-2.79 _{93.4}	0.006 *

4.4.4 Use of GoPro video footage

A total of 67 chick feeding events were noted during timed observations of chicks. Of these 56 were also recorded on the contemporaneous video footage. The remaining 11 feeds all took place 'off camera', outside of frame of the video capture. All missed feeds occurred during the final observation period on the 4th July 2022 when the observed chicks were over two weeks of age and highly mobile. Examination of video footage also showed two chick feeds which had not been recorded during timed observations undertaken on the 4th July.

In 45% of instances the prey items identified by direct observation and by examination of video footage were identical. Only in 5% of records were prey items identified differently depending on the method of data collection used. However, in 50% of instances prey item were classified as 'unidentified' using either or both methods (Figure 4.7).

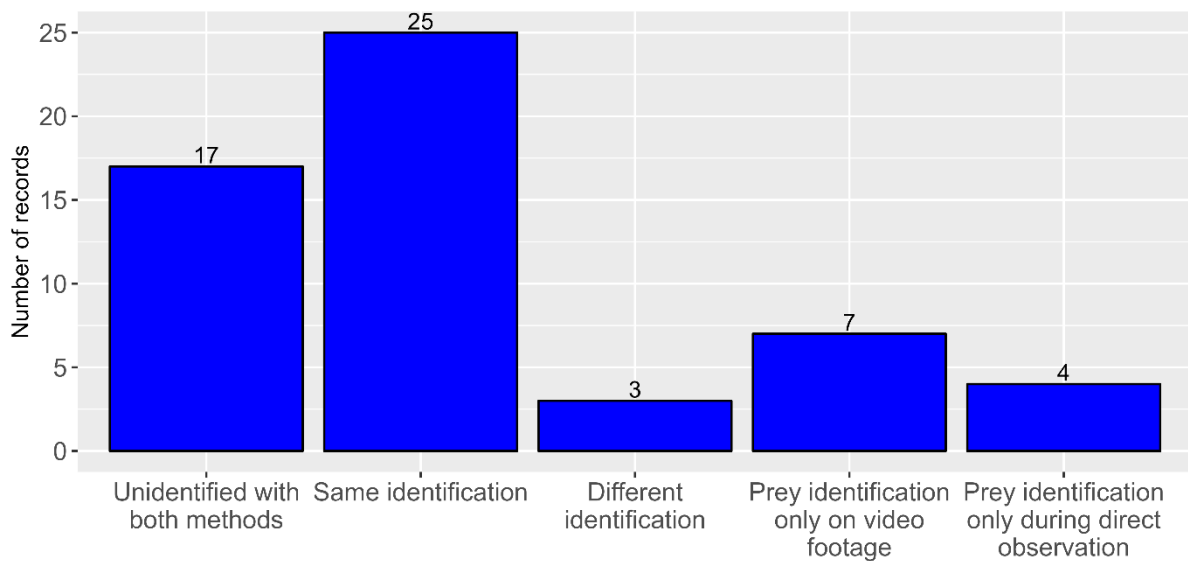


Figure 4.7. A comparison of the results of prey identification made using contemporaneous field observation and video footage captured on GoPro (number of feeding events compared = 56)

Prey size estimates obtained from direct observation and by review of video footage were identical in 39% of recorded chick feeds and differed in 20% of feeds. In 41% of feeds no size estimate could be determined using one or both methods (Figure 4.8). The mean difference in estimated prey size between methods was 0.3cm (range 0 to 0.76 cm).

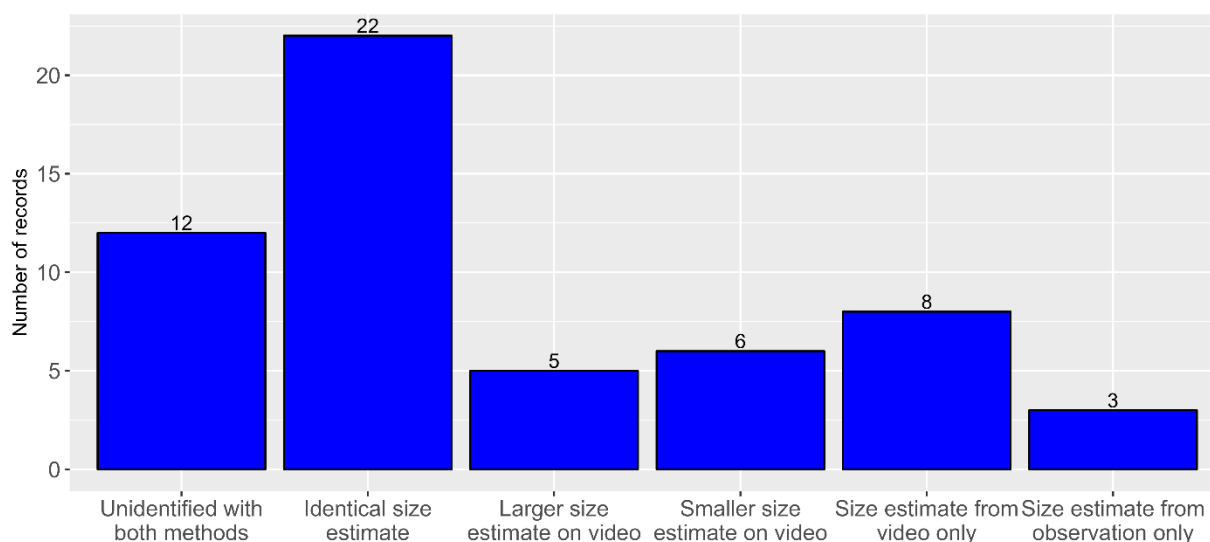


Figure 4.8. A comparison of prey size estimates made using contemporaneous field observation and video imagery from GoPro (number of feeding events compared = 56)

4.5 Discussion

4.5.1 Use of video footage to validate the results of field observations

Due to issues with the performance of camera traps it was possible to validate only a small number of chick feeding records collected in the field. Despite the small sample size, the available feeding records suggest that there is a high degree of consistency in the identification of prey types and estimated prey length regardless of whether data are collected in the field or through a review of video images. The results from the review of GoPro footage of chick feeding taken in 2022 also support this view.

When undertaking timed feeding observations in the field, prey items were only recorded at the taxonomic level of family. This reflects the small size of the prey items provisioned to Little Tern chicks and the practical difficulties involved in identifying clupeids and Sandeel to species level without access to physical specimens. Video footage, including imagery captured by camera traps only a few metres from chicks, did not allow for any more detailed taxonomic classification of prey items than did field observations. However, these results suggest that, at least at the level of the individual recorder, the choice of data collection methodology does not seem likely to add any additional bias to data collection.

4.5.2 The use of video footage in Little Tern feeding studies

Despite the difficulties encountered in using camera traps to capture contemporaneous footage of chick feeding recorded through field observations, the general patterns of diet composition and of prey size distribution obtained using the two data collection methods were similar. The only significant difference found in diet composition was a lower proportion of unidentified prey items obtained when examining camera trap footage. This reduction in unidentified prey appeared to increase the recorded proportion of clupeids during 2017 and 2018, and the proportion of Sandeel in 2018 but these differences were not statistically significant and did not alter the broad conclusions about the relative importance of different prey types within any one year. Similar, there was no statistically significant difference found in the mean estimated size of prey recorded using the two methodologies, with the exception of clupeids in 2019. In that instance the difference in mean size was only 0.27cm which given the prey sizes are only an estimation is unlikely to be ecologically significant.

There are many practical difficulties in studying Little Tern and the use of timed feeding observations to monitor chick diet can be constrained by the time available to site wardens at breeding colonies. At other locations such as Langstone Harbour in Hampshire, one of the colonies from which diet information was made available through the Little Tern Recovery LIFE project (see Chapter 2), the use of direct feeding observations may not be possible due to issues with access or bird disturbance. The number of prey records obtained from camera trap footage is generally good when compared with the results of direct feeding observations. The poorest year in terms of data from camera trapping was 2018 still managed to produce 73 individual prey records, which is more than was obtained by direct observation by the LIFE Project in six of the 12 colonies studied.

The results presented in this Chapter suggest that the use of camera traps can be a valid way of passively collecting data on chick diet in the absence of direct surveys, or as a means of supplementing direct surveys. In contrast to the use of camera traps in studies of prey composition, the results presented here suggest that camera traps

persistently fail to capture a percentage of chick feeds and so may not be appropriate for use in studies of rates of food delivery to chicks.

The camera traps deployed at Long Nanny were subject to a number of practical difficulties which affected their use for collecting chick feeding data. The short time windows available for setting out or moving camera traps at Long Nanny meant that any issues were often not detected until devices had been in place for several days and not possible to rectify until some days after that. The most common issues involved the timing and location of trap placement. Some of these issues involved the original choice of location for trap placement but more frequently involved the movement of chicks to new locations within the colony. Low battery life was also a significant issue in 2019 and led to lower than anticipated rates of data capture.

The collection of GoPro footage via digi-scoping was trialled in 2022, to investigate whether it offered an alternative to camera trapping which could be more flexible and responsive to changes in chick location. The data obtained indicate that, in contrast to camera trapping, the majority of chick feeds recorded during field observations were also captured on contemporaneous video footage. Those feeds which were not present on the video footage were missed were of older, mobile, chicks which were fed outside of the field of view of the recording device. This suggests that for younger, less mobile, chicks the use of digi-scoped video provides an alternative mechanism for collecting data on feeding rates. In common with camera trapping there appeared to be good agreement in prey identification and estimated prey size when compared with contemporaneous field records. In addition, review of the digi-scoped footage provided two additional feeding records of chicks which were not included in timed feeding observation (on both occasions from older mobile chicks) and picked up additional feeding records of chicks which were not included within the timed feeding observations but were present within adjacent areas. Digi-scoped images were less successful than camera trapping in providing a positive identification of prey items although still appeared to provide a minor improvement in the number of prey identifications. However, this lower rate of prey identification may have been the result of the long distance from the observed chicks in the majority of recordings and from

lower image quality due to wind shake and heat hazes. Further investigate into the influence of distance into the ability to identify prey would be useful but was not possible within the timescales available for this work.

Digi-scoping also differed from camera trapping in the timescales over which images were collected. Camera trapping allows imagery to be collected over a 24-hour period across several days although only when triggered by bird movement. In contrast, digi-scoping takes place over a shorter defined time period, limited by battery life, storage capacity, and available day light. Both approaches require an investment of time to review footage and extract feeding records. The time taken to review digi-scoped video is at least equivalent to the time taken for direct observations in the field and offers no time savings when compared to direct observation. However, it does allow the time commitment to be deferred to a later date, which for staff in breeding colonies may always greater flexibility in how they use their available resources.

No reference specimens were collected as part of the study so it was not possible to independently verify how well prey identification or size estimation from either field observation or review of video footage matched the true size and identity of food item being observed. While at the level of the individual observer there appeared to be good agreement between methods in prey identification and prey size estimation, the potential issues of consistency and bias between individuals, as identified by Cezilly and Wallace (1988), Goss-Custard *et al.* (1987) and Lee and Hockey (2001), still remain. Use of photographic images to provide a proxy for voucher specimens may be one potential method to assess observer variation in situations where a number of individuals are involved in data collection. Gaglio *et al.* (2017) have produced a methodology for estimating the size of Anchovy *Engraulis encrasicolus* from photographs as part of a study into the diet of the Greater Crested Tern *Thalasseus bergii*. A useful future line of research might be to develop a similar methodology for estimating the size of common prey species of UK tern species.

To conclude, these results show a potential role for video capture in future Little Tern feeding studies, particularly as a way of supplementing more traditional means of data

collection. The means of image capture used will depend on local circumstances and on the research question being posed with camera traps being of potential use in studies of diet composition, particularly in locations where direct feeding observations are not possible, while use of digi-scoped video footage is likely to be of greater use in studies of chick feeding rates.

Chapter 5. Foraging behaviour of Adult Little Terns: a comparison from two colonies

5.1 Abstract

An understanding of the core foraging areas used by Little Terns around their breeding colonies is important for protection of key feeding areas and can give insights into potential impacts of any future changes in prey availability. Here, I made observations of adult Little Tern at locations around breeding colonies, at Long Nanny in Northumberland and at Seaton Carew on Teesside, with the aim of understanding the factors influencing the use of the coast by foraging birds and to document any differences in foraging behaviour between the two locations.

I used Generalised Linear Models to investigate the factors which influenced the numbers of Little Tern recorded during bird counts at observation points around the two colonies. There was evidence that tidal state influenced the numbers of foraging birds seen at both locations, although different tidal states were associated with peak numbers at the two locations. Numbers of Little Tern were influenced by wave state and estimated air temperature at both colonies. Foraging distances and distributions of adult birds differed strongly between the two locations.

I discuss the possible reasons for these differences and what they might suggest about available food resources at the two locations. I also discuss potential additional future areas of research including the use of remote tracking of birds.

5.2 Introduction

Effective conservation of mobile organisms requires an understanding of their movement and habitat use (Ronconi *et al.* 2022). For seabirds, knowledge of foraging behaviour and locations has been applied both to define the boundaries of Marine

Protected Areas and to assess the possible environmental impacts of proposed new activities or developments within the coastal zone (Donazar *et al.* 1993, Lascelles *et al.* 2012, Thaxter *et al.* 2012).

As central place foragers, seabirds must make a number of trade-offs during the breeding season between meeting their own energy needs and that of their growing offspring. These can influence foraging choices for food, including decisions on foraging distances and habitat use. Coastal waters are a highly dynamic environment with regular variations in tide, water depth, and turbidity (Fijn *et al.* 2017). The distribution of prey species may be changeable and patchy so seabirds need to be able to adapt their foraging strategies in response to cues in their environment which may indicate the presence of available prey (Darby *et al.* 2022, Urmy and Warren 2018). Such environmental cues may be biotic or abiotic and a well-established body of literature which identifies the impacts of factors such as wind, turbidity or currents have on seabird foraging behaviour (Eglington and Perrow 2014).

Little Tern *Sternula albifrons* is a single prey loader (a species only able to carry one prey item at a time) which feeds in shallow waters typically less than 1m in depth in areas close to shore (Fasola *et al.* 2002). The foraging range of adults from colonies is smaller than that found in other UK Tern species (Parsons *et al.* 2015). Thaxter *et al.* (2012) quote a mean maximum range of 6.3km, although they express low confidence in this assessment due to data limitations. Eglington and Perrow (2014) have noted that most studies indicate a foraging range of less than 4km of nest colonies. There is evidence that foraging range differs between the egg incubation and chick feeding periods, with adults foraging closer to their breeding colony during the chick feeding period (Eglington and Perrow 2014). Colony size and density appears only to have a weak influence on foraging range (Parsons *et al.* 2015).

Within the UK, studies of foraging locations of adult Little Tern have largely concentrated on quantifying foraging extent around colonies, linked to the identification of boundaries for Marine Protected Areas (e.g. Parsons *et al.*, 2015), rather than investigating foraging on a fine scale. This is partly due to the more restricted inherent range and lack of

habitat data at a suitable resolution or location (Parsons *et al.* 2015). Use of telemetry to record movements and location is less commonly used on Little Tern than for other bird species, with the exception of work carried out by Perrow *et al.* (2006). This is in part because until recently there has been limited access to radio tracking devices or geolocators which are lightweight enough to be used on Little Tern and in part because of the rigorous licencing requirements for tagging of Little Tern and the need to demonstrate why less invasive methods of data collection cannot be used.

This current study looks at foraging ranges and locations of adult Little Tern at two colonies in the North East of England: Long Nanny in Northumberland and Seaton Carew in Hartlepool. The extent of adult foraging ranges of birds from the Long Nanny colony has previously been mapped through the work of Parsons *et al.* (2015) but no attempt to identify bird usage within that wider area has previously been attempted. The colony at Seaton Carew is only known to have been used by breeding Little Tern since 2019 (RSPB 2019a) and no information about the extent of adult foraging from the colony is available.

The aim of this study is to determine range and core foraging areas by Little Terns around Long Nanny and Seaton Carew colonies and compare differences between the two.

Due to the logistical, licencing, and welfare issues inherent in using tracking devices on Little Tern, the study has been carried out using shore-based observations of birds. However, it is hoped that the work can be used to identify future research questions for which tracking of birds may be the most appropriate method of data collection.

5.3 Methods

5.3.1 Study Colonies

This study looked at the foraging locations of adult Little Tern in the area surrounding two breeding colonies: Long Nanny in Northumberland and Seaton Carew near Teesside. A full description of both colonies is given in Chapter 1, Section 1.5.

In addition to the main breeding colony at Seaton Carew, a small satellite colony of 2-4 pairs of scraping Little Tern established themselves at the north end of North Gare beach (1.8km from the main colony). There were also some early attempts to scrape at the former breeding colony at Crimdon (approximately 7km north of Seaton Carew) but these were abandoned before the start of June (Durham Wildlife Trust 2021, RSPB 2021).

5.3.2 Field observations

Shore-based observations of the use of inshore waters by adult Little Terns were undertaken on areas of coast surrounding the Long Nanny colony in Northumberland and the Seaton Carew colony in the lower Tees Valley. Counts of adult birds were collected using a combination of timed observations from observation points (Figures 5.1a and 5.1b) and from walks along sections of beach. Observations at Long Nanny were predominantly made during 2022 (21st May to the 23rd July) with some field work also occurring during 2018 (1st June to 13th July) and 2021 (2nd June to the 7th July). Field work at Seaton Carew took place in 2021 between the 16th June and 24th July.

Observations at Long Nanny spanned the period from before egg hatching until the start of chick fledging. Observations at Seaton Carew commenced after the first chicks in the colony had hatched until the start of chick fledging. Observations were carried out between 10am in the morning up to 8pm in the evening. At Long Nanny, 69.5% ($\pm 7.6\%$) of fixed-point observations were carried out between 10am and 3pm (range 46.6% to 96.6%) and 80.1% ($\pm 4.8\%$) of beach walks were carried out in the same period (range = 66.7-100%). At Seaton Carew, 79.7% (± 4.0) of fixed-point observations took place between 9am and 3pm (range 55.6 – 100%) and 90.1% ($\pm 7.6\%$) of beach walks were commenced during the same period (range = 73.6 – 100%). A further breakdown of recording effort at both sites is provided in the section 5.6 appendices (Tables 5.A1 to 5.A4).

All observation points had an unobstructed view of the coast and were chosen at points to the north and south of breeding colonies in areas of public access. During 2018 observations were undertaken for periods of one hour ($n = 13$). This was reduced in

subsequent years to allow for observations to be collected from a greater number of points within the time available. The majority of observations were made for periods of 20 minutes, with a small number ($n = 17$) of observations in 2021 and 2022 extended up to 30 minutes when foraging activity was still ongoing at the end of a 20-minute period. Locations for fixed point locations are shown in Figures 5.1a and 5.1b and described in more detail in Tables 5.A1 and 5.A3 (section 5.6).



Figure 5.1a. Locations of observation points from where data were collected on foraging behaviour of Little Terns in the areas surrounding the Long Nanny.

Observations at Long Nanny were carried out during May to June in 2018, 2019, 2021, and 2022. See Table 5.A1 (section 5.6) for a breakdown of observation effort between years. Base map attribution: *Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community*



Figure 5.1b. locations of observation points from where data were collected on foraging behaviour of Little Terns in the areas surrounding the Seaton Carew colony near Hartlepool. Observations were carried out during May to July 2021. See Table 5.A4 (section 5.6) for a breakdown of observation effort between years. Base map attribution: Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Beach walks were undertaken on defined sections of the coast. The chosen section of beach was walked and observations of any sightings of Little Tern were recorded. Walks were undertaken on the shore itself where possible or from adjacent footpaths where this was not possible. A series of regular stopping points were identified on each section of coast which were observed for 5-minute periods. Birds seen during walks between points were also recorded. At Long Nanny, seven sections of beach were walked in the area between Seahouses Golf Course, 4km to the north of the colony to Dunstan Steads, 5.4km south of the colony. Of these, six sections of coast were walked less regularly. The less regularly walked section was the short (0.5km) section of shore immediately in front of the colony which was difficult to access at some stages of the tide without causing disturbance to nesting birds. Due to the more developed nature of the coast around Seaton Carew walks were only undertaken in three areas covering

Hartlepool Bay and on North Gare beach, extending 2.9km north of the colony and 2.8km to the south. All distances are measured as the shortest distance between two points and do not take into account the likely route taken by birds along the shoreline. Details of beach walk sectors are given in Tables 5.A2 and 5.A4 (section 5.6).

All Little Terns sighted during timed observations or beach walks were recorded and a note made of their location, behaviour and direction of travel. Behaviour was classified as falling into one of the following categories:

- Locally foraging – birds hovering or actively diving for food or actively searching for food in the location being observed
- Birds in passage – birds flying through an area but showing no signs of current foraging behaviour in the location.
 - Also included in this category were birds which had been foraging outside of the area under observation and which were returning to the colony carrying food in their bills. A separate note was also made of these. Where possible the prey being carried was identified to Family. Number of birds passing through carrying food are recorded in Tables 5.A5 and 5.A6 (section 5.6)
- Loafing birds – birds resting on sand or rocks

For each beach walk or timed observation the following information was also recorded:

- Estimated wind speed (Beaufort Scale)
- Wind direction
- Estimated sea state (Douglas Sea Scale)
- Estimated cloud cover in oktas
- Estimated air temperature (taken from local online weather forecast) and assigned to bands of 10-15°, 15-20°, and 20° or more
- Precipitation

5.3.3 Use of the lower Long Nanny Burn

Separate observations of Little Tern usage of the lower section of the Long Nanny Burn were made using timed observations from viewpoints upstream of the footbridge (55°32'15.24"N, 1°38'32.02"W) and from the dune ridge to the south of the colony (55°32'16.52"N, 1°38'15.67"W). See Figure 5.1 a. These were combined with observations from the coastal viewpoint at the mouth of the Burn (55°32'29.37"N, 1°38'7.96"W) to gather data on the numbers and locations of foraging birds. Due to access restrictions, it was not possible to assess any usage of the higher sections of the Long Nanny Burn.

5.3.4 Modelling the presence of Little Tern

Generalised Linear Models (GLMs) with a Poisson error structure were used to investigate the factors influencing the counts of Little Tern (both foraging and overall, see below) made at observation points. The predictors included within the model were location, tidal stage, sea state, and estimated air temperature. Data on wind speed were also collected as part of observations but were not included in the model due to interaction with sea state, with roughness of the sea being influenced by local wind conditions. Data on rainfall during were not included in the model due to a low range of conditions present during observations, with rain recorded during two of the fieldwork days at Seaton Carew and on four of the fieldwork days at Long Nanny. Observation length (in minutes) was used as an offset in the model. Two models were produced for both Long Nanny and for Seaton Carew. The first model used the overall numbers of Little Tern recorded at observation points (excluding loafing birds) as the response variable, while the second model used numbers of locally foraging Little Tern as the response variable.

Tidal stage was defined as High, Low, Rising or Falling based on reference to published Tide Tables for the closest port or harbour to the colony. High and low tides were taken as lasting one hour either side of the time of low and high tide. Sea State was expressed as being either "calm-slight" (Douglas Sea Scale values 1 to 3) or "moderate" (Douglas Sea Scale values 4 and 5). Air temperature was taken from local weather forecasts and expressed as being either less than 15°, 15-20°, or greater than 20° at Long Nanny. At

Seaton Carew only two observation periods included estimated temperatures about 20°C so the categories less than 15°C and more than 15°C were used.

5.3.5 Foraging Habitats

Records of locations of foraging Little Terns at Long Nanny were compared with a with available habitat mapping from the “Marine Designated Site Features Open Data (England)” page on the www.data.gov.uk website (Natural England. 2024). Little Tern sightings were broadly classified as either rocky reef or on soft sediment.

It could not be established that each foraging record of Little Tern represented a unique individual and there was some evidence to suggest that some records were return foraging trips by the same or a small number of individuals. Therefore, because of the risk of pseudo-replication in the data, no statistical analysis of foraging within different habitats was undertaken. Likewise no attempt was made to produce a habitat preference index, such as Jacob’s Preference Index, to further analyse habitat usage by birds. These was due to uncertainty on how most appropriately to define the seaward extent of the area used by Little Tern and because the high risk of pseudo-replication.

There was limited habitat diversity in the area around the Seaton Carew colony, with the coast being dominated by soft sediment with only small areas of rock or artificial hard structures. For this reason, no analysis of relative use of different foraging habitats was undertaken.

5.4 Results

5.4.1 Little Tern Foraging around the Long Nanny colony

A total of 148 timed observations were made from six main observation points and 72 walks undertaken across seven sections of beach. Little Terns were recorded at all observations points and on all sections the coast walked (Tables 5.1a and 5.1b), although birds were not consistently present at any single location. No birds were recorded at a distance greater than 3.6Km north of the colony or 5.4km south of the

colony (at Dunstan Steads, the southernmost observation point and the southern limit of the beach walks). Only a single record of a Little Tern flying into view from the south of Dunstan Steads was made, suggesting that birds did not regularly use the coast south of this point.

The frequency of sightings at each observation point ranged from 0.02 to 0.29 Little Tern/minute of observation, with birds most frequently observed within 0.5km of the breeding colony (Figure 5.2). The highest frequency of Little Tern sightings from beach walks were made on Embleton Bay (0.08 Little Tern/minute) and on the colony shore (0.13 Little Tern/minute).

Table 5.1a. Summary of sightings of Little Tern at individual observation points at Long Nanny. Observations points listed from the most northern to the most southern. Visits were made during 2018, 2021 and 2022. See Table 5.A1 (section 5.6) for a breakdown of recording effort by year.

Observation Point	Distance from Colony (Km)	Number of observation periods	Total duration of observations (mins)	Mean duration of observations (minutes \pm se)	% of observation with Little Tern	% of observations with locally foraging Little Tern
Annstead Rocks	3	14	300	21 \pm 1.0	57%	43%
Beadnell Harbour	1.4	21	420	20 \pm 0.0	52%	33%
Mouth of Long Nanny Burn	0.2	30	590	20 \pm 0.3	97%	37%
Southern end of colony	0.45	25	510	20 \pm 0.7	73%	8%
Football Hole	2	27	585	22 \pm 0.7	52%	37%
Dunstan Steads	5.4	31	633	20 \pm 0.3	32%	32%

Table 5.1b. Summary of sightings of Little Tern with individual beach walks at Long Nanny. Sections of beach are listed from the most northern to the most southern. Beach walks were made during 2021 and 2022. See Table 5.A2 (section 5.6) for a breakdown of recording effort by year.

Section of beach	Number of walks	Total duration (mins)	Mean walking rate (km/min \pm se)	% walks with Little Tern	% walks with locally foraging Little Tern
Beadnell Haven to Golf Course	11	659	0.036 \pm 0.002	36%	36%
Beadnell Harbour to Beadnell Haven	13	507	0.03 \pm 0.005	38%	38%
Beadnell Bay North	14	445	0.04 \pm 0.003	57%	43%
Colony shore	4	47	0.04 \pm 0.01	75%	0%
Beadnell Bay South	15	363	0.06 \pm 0.03	33%	7%
Low Newton to Beadnell Bay	4	117	0.05 \pm 0.01	50%	50%
Embleton Bay	11	600	0.05 \pm 0.01	73%	73%

Foraging behaviour by Little Terns was observed at locations along the coast from Dunstan Steads 5.4km to the south to Annstead beach 3.5km to the north of the colony. The numbers and presence of foraging Little Tern varied at all locations (Tables 5.1a and 5.1b). The frequency of foraging birds observed at each observation point ranged from 0.02 to 0.06 Little Tern per minute (median 0.03). The proportion of overall bird numbers which were recorded as actively foraging at observation points were lowest at locations closest to the colony, suggesting that most birds were travelling away from the colony to feed (Figures 5.2a and 5.2b). Foraging birds were also observed to use the Long Nanny Burn in the area behind the colony (see Section 5.4.1.1).

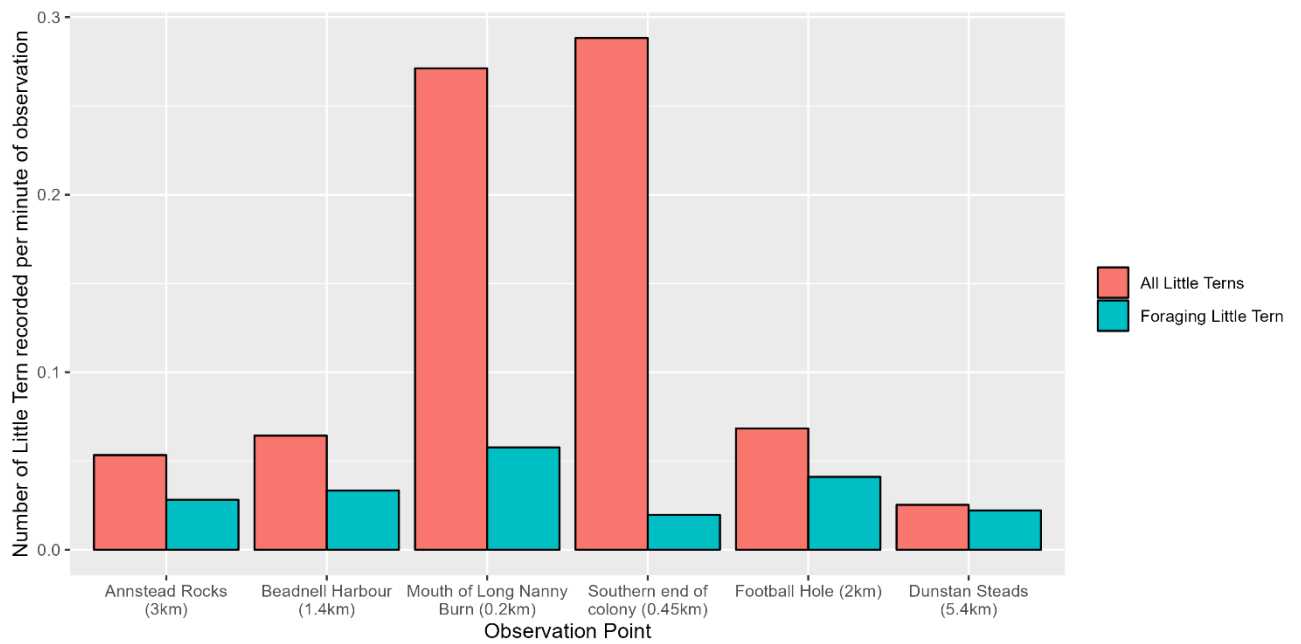


Figure 5.2a. Summary of sighting rate of Little Terns during fixed-point observations. Distance from colony is given in brackets. The category ‘all Little Tern’ includes sightings of all birds, including those flying through the observation area. ‘Locally foraging Little Tern’ are birds which were showing active foraging behaviour in the area. Birds which were observed flying through the area carrying food, and which had presumably been foraging at another location, were not included in the locally foraging category.

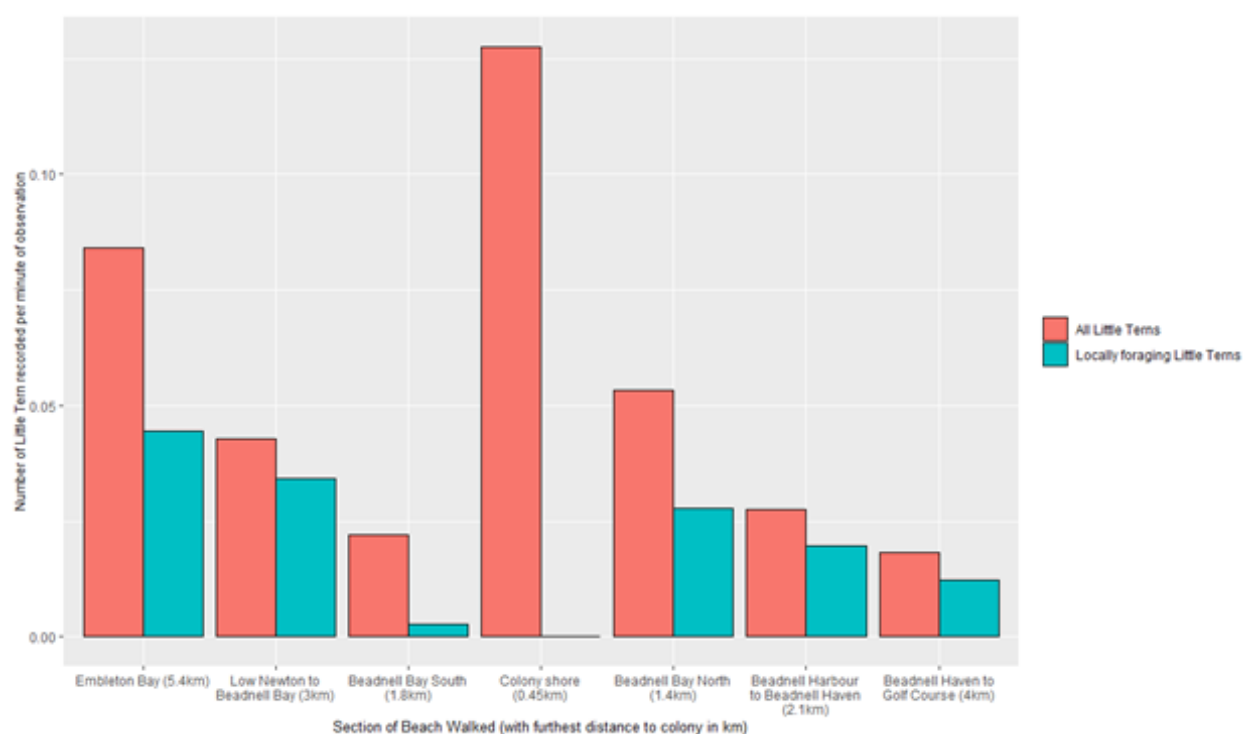


Figure 5.2b. Summary of sighting rate of Little Terns during beach walks. Furthest distance from colony given in brackets. See legend on Figure 5.2a for an explanation of categories.

Approximately 55% of all records of foraging Little Tern occurred within a 2km radius of the colony, with 87% of foraging activity being recorded within 4Km of colony (Figure 5.3).

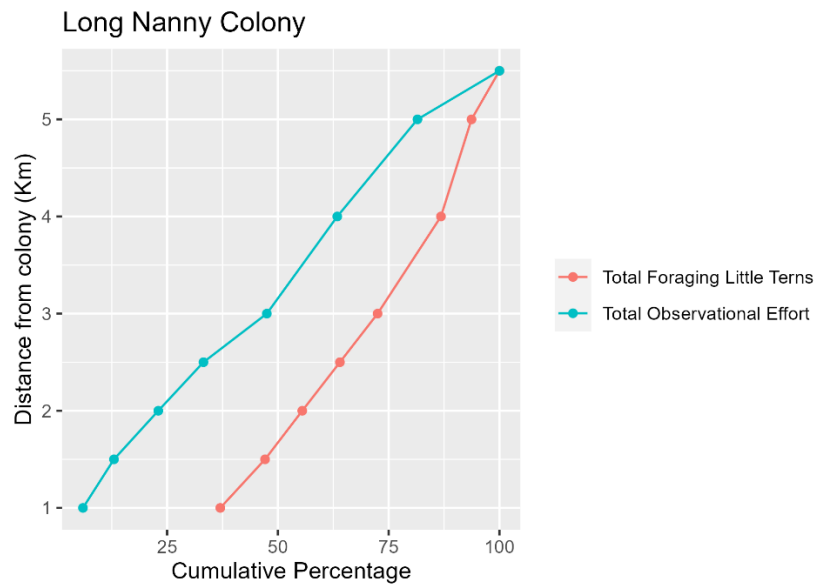


Figure 5.3. Cumulative sightings of foraging Little Tern by distance from the Long Nanny colony. Total observation effort includes time spent on fixed-point observations and beach walks.



Figure 5.4. Sightings of foraging Little Tern within the area between Dunstan Steads (Embleton Bay) and Seahouses Golf Course. Records are taken from fixed-point observations and beach walks from 2018, 2021, and 2022.

A detailed breakdown of the numbers of Little Tern recorded at fixed observation points and beach walks, their behaviour and direction of travel, is given in Table 5.A5 (section 5.6).

5.4.1.1 Little Tern foraging in the Long Nanny Burn

Records of Little Tern use of the lower reaches of the Long Nanny Burn, adjacent to or upstream of the colony, were made from 21 timed observations totalling 430 minutes. These were in addition to the 590 minutes of observations made at the mouth of the Burn (section 5.4.1). Foraging Little Tern were recorded in low numbers during eight of these observations. Birds were generally present as single individuals, with a peak number of three being seen at any one time.

Foraging Little Tern were not evenly distributed throughout the Burn with birds most frequently seen foraging around the area where the Long Nanny Burn meets the sea (Section 5.4.1). Other locations adjacent to or upstream of the colony were also used for feeding (Figure 5.5), with 10 foraging records being made from the north side of the Burn in the area south of the footbridge (55°32'15.39"N, 1°38'30.17"W), three records of foraging being made from the channels in the area of saltmarsh upstream of the footbridge (55°32'13.59"N, 1°38'31.76"W) and four foraging observations being made from a curve in the Burn near the northern edge of the colony (55°32'22.72"N, 1°38'21.06"W).



Figure 5.5. Little Tern foraging records from the Long Nanny Burn

5.4.1.2 Foraging habitat at Long Nanny

Foraging Little Tern were recorded 161 times during fixed-point observations and beach walks. Habitat mapping indicates an even split between rock and sediment habitats in the inshore waters of the study area and foraging records appear to suggest that similar numbers of records occurred from these two broad habitat types (Figure 5.4). However larger numbers of foraging birds were recorded on the Long Nanny Burn and the area where the Embleton Burn meet the sea than on other areas of soft sediment (Table 5.2). These two areas combined represent only a small proportion of the area of coast surveyed and cover an area of around no more than 12ha in size. Foraging on wider soft sediment areas of the open coast was less common and made up 42% of all foraging records. A map showing foraging records overlaid on a habitat map is given as Figure 5.A5. (section 5.6)

Table 5.2. Numbers of foraging Little Tern by broad habitat type at Long Nanny. Figures of locally foraging birds taken from observation point records (n = 97) and beach walks (n= 64). Extent of rock habitat is shown in Figure 5.4 and represents approximately 50% of inshore waters.

Habitat	Numbers of foraging Little Tern recorded
Rocky reef	77
Soft sediment	84
- <i>Associated with Long Nanny Burn or Embleton Burn</i>	49
- <i>Associated with wider coast</i>	35

5.4.2 Little Tern Foraging around the Seaton Carew colony

A total of 94 timed observations for Little Tern were made across ten fixed observation points, and 20 walks undertaken across three sections of beach.

The presence of Little Terns was recorded at least once on all of the sections of beach walked and at six of the ten fixed observations points (Tables 5.3a and 5.3b). With one exception Little Tern were observed at a distance greater than 1.6km to the north of the main Seaton Carew colony and a distance 2.8km to the south. This exception was a single observation of a foraging adult near Spion Kop (5.7km from the colony) was made on the 16th June 2021. This was assumed to be, but impossible to prove, a bird from the abandoned colony at Crimdon Dene.

Table 5.3a. Summary of information for fixed-point observations at Seaton Carew. Observations points listed from the most northern to the most southern.

Observation Point	Distance from Colony (km)	Number of observations	Total duration (mins)	Mean duration of observations (minutes \pm se)	% of observation with Little Tern	% of observations with locally foraging Little Tern
Spion Kop	5.7	8	161	20 \pm 0.1	13%	13%
Heugh	4.3	8	160	20 \pm 0.0	0%	0%
South of marina	3.2	8	160	20 \pm 0.0	0%	0%
North of colony	0.2	13	260	20 \pm 0.0	77%	54%
Mid-colony	0	8	160	20 \pm 0.0	100%	88%
South of colony	0.3	15	300	20 \pm 0.0	93%	60%
North Gare Pier	1.8	9	200	22 \pm 1.5	89%	22%
North Gare (South)	2.8	9	180	20 \pm 0.0	38%	25%
Seal Sands Entrance	2.8	8	160	20 \pm 0.0	0%	0%
South Gare	3.25	9	200	20 \pm 0.0	0%	0%

Table 5.3b. Summary of information for beach walks at Seaton Carew. Sections of beach listed from the most northern to the most southern.

Section of beach	Number of walks	Total duration (mins)	Mean walking rate (km/min)	% walks with Little Tern	% walks with locally foraging Little Tern
Hartlepool Bay (North)	5	384	0.04 ± 0.003	83%	68%
Hartlepool Bay (South)	7	208	0.06 ± 0.008	86%	54%
North Gare Beach	7	376	0.03 ± 0.004	86%	31%

The frequency of sightings of birds at each observation point ranged from 0 to 0.39 Little Tern per minute of observation (Figure 5.6a). Some large aggregations of loafing birds were seen on North Gare beach in mid-July (for example, 54 birds on the 19th July 2021). These were assumed to be non-breeding or post-breeding adults preparing for migration.

The frequency with which foraging Little Tern were seen at each observation point ranged from 0 to 0.2 Little Tern per minute of observation (median = 0.01). For beach walks the frequency of foraging birds ranged from 0.09 to 0.11 Little Tern per minute (median = 0.1) (Figure 5.6b).

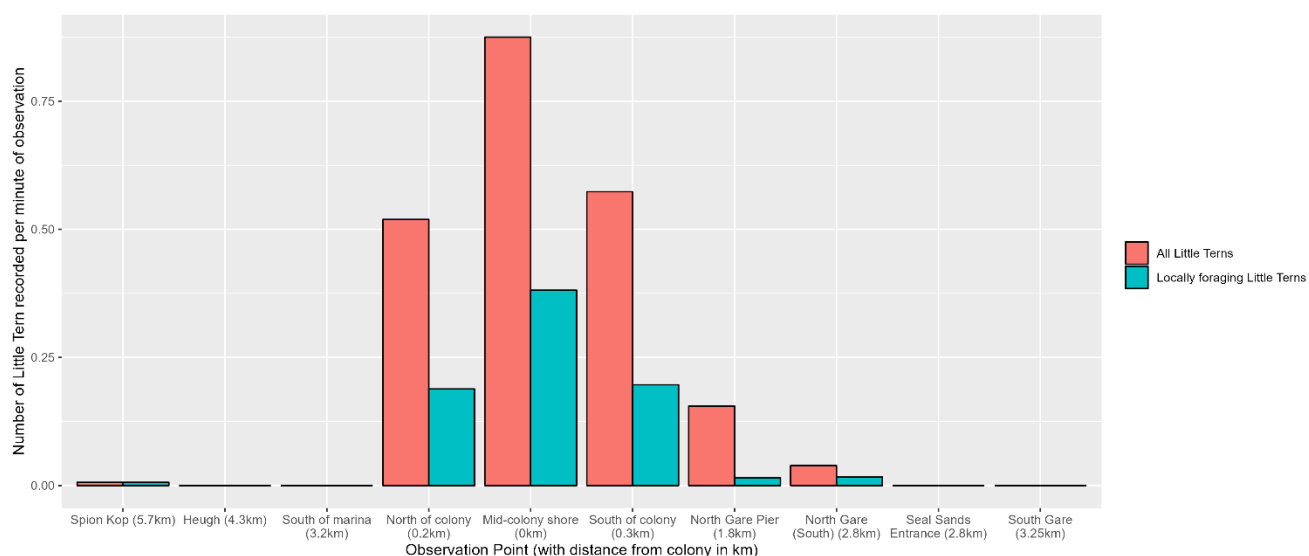


Figure 5.6a. Summary of sighting rate of Little Terns during fixed-point observations. Distance from main colony given in brackets.

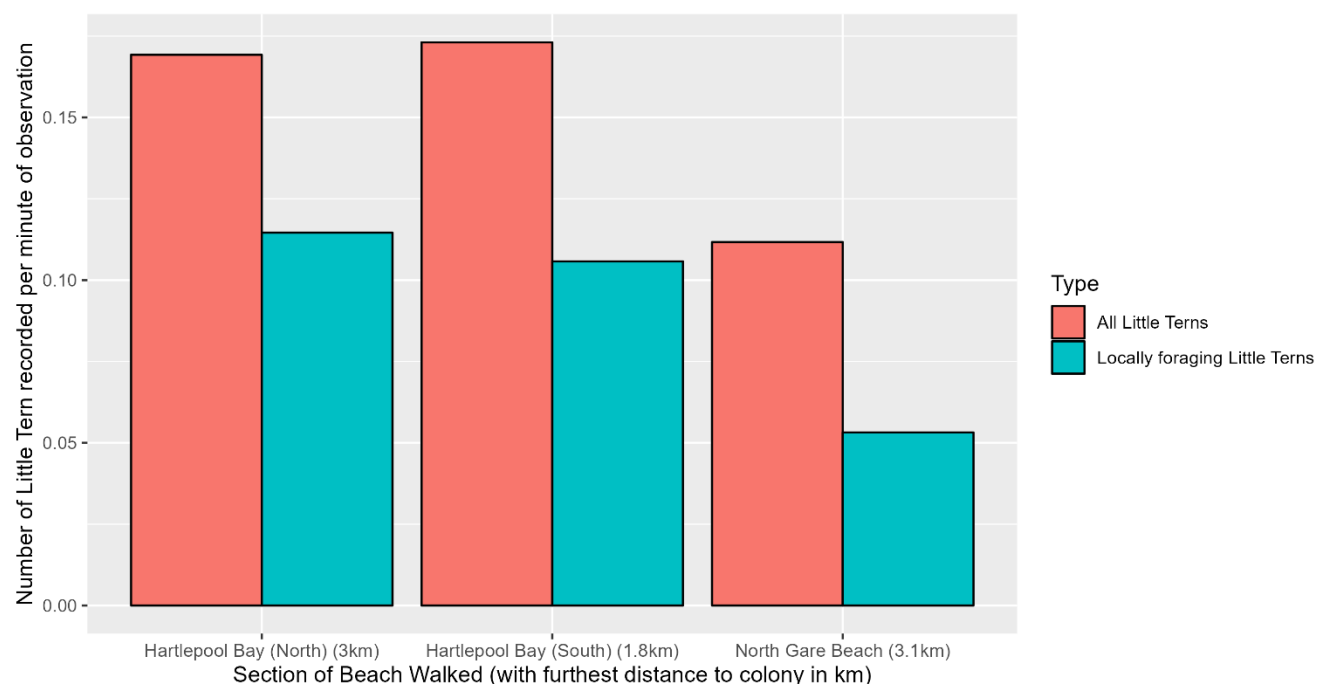


Figure 5.6b. Summary of sighting rate of Little Terns during beach walks at Seaton Carew. Furthest distance from main colony given in brackets.

The majority of foraging birds were seen feeding in the waters in front of or immediately adjacent to the breeding colony with approximately 85% of all sightings of foraging Little Tern being recorded within 1km of the Seaton Carew colony (Figure 5.7). Peaks of up to eight foraging Little Tern were also recorded in the waters adjacent to the rock

armouring along the north end of North Gare beach. It is likely that at least some of these birds were from the small satellite colony at North Gare.

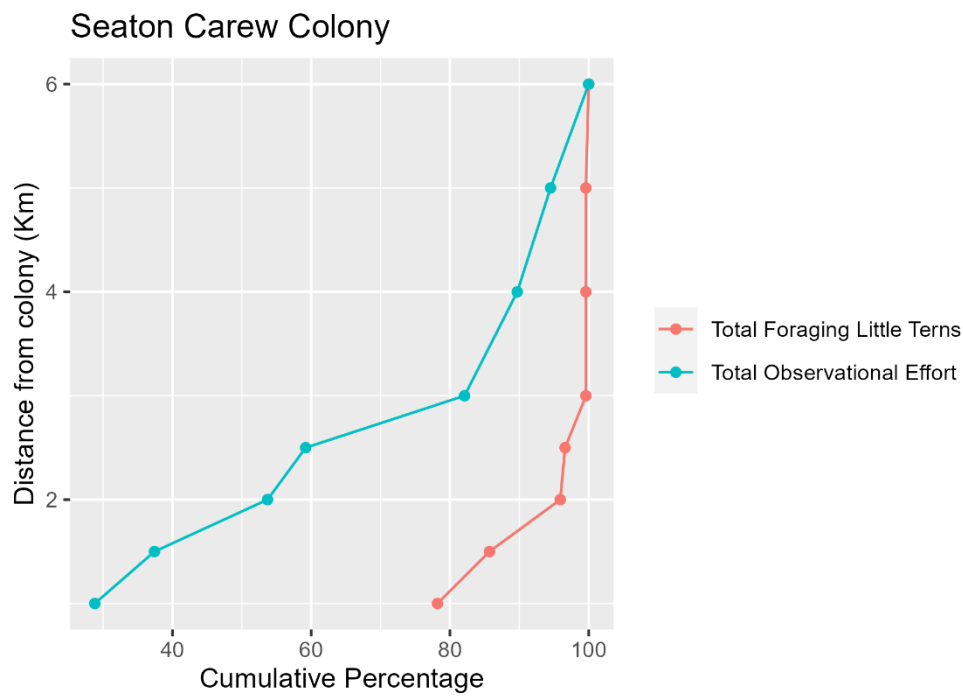


Figure 5.7. Cumulative sightings of foraging Little Tern by distance from the Seaton Carew colony. Total observation effort includes time spent on fixed-point observations and beach walks.

Marine habitats in Hartlepool Bay and North Gare are dominated by soft sediments with occasional small areas of rock. The distribution of foraging Little Tern appeared to reflect the distribution of underlying habitats and there was no evidence of selective foraging on any one habitat type (Figure 5.8).

A detailed breakdown of the numbers of Little Tern recorded at fixed observation points and beach walks, their behaviour and direction of travel, is given in Table 5.A6 (section 5.6).



Figure 5.8. Map showing location of sightings of foraging Little Tern within the area between Spion Kop and South Gare (NB: not all areas of coast between these points visited due to access restrictions)

5.4.3. Factors influencing bird presence

Generalised Linear Models were used to investigate the factors which influenced the numbers of Little Tern recorded as part of bird counts at fixed observation points in the areas around the Long Nanny and Seaton Carew tern colonies (Table 5.4). The numbers of Little Tern recorded at observations points around both colonies appear to have been significantly influenced by location, tidal stage, Sea State and estimated air temperature. There was evidence that all of these factors also influenced the numbers of foraging Little Tern observed around Seaton Carew, while at Long Nanny the model indicated that the numbers of foraging birds observed were only influenced by tidal stage and sea state, with no significant difference in numbers being found between observation points.

The variation in Little Tern numbers with location appears to be linked to distance from the colony with greater numbers of birds being seen at locations nearest to the breeding location (Figures 5.2a, 5.2b, 5.6a and 5.6b).

Table 5.4. Results of model results looking at factors influencing numbers of Little Tern seen at observation points at Long Nanny and Seaton Carew.

		χ^2	df	p-value
Long Nanny				
<i>All Little Tern</i>	Location	237.9	6	< 0.001
	Tidal stage	31.5	3	< 0.001
	Sea state	38.1	1	< 0.001
	Estimated air temperature	12.3	2	0.002
 <i>Foraging Little Tern</i>				
	Location	8.4	6	0.23
	Tidal stage	9.97	3	0.018
	Sea state	6.7	1	0.009
	Estimated air temperature	3.3	2	0.19
 Seaton Carew				
<i>All Little Tern</i>	Location	703.8	9	< 0.001
	Tidal stage	65.0	3	< 0.001
	Sea state	42.1	1	< 0.001
	Estimated air temperature	32.8	1	< 0.001
 <i>Foraging Little Tern</i>				
	Location	273.5	9	< 0.001
	Tidal stage	13.5	3	0.004
	Sea state	23.4	1	< 0.001
	Estimated air temperature	29.1	1	< 0.001

The influence of tide differed between the two colonies (Figure 5.9). At Long Nanny, the lowest sighting rate of birds (Little Terns seen per minute of observation time) were seen at low tide with high tide seeing the largest proportion of Little Tern per minute of observation. In contrast at Seaton Carew, high tide saw the smallest number of Little Tern sightings per minute of observation, while the highest sighting rate of foraging Little Tern were observed at low tide.

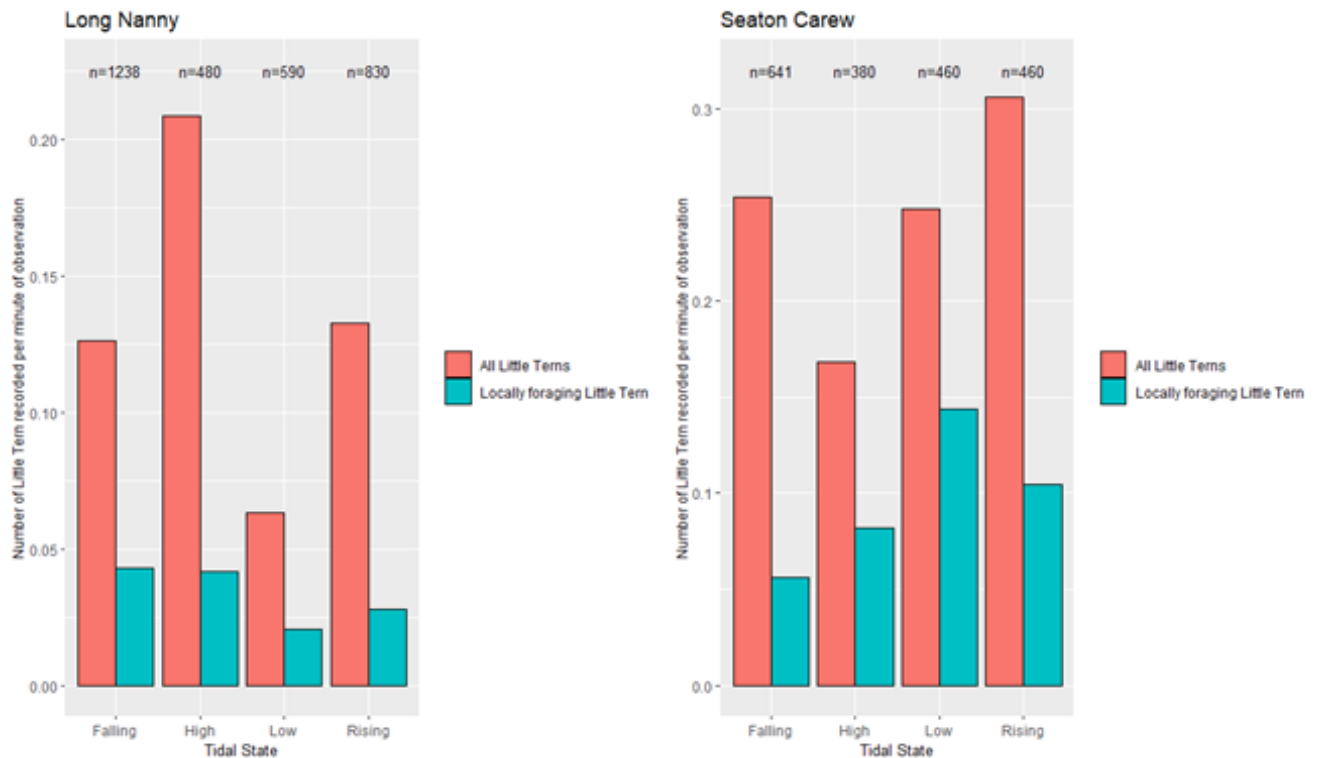


Figure 5.9. Variation in mean sighting rates of Little Tern at different stages of the tide. Figures exclude loafing birds. N= length of observation in minutes.

The results for variation with sea state were similarly mixed with Little Terns at Long Nanny being recorded at a higher rate during calm to slight sea conditions (Douglas Sea Scale 1 to 3) than during moderate sea conditions (Douglas Sea Scale 4 or 5). This pattern was reversed at Seaton Carew, although attention is drawn to the strong imbalance in observational effort between categories at both colonies (Table 5.5). At Long Nanny, higher estimated air temperatures appeared to be associated with greater sighting rates of Little Tern but had no detectable influence on sighting rates of foraging birds. At Seaton Carew, higher sighting rates of Little Tern appeared to be associated with lower estimated air temperatures, although again attention is drawn to the strong imbalance in observational effort between the two temperature categories used.

Table 5.5. Summary of differences in observed rates of Little Tern presence (Little Terns recorded per minute of observation) with Sea State and estimated air temperature at Long Nanny and Seaton Carew. Figures exclude loafing birds.

			Mean observation rate (Little Terns/minute ± se)	Total length of observations (mins)
Long Nanny				
<i>All Little Tern</i>	Sea state	Calm-Slight	0.16 ± 0.02	2438
		Moderate-rough	0.03 ± 0.009	600
	Estimated air temperature	>15 ^o C	0.08 ± 0.1	1318
		15 ^o to 20 ^o C	0.16 ± 0.03	1440
< 20 ^o C		0.2 ± 0.08	280	
Foraging Little Tern				
<i>Foraging Little Tern</i>	Sea state	Calm-Slight	0.04 ±0.007	2438
		Moderate-rough	0.02 ± 0.007	600
	Estimated air temperature	>15 ^o C	0.03 ± 0.009	1318
		15 ^o to 20 ^o C	0.03 ± 0.008	1440
< 20 ^o C		0.04 ± 0.03	280	
<hr/>				
Seaton Carew				
<i>All Little Tern</i>	Sea state	Calm-Slight	0.2 ± 0.05	1471
		Moderate-rough	0.4 ± 0.09	470
	Estimated air temperature	>15 ^o C	0.46 ± 0.1	410
		<15 ^o C	0.2 ± 0.04	1531
Foraging Little Tern				
<i>Foraging Little Tern</i>	Sea state	Calm-Slight	0.08 ± 0.02	1471
		Moderate-rough	0.14 ± 0.04	470
	Estimated air temperature	>15 ^o C	0.215 ± 0.06	410
		<15 ^o C	0.06 ± 0.02	1531

5.5 Discussion

This study used shore-based observation to determine the use by Little Tern of the coastal waters around two breeding colonies in the North East of England. The results indicated markedly different patterns of foraging being adopted by birds at these two colonies. Sightings of adult Little Tern at Seaton Carew mostly came from areas adjacent to the main breeding colony, with the majority of foraging birds being recorded within 2km the colony centre. In contrast, the distribution of sightings of adult Little Tern around Long Nanny was more dispersed and irregular and came from within greater distances of the colony. At both Seaton Carew and at Long Nanny, the overall numbers of Little Tern decreased with increasing distance from the colony, but at Long Nanny the numbers of activity foraging terns recorded did not appear to be influenced by distance.

The distribution of foraging birds can be expected to reflect both the distribution of available food resources and any energetic constraints in accessing those food resources (Bugge *et al.* 2010). The short maximum alongshore foraging distance of Little Tern record at Seaton Carew suggest that birds are able to access their necessary food requirements within the coastal waters immediately adjacent to the breeding colony and do not have to forage at great distances in order to meet their own energy requirements or those of their developing chicks. It has been suggested that food availability is the dominant factor determining the selection of colony location by Little Tern (Perrow *et al.* 2003). Little Tern is normally characterised by a high sensitivity to human disturbance (Brown and Grice 2005, Cabot and Nisbet 2013) and the presence of a good supply of prey items within a short distance of the colony may help to explain the choice of what might otherwise appear to be the sub-optimal breeding habitat of a heavily used recreational beach on urban Teesside.

The first breeding records of Little Tern at Seaton Carew come from 2019 so no existing estimates of the maximum foraging range of birds around the colony are available. The nearest comparable location is the nearby (and now abandoned) Little Tern colony at Crimdon Dene on the Hartlepool/County Durham border where Parsons *et al.* (2015) reported a maximum alongshore foraging extent of 5km north and south of the colony.

This would indicate a narrower foraging extent for birds at Seaton Carew, although the maximum foraging distances reported here are consistent with some of the shorter ranges identified by Parsons *et al.* (2015) at other UK colonies and it appeared that peak sightings of Little Tern around Crimdon were within 2km of the colony.

In contrast to Seaton Carew, Little Tern at Long Nanny foraged over a wider geographic area and their presence at any individual location was less predictable. While the overall numbers of Little Tern recorded from fixed-observation points decreased with increasing distance, modelling found no similar decrease in the presence of activity foraging Little Tern, suggesting that available food resources are dispersed spatially and/or temporally necessitating foraging birds to utilise a wide area of coast in order to meet their own feeding requirements and those of their chicks.

The maximum foraging range identified for birds at Long Nanny is consistent with that previously reported by Parsons *et al.* (2015) who undertook 4070 minutes of shore based observations around the site during 2009-2011 and recorded 518 Little Tern. These authors also found a small number of Little Tern foraging approximately 4km north of the colony, beyond the northern limit of the fixed-point surveys present here. Neither this study nor the Parsons *et al.* (2015) conducted observations further than 6km south of Long Nanny. While it is possible that there may be some use of the coast further south than this the results presented here suggest that this is a rare occurrence, with only a single recorded of a bird travelling into the survey point from the south. The density of Little Terns observed in this current study are also comparable with those of Parsons *et al.* with, for example, approximately 75% of total Little Tern sightings being found within 3km of the colony in both studies.

Little Tern were also recorded using the Long Nanny Burn on a regular basis, although generally small numbers. The foraging areas used by birds included the channels in the area of saltmarsh to the west of the colony. This saltmarsh area is outside of the boundary of the Northumberland Marine Special Protection Area (SPA) was designated in 2017 specifically to protect the foraging grounds used by breeding terns and other

seabird on the Northumberland coast (Defra 2017). Any future review of the SPA boundary should consider including this area.

A comparison of foraging records from Long Nanny with habitat mapping appeared to show that the distribution of birds was almost equally split between areas of rocky reef and areas of soft sediment. However, foraging Little Tern did not appear to be equally distributed within these habitats with what appeared to be distinct clusters in the locations of records (Figure 5.4). In particular, the numbers of records obtained from areas where coastal streams met the sea (such as the mouths of the Embleton Burn and the Long Nanny Burn) appeared to be disproportionately large compared to the area these covered (approximately 12 ha). This could not be tested statistically due to potential issues of pseudo-replication in the data but merits additional investigation. The number of records from the mouth of the Long Nanny Burn is likely to be caused, in part, by proximity to the colony. However, other areas equally close produce few if any records of foraging birds.

Inshore coastal waters are a highly dynamic environment where the distribution of prey species can be patchy and variable. Areas of rocky reef or tidal channels might be expected to experience high water flow velocities and turbulence at certain tidal stages, during which prey items are more likely to be exposed to surface feeding birds (Schwemmer *et al.* 2009). Such areas may be favoured by foraging seabirds either because they offer access to a greater quantity of prey than other nearby habitat or because they provide relatively predictable access to prey in an otherwise changeable environment (Urmy and Warren 2018). No similar comparison was made at Seaton Carew due to a lack of contrasting habitat types within the main Little Tern foraging area, the majority of intertidal and sub-tidal habitats consisting of sandy sediments. It is possible that there may have been other environmental variables such as water depth or the presence of subtidal sandbanks which influenced Little Tern foraging within this broader area but investigation of this was outside of what could be determined through shore-based observations. Further investigation would require improved habitat mapping and tracking of individual Little Terns through use of GPS or telemetry, to obtain precise foraging locations.

At both locations in this study, the overall numbers of birds recorded were significantly influenced by location, tidal stage, sea state, and air temperature. These same factors also appeared to influence the numbers of actively foraging Little Tern seen at Seaton Carew. Weather, tide and sea state have all been identified in previous study as influencing foraging behaviour and foraging success in seabirds (e.g. Becker *et al.*, 1993, Elliott *et al.* 2014, Pistorius *et al.*, 2015). Perhaps most notable was the lack of any significant difference in numbers of actively foraging birds at Long Nanny with viewpoint location. While the overall number of birds seen decreased with distance from the colony, the number of birds which were actively foraging remained at similar numbers at around 0.3 birds per minute. This provides additional support the suggestion that access to food suppliers at Long Nanny are more dispersed and less spatially predictable than at Seaton Carew. However, it should be noted that the number of foraging records used to support the production of the Generalised Linear Models was relatively low and that additional data would help to increase confidence in their outputs.

Another notable aspect of this study is that although tide and sea state both appeared to influence the numbers and locations of foraging adults at Long Nanny there was no evidence that these changes in foraging patterns are translated into any observable difference in the rate at which food is delivered to chicks (see Chapter 3), suggesting that foraging adults were adjusting their behaviour to provide a constant rate of food provisioning for their offspring. Further study would be needed to examine the linkages between observed patterns of parental foraging and observed patterns of chick provisioning. Such a study would probably require tagging and tracking of adult birds.

The results from Seaton Carew came from within a single year with no data available to indicate what, if any, inter-annual variation in foraging behaviour might occur. An additional complication was provided by the presence of addition a small number of breeding Little Tern at locations outside of the main Seaton Carew colony. Observations during the 2021 breeding season noted aborted attempts by some birds to scrape at Crimdon Dene during May, and the establishment of a small number of scraping birds

next to the North Gare breakwater during June. The record of a single foraging Little Tern at Spion Kop during May of 2021 is an obvious geographic outlier in the observations and it seems reasonable to suspect that this may have been a remaining bird from Crimdon Dene. It appears probable that some of the foraging Little Tern recorded from Hartlepool Bay and North Gare beach will have been birds from the small satellite colony at North Gare breakwater. However, given the small number of birds present at the satellite colony and its close proximity to Seaton Carew it seems likely that any impacts on the determination of maximum foraging range will have been negligible.

A number of other caveats need to be raised in connection to both Seaton Carew and Long Nanny. Overall the numbers of actively foraging Little Tern used to populate the modelling at both sites was low and it is likely that some individual may have been counted more than once if they made repeat foraging visits to a location within the same observation period. There was also no means available to determine whether the breeding status of the individual birds observed during surveys. Non-breeding individuals, individuals who are incubating eggs, and individuals who are rearing chicks may show different foraging ranges and behaviours (Eglington and Perrow 2014). Foraging data from Long Nanny are most likely to be affected by this potential issue as the status of the Little Tern present on the site varied across the years in which observations were made. However, the maximum distance at which birds were recorded was similar in each of the years of observation despite the different numbers of birds and likely different breeding status of the birds present in each year suggesting that, for the area of coast covered by surveys, there was little if any impact.

Foraging Little Tern appeared to be restricted to within 0.5 to 1.0km of the shoreline at both locations. This is in contrast Parsons *et al.* (2015) who reported that boat-based surveys showed a mean seaward extent for Little Tern at Long Nanny of distances exceeding 2km and a mean seaward extent at the now defunct Teesside colony at Crimdon of in excess of 3km. It is therefore possible that birds foraging beyond 0.5km were missed during shore-based observations due to lack of visibility. The seaward extent of foraging Little Tern remains an area meriting additional research but would

require either boat surveys or the use of telemetry, both of which were outside the scope of this present study.

The use of tracking devices such as radio tags, satellite tags and data loggers has been used extensively in seabird foraging research (Bernard *et al.* 2021) but guidelines on the recommended maximum weight of logging devices has meant that until recently there were few devices suitable for use with small seabirds such as Little Tern. In the UK the use of bird-mounted device also requires a licence from the Special Methods Technical Panel (SMTP) of the BTO Ringing Committee (Cook *et al.* 2023). Because of these issues this current project has relied solely on foraging observation collected through shore-based surveys. However, future use of tracking devices may have a role in helping to address any outstanding questions or uncertainties. In particular, the use of tracking devices may be able to provide fine-gained information about how individual foraging birds are utilising particular habitats or areas of sea, give greater insight into how far out to sea birds are foraging, and provide insight into the relationship between patterns of parental foraging and food provisioning of chicks.

5.5.1 Conclusions

The results presented in this study provide a comparison of alongshore travel distances at two contrasting Little Tern colonies in the Northeast of England. The majority of Little Tern at Seaton Carew could regularly be found foraging within less than 2km of the colony, suggesting that good food resources, sufficient to meet the needs of adult birds and their chicks, were available close to the breeding site. In contrast, alongshore foraging distances at Long Nanny were greater and the presence of Little Tern at any one location was less predictable suggesting that to meet the needs of themselves and their chick, birds needed to travel longer distances to find changing patches of high prey availability. A comparison of foraging records against habitat mapping for Long Nanny suggested foraging birds might be selective in the areas in which they fed, for example being apparently recorded in greater numbers on intertidal channels. It was not possible to test this statistically and further study is needed. No similar analysis of foraging habitat could be carried out at Seaton Carew as the majority of foraging

locations consisted of soft sediment and it was beyond the scope of the current study to investigate into linkage between foraging location and habitat variables, such as water depth or presence of subtidal sandbanks.

Data collection was undertaken solely using shore-based observations. There is scope for additional future work using tracking devices attached to adult birds. This would come with some logistical and licencing issues but could help to provide information about foraging locations and habitats at a finer-grain than is possible from shore-based observations alone and would help clarifying the extent of seaward foraging by Little Tern.

5.6 Appendices

Table 5.A1. Summary of observation points in the area around Long Nanny

Observation Point	Total Duration of observations (mins)	Duration of observations 2018 (mins)	Duration of observations 2021 (mins)	Duration of observations 2022 (mins)
Annstead Rocks	300	0	50	250
Beadnell Harbour	420	0	40	380
Mouth of Long Nanny Burn	590	0	60	530
Southern end of colony	510	0	70	440
Football Hole	585	0	90	495
Dunstan Steads	633	363	20	250

Table 5.A2. Summary of beach walks in the area around Long Nanny.

Section of beach (approx. length in km)	Northern Extent	Southern Extent	Total duration of walks (mins)	Duration of walks in 2021 (mins)	Duration of walks in 2022 (mins)
Beadnell Haven to Golf Course (2km)	55°34'33.88"N, 1°38'34.18"W	55°33'28.01"N, 1°37'48.29"W	659	168	491
Beadnell Harbour to Beadnell Haven (1.2km)	55°33'18.41"N, 1°37'41.82"W	55°33'2.60"N, 1°37'28.20"W	507	136	371
Beadnell Bay North (1.25km)	55°33'2.86"N, 1°37'31.04"W	55°32'29.67"N, 1°38'8.53"W	470	85	385
Colony shore (0.5km)	55°32'29.67"N, 1°38'8.53"W	55°32'9.67"N, 1°38'1.96"W	47	0	47
Beadnell Bay South (1.25 km)	55°32'9.67"N, 1°38'1.96"W	55°31'34.81"N, 1°37'20.44"W	363	0	363
Low Newton to Beadnell Bay (1.2km)	55°31'34.81"N, 1°37'20.44"W	55°30'53.77"N, 1°37'5.61"W	117	0	117
Embleton Bay (2.7km)	55°30'53.77"N, 1°37'5.61"W	55°29'39.51"N, 1°36'20.50"W	631	0	631

Table 5.A3. Summary of observation points and beach walk location near Seaton Carew.

Observation Point	Total Duration of observations (mins)
Spion Kop	161
Heugh	160
South of marina	160
North of colony	260
Mid-colony Shore	160
South of colony	300
North Gare Pier	200
North Gare (South)	180
Seal Sands Entrance	160
South Gare	200

Table 5.A4. Summary of beach walk location near Seaton Carew.

Section of beach	Northern Extent	Southern Extent	Total duration of walks (mins)
Hartlepool Bay (North)	54°38'48.25"N, 1° 9'44.78"W	54°38'4.02"N, 1° 9'44. 76"W	384
Hartlepool Bay (South)	54°39'24.08"N, 1°10'47.22"W	54°38'49.80"N, 1° 9'54.31"W	208
North Gare Beach	54°40'56.62"N, 1°11'55.21"W	54°39'38.71"N, 1°11'4.14"W	376

Table 5.A5. Summary of observation point records for the area around Long Nanny.

Location	Away from colony				Towards colony				No direction				
	Total Little Terns	In passage (All)	In passage (carrying food)	Foraging	Total Little Terns	In passage (All)	In passage (carrying food)	Foraging	Total Little Terns	In passage (All)	In passage (carrying food)	Foraging	Loafing
Annstead Rocks	4	0	0	4	5	3	2	2	5	0	0	3	2
Beadnell Harbour	22	13	0	9	2	0	0	2	3	0	0	3	0
Mouth of the Long Nanny Burn	53	35	1	18	83	78	43	5	22	15	2	3	4
Southern end of colony	24	21	0	3	122	115	81	7	1	1	0	0	0
Football Hole	25	8	0	17	13	8	0	5	2	0	0	2	0
Dunstan Steads	11	0	0	11	1	1	0	0	3	0	0	3	0

Table 5.A6. Summary of observation point records for the area around Seaton Carew.

	Away from colony				Towards colony				No direction				
Location	Total Little Terns	In passage (All)	In passage (carrying food)	Foraging	Total Little Terns	In passage (All)	In passage (carrying food)	Foraging	Total Little Terns	In passage (All)	In passage (carrying food)	Foraging	Loafing
Spion Kop	1	0	0	1	0	0	0	0	0	0	0	0	0
Heugh	0	0	0	0	0	0	0	0	0	0	0	0	0
South of marina	0	0	0	0	0	0	0	0	0	0	0	0	0
North of colony	66	31	0	35	54	54	26	0	14	0	0	14	0
Mid-colony	75	28	2	47	56	50	21	6	8	0	0	8	0
South of colony	72	43	3	29	72	63	28	9	24	3	0	21	0
North Gare Pier	18	17	1	0	6	5	1	1	4	71	0	8	63
North Gare beach (South)	2	1	0	1	3	2	1	1	56	1	0	1	54
Seal Sands Entrance	0	0	0	0	0	0	0	0	0	0	0	0	0
South Gare	0	0	0	0	0	0	0	0	0	0	0	0	0

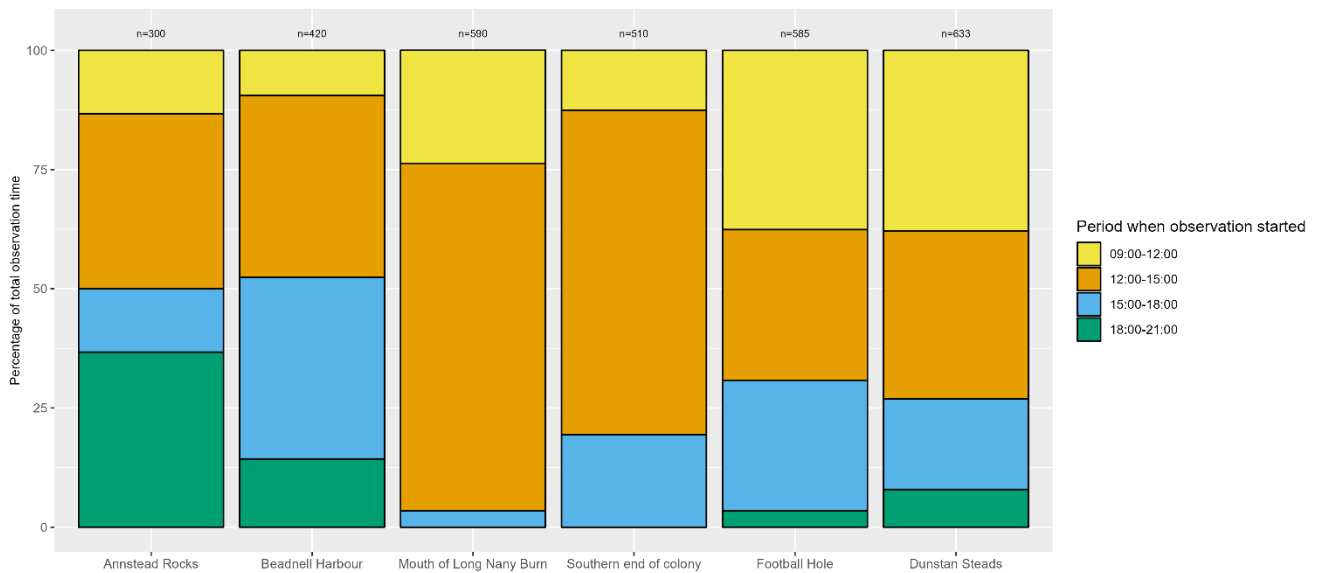


Figure 5.A1. Observation point recording effort at Long Nanny by time of day. N=total length of observations in minutes.

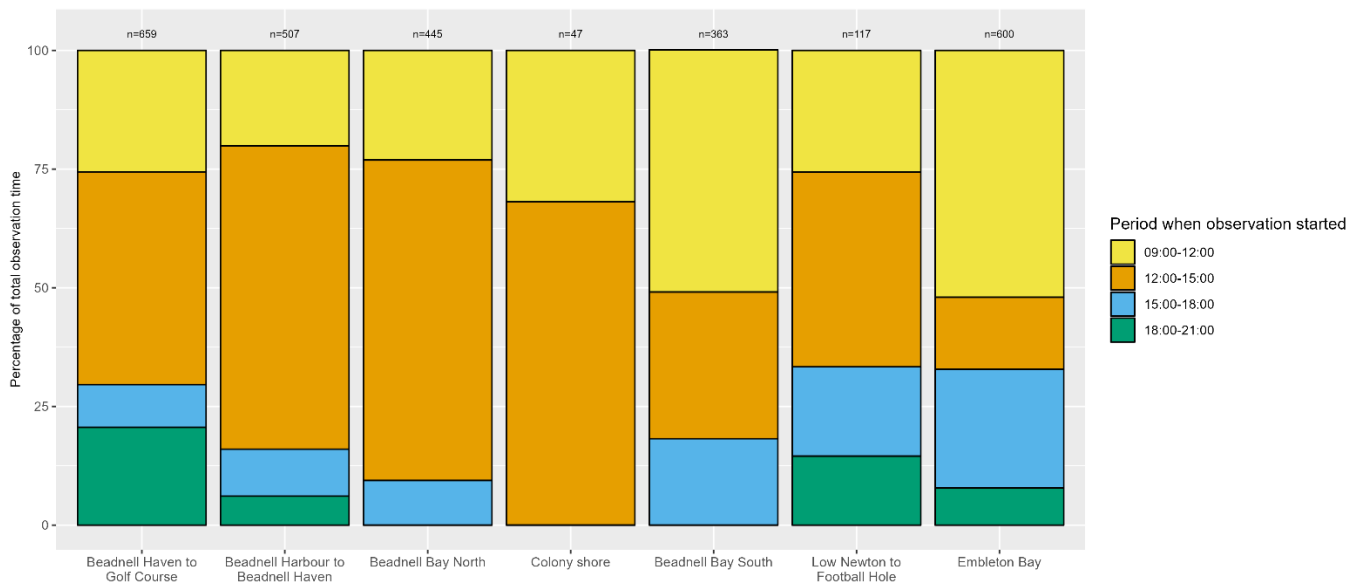


Figure 5.2A. Beach walk recording effort at Long Nanny by time of day. N=total length of observations in minutes

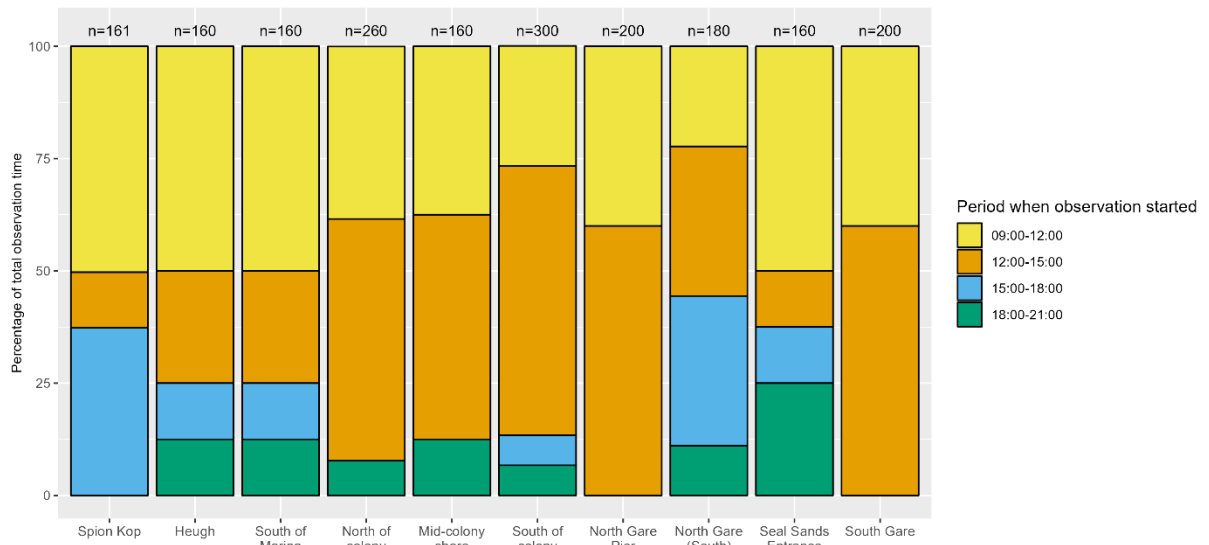


Figure 5.A3. Observation point recording effort by time of day at Seaton Carew. N=total length of observations in minutes

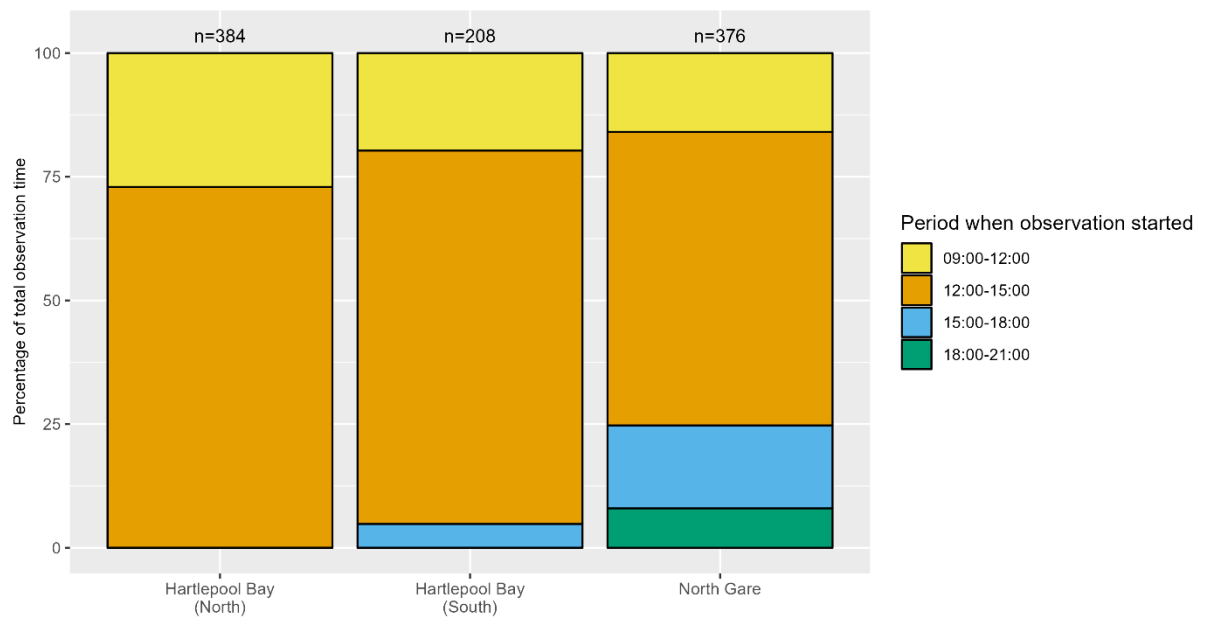


Figure 5.A4. Beach walk recording effort by time of day at Seaton Carew. N=total length of observations in minutes

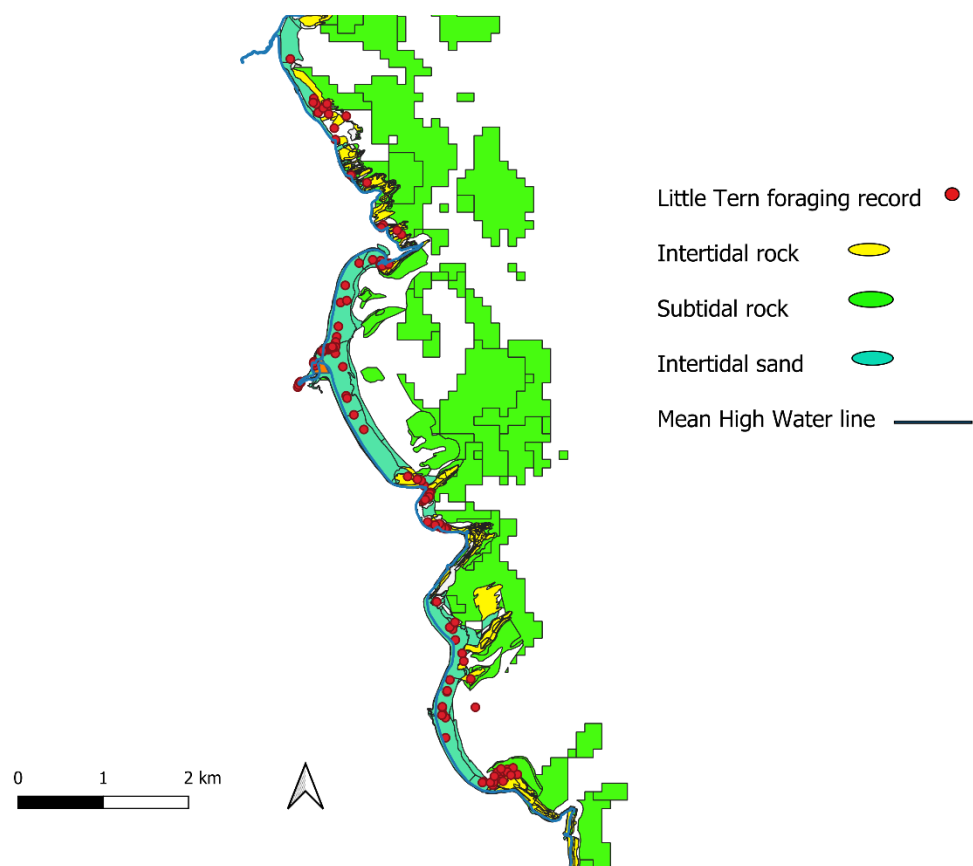


Figure 5.A5. Little Tern foraging records from Long Nanny overlaid on details from marine habitat map. Mapping taking from Natural England (2024)

Chapter 6. General Discussion

6.1 Context and aims of the study

The link between poor breeding success and low feeding rates in seabirds is well established and has been the subject of a wide range of published studies, with available food resources having been identified as a factor influencing a range of reproductive parameters including clutch size, date of egg laying and chick growth, and fledging success (Barrett *et al.* 1987, Daunt *et al.* 2008, Dias *et al.* 2019, Fayet *et al.* 2021, Furness and Barrett 1985, Klaassen 1994, Mcleay *et al.* 2009, Monaghan *et al.* 1989, Ramos *et al.* 2013). Tern species have a small size and during the breeding season are limited in the distance they can travel to forage and the number of prey items they can carry in their beaks. As a result, reproductive success in tern spp. is widely considered to be more sensitive to low food availability than is the case for larger species of seabird (Monaghan 1996, Daunt *et al.* 2008, Furness and Tasker 2000). The relationship between diet and foraging and reproductive output and productivity has been studied in several different species of tern with perhaps the Arctic Tern *Sterna paradisaea* being one of the mostly widely investigated (for example, Monaghan *et al.*, 1992, 1989). In contrast, the feeding ecology Little Tern has received relatively less attention, perhaps due to many of the difficulties in studying the species with frequent individual brood and whole colony failures and movements of colonies between years (Cabot and Nisbet 2013).

The purpose of this study has been to investigate the feeding ecology of Little Tern and to link this to the wider conservation of the species. In undertaking the study I have, in addition to my own fieldwork, had access to data on chick feeding from the EU LIFE funded Little Tern Recovery Project which ran from 2014 to 2019 and was led on by the RSPB (Wilson *et al.* 2020). A key purpose of the study has been to analyse this data and to make the results more widely available. The specific aims of the study were:

- To elucidate the diet of Little Tern chicks in the UK (Chapter 2)

- To identify the main factors driving rates of chick provisioning and to understand how differences in chick provisioning rates may relate to Little Tern productivity (Chapter 3)
- To assess the potential application of camera traps and video capture in feeding studies of Little Tern chicks (Chapter 4)
- To better understand how adult Little Terns are using the North East coast for foraging (Chapter 5)

In this final discussion chapter, I review progress against these aims, discuss some wider issues which arise out of the work, identify potential future avenues for additional research, and give a brief recommendation for future conservation work on Little Tern.

6.2 Reviewing the aims of this study

6.2.1 Aim 1: To elucidate the diet of Little Tern chicks in the UK

In Chapter 2, I reviewed the available information sources on Little Tern diet in the UK. I drew on three main sources of data: i) chick feeding records obtained from a literature review of published and unpublished sources; ii) LIFE project timed observations of chick feeding (from twelve colonies); iii) LIFE project camera trap observations from Langstone Harbour. Information from the LIFE project was compared with information from existing sources to identify similarities and differences. As part of the review of existing sources I also presented an analysis of data on chick diet contained within unpublished colony reports from Long Nanny in Northumberland covering a period of 17 years. Data on chick diet from the LIFE project were analysed to detect any differences between colonies and between years. Since relative proportions of different prey types found within samples are not independent of each other, compositional analysis was used to examine patterns of chick diet (Aebischer *et al.* 1993).

Both existing sources of data and work presented in this thesis support the view that Little Terns are generalist feeders capable of utilizing a wide range of different prey. However, observed chick diets were dominated by two main types of energy rich prey: Sandeel *Ammodytes* spp. and clupeids (members of the Herring family). Together these up 82% of all recorded prey items from LIFE project data. There has previously been some contradictory evidence over the relative importance of fish and invertebrate in

chick diet (Cabot and Nisbet 2013). Data from the spread of colonies in different parts of the UK included in the LIFE project was able to confirm that although invertebrates such as crustaceans are regularly recorded in low numbers as part of chick feeding observations there was little evidence that these routinely make up a significant proportion of total chick diet. The composition of chick diet differed significantly between colonies due to differences in the relative contribution of Sandeels and clupeids, but there was no evidence within individual colonies of a statistically significant difference between years. In contrast, analysis of historic chick feeding data showed evidence of statistically significant differences in recorded Sandeel numbers between some years.

6.2.2 Aim 2: To identify the main factors driving rates of chick provisioning and to understand how differences in chick provisioning rates relate to Little Tern productivity

In Chapter 3, I examined the data on food delivery to chicks collected by the LIFE project. Two measures of chick provisioning are presented: i) food delivery rates (numbers of feeds per chick per hour); and ii) estimated energy delivery rates (estimated energetic content of food delivered in kJ per chick per hour. Sources of variation in these measures are analysed and an attempt made to relate measures of chick provisioning to colony productivity.

The greatest single predictor of provisioning rates was found to be chick age. Older chicks were fed more frequently and with larger prey items than were younger chicks. There was also evidence that provisioning rates varied between colonies and between years. Contrary to expectations, no evidence was found that provisioning rates to chicks changed with time of day or with tide.

Due to high levels of chick mortality from causes such as predation and tides/weather, it was not possible to link differences in chick provisioning with differences in chick fledging rates or other measures of colony success. Participation in chick feed studies came to a total of 30 colony/years across the period of the LIFE project. Out of these 30 colony/years, 21 reported substantial losses of chicks or eggs due to predation, tidal flooding or bad weather. The sample size to test the relationship between provisioning

rates and breeding success was limited to eight years. Results were not significant which is not surprising given the limited sample size. Chick provisioning and food availability do not in themselves appear to be good predictors of likely fledging success in Little Tern, in contrast to some other seabird species, but this may be a consequence of the large number of years in which other factors explain poor breeding performance.

6.2.4 Aim 3: Assess the potential application of camera traps and video capture in feeding studies of Little Tern chicks

In Chapter 4, I investigated the use of video imagery in Little Terns feeding studies. There were two specific drivers for this: i) to attempt to validate the results of direct feeding observations of chicks and to use video footage as a point of comparison for prey identification and size estimates; and ii) to investigate whether video capture could be reliably used as an additional research tool for use in dietary studies and provisioning rate studies on Little Tern. I deployed camera traps to capture footage of chick feeding at the Long Nanny colony during 2017, 2018 and 2019. During 2022, I used an action camera (GoPro) attached to a spotting scope to collect footage of chick feeding. The feeding records obtained from video were compared with the results of direct feeding observations made on site.

Due to a variety of issues a direct comparison of the results of feeding surveys in the field and imagery of chick feeds caught by the camera traps was only available for 12 observation periods. Despite this, there was good agreement in prey identification (82% of feeds). Agreement in prey size estimation was found for 44% of feeds. Use of a digi-scoped GoPro camera provided a better comparison of methodologies with 56 out of 67 chick feeds recorded in field surveys also being captured on video footage. There was greater variation in prey identification from digi-scoped imagery with only 45% of instances the prey items identified by direct observation and by examination of video footage were identical. In 50% of instances prey item were classified as ‘unidentified’ using either or both methods.

A review of chick feeding records from camera trap data as a whole (not just those which were contemporaneous with direct feeding observations in the field) indicated that the proportion of Sandeel and clupeids in chick diet in data from camera trap footage was

broadly comparable with data obtained through timed feeding counts. The proportion of unidentified prey items was significantly lower in camera trap data. Average prey size estimates were similar in all years with the exception of clupeid records obtained in 2019 and Sandeels records obtained in 2018, when statistically significant but small (less than 0.5cm) differences were found. Based on the results presented I concluded that camera traps may be of potential use in studies of diet composition, particularly in locations where direct feeding observations are not possible, while use of digi-scoped video footage is likely to be of greater use as an alternative means of capturing data on chick feeding rates.

6.2.5 Aim 4: To better understand how adult Little Terns are using the North East coast for foraging

In Chapter 5, I presented data on the distribution and foraging behaviour of Little Tern collected from two separate colonies: Long Nanny in Northumberland and Seaton Carew in Hartlepool. An assessment of foraging distances ranges of adult birds from Long Nanny had previously been undertaken by (Parsons *et al.* 2015) although no work had been done to how foraging birds were using the coast within these foraging radii. No previous assessment of either foraging ranges or foraging locations had been undertaken at Seaton Carew. Statistical models were used to identify some of the factors influencing the presence and distribution of foraging birds.

Markedly different patterns of foraging were seen at these two colonies. Sightings of adult Little Tern at Seaton Carew mostly came from areas adjacent to the main breeding colony, with the majority of foraging birds being recorded within 2km the colony centre. In contrast, foraging birds were seen at greater distances from Long Nanny and the presence of Little Tern at any one location was less predictable, birds needed to travel longer distances in order to find changing patches of high prey availability. There was some indication from Long Nanny that foraging birds occurred in larger numbers in some areas, particularly with locations where coastal streams entered the sea. I speculate that these habitats may offer predictable access to prey at some tidal stages. No similar analysis of foraging habitat could be carried out at Seaton Carew as the majority of foraging locations consisted of soft sediment. At both colonies the numbers of foraging birds present appeared influenced by sea state (waviness) and tidal stage.

Observations from Long Nanny identified low-level but regular usage of the Long Nanny Burn by foraging Little Tern. This included areas of the burn which are outside of the boundary of the Northumberland Marine Special Protection Area, the designated site intended to protect the feeding areas of the internationally important breeding seabird population of the Northumberland coast (Natural England. 2019).

6.3 Discussion of wider issues

6.3.1 The importance of food to Little Tern breeding success and conservation

One of the initial drivers for the inclusion of monitoring of chick feeding within the LIFE project was to investigate whether any differences in the rate at which chicks were fed was reflected in chick survival and fledging success. The analysis presented in this thesis has found no clear evidence that food supply is a regular cause of low colony productivity at breeding sites in the UK. Examination of the relationship between food delivery rates and final colony productivity did not produce a statistically significant correlation. However, it is important to note that the power of such an analysis is low because of the small number of locations (n=8) available for analysis once colonies which suffered losses due to predation, high tides or poor weather (21 out of the 30 available colony/years) were set aside. As such, there was insufficient evidence to draw any robust conclusions about what influence of food supply may have in the breeding success of Little Terns when other mortality factors are absent. This question remains an area for further study.

Food supply plays an important role in the productivity of many seabird species such as, for example, Arctic Tern (Schreiber and Kissling 2005), or Atlantic Puffin *Fratercula arctica* (Fayet *et al.* 2021). Little Tern appear to suffer from declining population recruitment (Ratcliffe N. *et al.* 2000) the main reported causes of chick death relate to predation or issues with tidal flooding and weather (Wilson *et al.* 2020). While there are reports of food shortages causing chick mortality at UK colonies, for example at

Holkham and Scolt Head in 2015 (RSPB 2015a), these do not appear a regular cause of colony failure and there was insufficient evidence to determine whether food acts as a limiting factor in colony success when other causes of chick or egg loss are absent. Impacts of food availability on breeding success in Little Tern could occur through their influence on other measures of life-histories, such as the condition of adult birds, and through reproductive choices such as date of egg lay and clutch size. This is an area that was outside of the scope of this present study, but which merits further research.

There are several factors which potentially may make Little Tern more resilient than some other seabird species to the impacts of low food availability. One of these is the flexibility of their diet and the wide range of potential prey species which they will consume. Another is their flexibility in selection of breeding sites which could buffer Little Tern from the impacts of food shortages. The location of Little Tern colonies can change from year to year (JNCC 2016, Brown and Grice 2005) which contrasts with greater breeding site fidelity in species such as Common Tern *Sterna hirundo* or Arctic Tern (González-Solís *et al.* 1999, Morten *et al.* 2022). Perrow *et al.* (2003) have offered evidence that food availability is a main driver of colony location in Little Tern, with birds apparently choosing to nest in areas of be sub-optimal habitat (for example in areas with high disturbance) if these are close to good food suppliers in adjacent foraging areas. Such behaviour would be expected to make Little Tern less exposure to changes in local food supplier than for seabird species which show greater fidelity to breeding sites by allowing them the flexibility to relocate to new locations with better access to prey.

Climate change is a factor that could cause significant future changes to the type, quality and distribution (temporal and/or spatial) of food resource available to Little Tern and to other seabird species (Mitchell *et al.* 2020a). Sandeel is one of the main prey items identified in the diet of Little Tern chicks in the LIFE project data and in other studies, with the breeding success of Little Tern is considered vulnerable to declines in Sandeel numbers (Daunt *et al.* 2008, Furness and Tasker 2000). Changes in distribution and nutritional quality of Sandeels in UK waters have been documented, due to the impacts of warming seas . While there is no evidence yet of Sandeel declines impacting on Little Terns, any future shifts in distribution or availability may change the quality of feeding areas around some existing UK colonies and may, if we assume that the quality

of adjacent feeding habitats is a significant factor in colony location, result in changes in preferred breeding sites. Future changes in prey availability may also see changes in Little Tern diet to include a greater proportion of lower quality prey items. This could place foraging greater burdens on adult birds as they may need to increase the rate at which they deliver food to their growing chicks to ensure that their energy requirements are met.

6.3.2 The EU LIFE Little Tern Recovery Project

6.3.2.1 Monitoring of chick feeding by the LIFE Project

The EU LIFE Little Tern Recovery Project (referred to as “the LIFE project” throughout this thesis) represented a coordinated and strategic approach to the conservation of Little Tern in the UK (Wilson *et al.* 2020) and is akin to a citizen science project in terms of much of the data used in this thesis. Efforts to collect data on chick feeding were a relatively minor part of the project as a whole still nevertheless provided a valuable insight into chick diet and chick provisioning. Until the LIFE project, information on the feeding of Little Tern chicks came from a relatively few studies at a small number of sites (see Table 2.A1 in Chapter 2), with much of the available information being contained in ‘grey literature’ sources such as student dissertation or annual reports from breeding colonies.

While the information on food provisioning collected by the LIFE project provides a valuable resource, the data are not without issues. The primary weakness of the chick feeding workstream of the LIFE project was that it was not backed up by a data acquisition plan, so although a standard methodology existed it was left to individual participants from colonies whether they participated in feeding surveys and the number of surveys which they carried out. As a consequence, data acquisition effort between colonies was unbalanced, with the total duration of chick observations undertaken at any one colony in any one year ranging from 5230 minutes to 114 minutes (median length of observations per colony per year = 632 minutes). Low sample sizes are often associated with Type II errors (Dytham 2003) and relatively small number of chick feeding surveys from some of the participating colonies had the potential to reduce the likelihood of detecting true difference when comparing food delivery rates.

Data collection using timed observations of chick feeding should be underpinned by clear research aims, with consideration given to what use will be made of the data, how it will be analysed, and what number of observations are needed to provide the necessary statistical power. Although the LIFE project identified questions which it wished to answer using chick provisioning data, there was no data acquisition strategy to ensure that the data needed was collected in a systematic way or was robust for purpose intended. Colony managers may have had reasons for collecting chick feeding data without a strong research objective. For example, data might be being collected as a way of assessing the main prey species available in any given year or to identify any early indications of food shortages. However, if data are to be used to make comparisons between years or between locations then the required level of observational effort in each year should be considered. If part of the objective of making observations of chick feeding is to analyse or compare differences in chick provisioning, then the influence of chick age should be considered and the need to sample different age groups of chicks incorporated into plans for data collection. It is recognised that this may be challenging or impossible in some locations in some years particularly where there is high chick mortality.

6.3.2.2 What did we learn from the LIFE projects work on chick feeding?

The LIFE project represented the first attempt in the UK to collect data on the food provisioning of Little Tern chicks across multiple colonies, in the same timeframe, using the same methodology. As such it provided an opportunity to compare differences between colonies and between years. The data has been particularly useful in providing an insight into the range of prey items fed to Little Tern chicks when compared to the small number of studies previously available. It has helped to clarify the relative importance of fish and invertebrates in chick diet and shown that despite feeding on several different types of prey Little Tern chick diet is dominated by a small number of energy-rich marine fish.

6.4 Recommendations for further research

6.4.1 Alternative methods of data collection

Little Tern is a challenging species to study in the field. The species is sensitive to disturbance, prone to fluctuations in colony numbers and locations, often suffers from heavy chick mortality and has chicks which become highly mobile within a few days of hatching. In addition, there are regulatory and licencing considerations to working with Little Tern due to its protected status under the Wildlife and Countryside Act 1981 (as amended).

The majority of data on chick feeding and chick diet presented in this thesis were obtained through direct observations of chicks in the field. This is a well-established technique in seabird feeding studies and has many advantages, particularly for the study of a protected species such as Little Tern, among them being that the method is non-invasive, minimising potential disturbance to bird and is relatively simple for non-specialists to use. However, there are also several potential limitations to this methodology, particularly around validation of prey identification and prey size estimates (Barrett et al. 2007, Cezilly and Wallace 1988, Goss-Custard et al. 1987, Lee and Hockey 2001). When applied to Little Tern there is also the issue of chick mobility, which can cause difficulties when make attempting to find chicks and observe them for the required period of time. Some of these issues could be mitigated through using alternative methods of data collection. While no perfect method exists that address all issues or is right for all studies there is scope to use other techniques to supplement field observation or as an alternative to field observation.

The use of camera traps and video imagery has been examined as part of this thesis and provide one potential alternative method to identify food items and estimate food size. This has indicated that such techniques may be of use in certain circumstances, particularly when collecting data on diet composition in locations where direct observation of chick feeding may be difficult. The work undertaken as part of this thesis gives some reassurance about the consistency of prey identification and size estimates at the level of the individual observer but does not address the potential issue of variation between individual observers. Ideally, to address issues of potential variation

between individual observers, voucher specimens would be obtained in the field to validate prey identification and prey size estimates. There are practical difficulties with obtaining voucher specimens however, especially when studying a species such as Little Tern where colony disturbance needs to be kept to a minimum. The use of photography provides a potential method of providing a proxy for voucher specimens and has recently been used to investigate the diet of the Greater Crested Tern *Thalasseus bergii* (Gaglio et al., 2018, Gaglio et al., 2017). As part of this research a methodology for estimating the size of Anchovy *Engraulis encrasicolus* from photographs. Development of similar methodologies for estimating the size of common UK prey species would seem a potentially very useful area of research which would be of use in future studies of Little Tern and other seabird species.

A range of more specialist techniques are available to study tern diet (Barrett *et al.* 2007). These include stable isotope analysis (Ismar *et al.* 2014a), DNA barcoding of faecal material (Jo *et al.* 2022) or examination of scales and otoliths in regurgitated food pellets (Correia *et al.* 2016). However, these are all likely to be more applicable to the study of adult diet as opposed to chick diet and come with a requirement a level of access to colonies to collect samples.

6.4.2 Food and adult breeding condition

It can be speculated that food availability may influence the breeding condition of adult birds and reproductive parameters such as date of egg lay and clutch size as is the case in other seabird species (e.g. Fayet et al. 2021, Regehr and Montevecchi 1997). This is an area for further study and is given additional urgency by some of the predicted impacts of climate change on the quality and availability of prey (Mitchell *et al.* 2020a). Related to this further research to elucidate the on the relationship between large-scale climatic phenomena such as the North Atlantic Oscillation on the seabirds and on the quality and availability of their prey would be useful.

This study has only looked at Little Tern in the UK context. There appears to have been few studies into the feeding ecology of the species in their African wintering grounds of with the exception of the work of Brenninkmeijer *et al.* (2002) and there is scope for more

research to determine any impacts which winter food availability may have on future reproduction and survival.

6.4.3 Tracking of foraging adults

This thesis examined adult foraging behaviour at two colonies using data obtained from shore-based observations. While this was sufficient to provide insights into the distances covered by adult Little Terns and information about preferred foraging locations around colonies the use of tracking devices attached to adult birds could help to provide information at a finer-grain than is possible from shore-based observations alone. The use of tracking devices such as radio tags, satellite tags and data loggers has been used extensively in seabird foraging research (Bernard *et al.* 2021) but guidelines on the recommended maximum weight of logging devices has meant that until recently there were few devices suitable for use with small seabirds such as Little Tern. The trapping and tagging of adult birds require a licence and needs to be supported with clear evidence of need and for a species such as Little Tern is not without practical and conservation concerns.

Tracking data when combined with habitat mapping would provide greater information about how individual foraging birds are utilising particular habitats or areas of sea. This when combined with other habitat or oceanographic data could help to identify particular physical or habitat features such as subtidal sandbanks which are of importance to foraging birds but which might not be readily identifiable from the shore. In addition, shore-based observations are useful in determining the usage of the shoreline and immediate inshore areas by birds but are less accurate when used to determine the seaward extent foraging journeys. Boat surveys have been used by Parsons *et al.* (2015) to determine the extent to which Little Tern forage at sea. However, access to boat surveys is expensive and can be logistically challenging. Tracking of birds offers one potential alternative to this.

This study has looked at both chick provisioning and adult foraging at the Long Nanny tern colony in Northumberland. One notable feature of the results from these studies is that, despite several years of data, no impact of tidal state could be detected on food delivery rates to chicks, yet tide appeared to influence the numbers for foraging adult

birds and their location. This would suggest that adult birds were adjusting their behaviour to provide a constant rate of food provisioning for their offspring. The relationship between observed patterns of parental foraging and observed patterns of chick provisioning merit further study, which is an area of work which tracking of adult birds could help with.

6.4.4 Assessment of local prey availability

The availability of good food resources in foraging areas around breeding sites is clearly an important consideration for the conservation of Little Tern but fisheries data for the area around colonies is often absent or inaccessible. Data on prey abundance and availability can provide additional insight into the results of chick feeding surveys. For example, fish surveys undertaken taken at Langstone Harbour (Maccallum 2015, 2016) were able to offer some assurance that the high proportion of Goby *Gobius* ssp. in chick diet identified through camera trapping probably represented a reflection of local prey availability. With the exception of some previous studies in Norfolk (Perrow *et al.* 2003, Perrow *et al.* 2011) few attempts to link data on food resources with data on chick provisioning. This would be a valuable research area and would help address some uncertainties about the degree to which prey selection influences the composition of chick diet e.g. by identify the presence of potential food species which are absent or under-represented in recorded chick diet. Such research could also provide an early warning of future problems especially if combined with ongoing surveys of chick diet and monitoring of colony productivity.

6.5 Implications for future conservation action

Little Tern is a species which is subject to a high level of conservation management, for example through the physical protection of breeding sites, through visitor management and public outreach, and through predator control. All of these interventions will need to continue in future if Little Tern populations in the UK are to be maintained or increased.

The impacts of future climate change and ocean warming are not yet known but it seems probable that these will result in changes to the distribution, type and quality of prey available to Little Tern. One possible implication of this is that we may see shifts in

the locations of breeding colonies as birds seek access to better foraging areas. Any such change would likely require a flexible and rapid response from nature conservation organisations, site wardens and others involved in the protection of nesting colonies. This would be especially true if attempts are made to breed on busy public beaches outside of current conservation management or on otherwise sub-optimal habitat. Action to strategically and pro-actively manage more areas of the coast to provide suitable locations for nesting shorebirds would be advantageous if there is increased movement of Little Tern colonies in future in response to changes in food availability. Such action would also be of benefit to a wider range of breeding coastal birds.

6.6 Conclusions and final remarks

The availability and quality of food resources plays in an important role in the breeding success of seabirds and for some species is a primary factor in determining productivity. Little Tern is a species which has suffered significant declines in the UK in recent decades due to low population recruitment. From the data presented here and in the analysis of Wilson *et al.* (2020) the main causes of egg and chick loss at UK colonies are predation, tidal flooding and bad weather. No statistically significant evidence was found to suggest that poor chick feeding was a regular or frequent cause of poor productivity the data obtained through the LIFE project. However, the data were of low statistical power and were insufficient to draw any robust conclusions about whether higher levels of chick provisioning are linked to higher productivity in the absence of other mortality factors. This is an area that still requires further research. However, availability of food resources is likely to be an influence on breeding parameters and demographics and on possibly on the choice of breeding location. Climate change and warming have the capacity to influence the availability, quality and distribution of available prey in future years. As a generalist feeder, Little Tern may be somewhat resilient to changing food availability, although within the UK they appear to rely heavily on a small number of prey types on which to feed their chicks. Change in prey availability may therefore yet impact on Little Tern, particularly if there are shifts in breeding location as birds seek out better foraging areas.

APPENDIX: Variation in food provisioning between chick broods

Summary

Timed observations of chick feeding are an established method of gathering data on seabird diet. When applied to tern species, most researchers make observations of multiple scrapes/broods within the observation period. The chicks of Little Tern are precocial and often wander distances (10s or even 100s of metres) from their scrapes (see Chapter 1), providing a challenge when making observations of multiple broods. For this reason, observations of Little Tern chick feeding are generally made on a single brood. However, this approach risks bias if there are significant differences in food provisioning between broods as a result, for example, of differences in parental experience. This potential influencing factor could not be investigated through the LIFE project data (Chapter 3) due to many broods not being provided with unique identifiers in records. This Appendix presents a comparison of food provisioning between separate chick broods using chick feeding data collected at the Long Nanny colony in Northumberland during 2018 and 2019. No evidence was found of any statistically significant variation within year between broods of similar age in mean food delivery rates, mean estimated energy delivery rates or mean prey size.

Methodology

Data were collected at the Long Nanny tern colony on Beadnell Bay during the 2018 and 2019 breeding seasons using methodologies described in Chapter 1 (section 1.4.3). Chick observations in 2018 took place between the 13th -15th June and the 16th - 26th July. Observations in 2019 took place between the 10th of June and the 25th July. The maximum number of broods observed simultaneously was four. Scrapes or broods were selected to observe and were watched for a minimum of 60 minutes (average observation time in 2019 = 62minutes \pm 0.6). Where possible a minimum of two separate broods were observed although this was not always possible depending on chick locations and movement.

Three different measures of chick provisioning were calculated from the data collected: food delivery rates, estimated energy delivery rates, and prey size. See Chapter 3, section 3.3.1 for details of how these were derived.

Data were analysed for normality using the Anderson-Darling test, and for homoscedasticity using Levene's test and found to be both non-normally distributed and heteroscedastic. Data transformations were unable to change the pattern of the data to conform to a normal (gaussian) distribution. Chick provisioning data were analysed using Welch's ANOVA and Welch's t-test. The high mobility of chicks produced a risk that the same brood could be recorded on different times and dates under different names. When comparing differences in chick provisioning between broods, care was taken to ensure that the data sample used in the analysis did not contain any replication. Where this could not be ruled out, broods were excluded from the analysis. This led to 20 food delivery estimates being omitted from the analysis of 2018 data and 31 food delivery estimates being omitted from the analysis of 2019 data. Generally only broods with five or more observations of food delivery rates were included for analyses, with data from broods with a low number of observations being set aside. Due to high frequency of unidentified prey items during observations it proved challenging to derive estimated energy delivery rates from feeding observations. Only 20 estimates could be derived in 2018 and 47 estimates in 2019, the remainder of feeding observations containing at least one unidentified prey item or prey item of unidentified size. Because of the sparsity of data available the broods were included in the comparison of estimated energy delivery rates when three or more estimates were available, with other records being set aside from the analysis. As with the comparison of food delivery rates, broods were omitted when replication could not be ruled out. Preliminary analysis of the data showed statistically significant differences in measures of chick provisioning between years and between chicks aged less than seven days and those aged seven days or more. For this reason, analysis was split between years and between age class of chicks.

Results

Variation in rates of food provisioning rates (feeds/chick/hour) between broods

Welch's ANOVA did not detect any significant difference between food delivery rate to chicks in the broods examined (Table A1, Figure A1).

Table A1: Results of Welch’s ANOVA to determine whether mean provisioning rates of chicks varied between chick broods. See Figure A1 for details of the broods compared and sample sizes.

Year	Age of Chicks	F-Value _(df)	<i>p</i>
2018	Under 7 days	1.41 _{2, 12.3}	0.28
2019	Under 7 days	1.52 _{5, 12.9}	0.25
2019	7 days or over	0.46 _{6, 27.8}	0.83

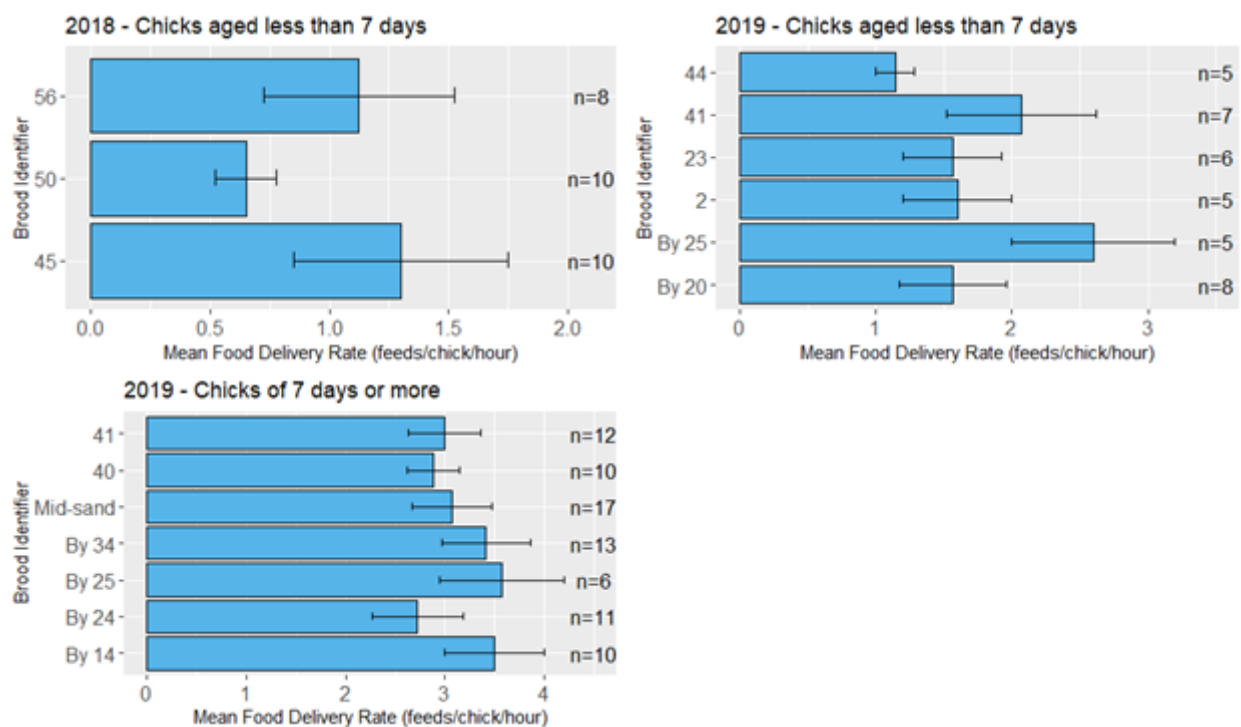


Figure A1: Comparison of mean chick provisioning rates between broods.

Bars show standard error of mean. Broods with fewer than 5 observations are excluded.

Variation in estimated energy delivery (kJ/Chick/Hour) to chicks

Because of the high number of unidentified prey items recorded during timed observations, it was only possible to calculate estimated energy delivery rates for 33 out of 67 timed observations in 2018 and for 54 out of 145 timed observations in 2019. Multiple estimates of energy delivery rates were only available for a small number of the broods observed (Figure A2).

No evidence was found that estimated energy per chick per hour varied between broods in either 2018 or 2019 (Table A2).

Table A2. Results of Welch's ANOVA comparing mean Energy Delivery Rate (kJ/chick/hour) between years and age bands of chick. See Figure A2 for details of the broods compared and sample sizes.

Year	Age of Chicks	F-Value _(df)	p
2018	Under 7 days	0.26 _{2,11.3}	0.77
2019	Under 7 days	3.18 _{2, 6.6}	0.11
2019	7 days or over	0.86 _{2, 24.6}	0.43

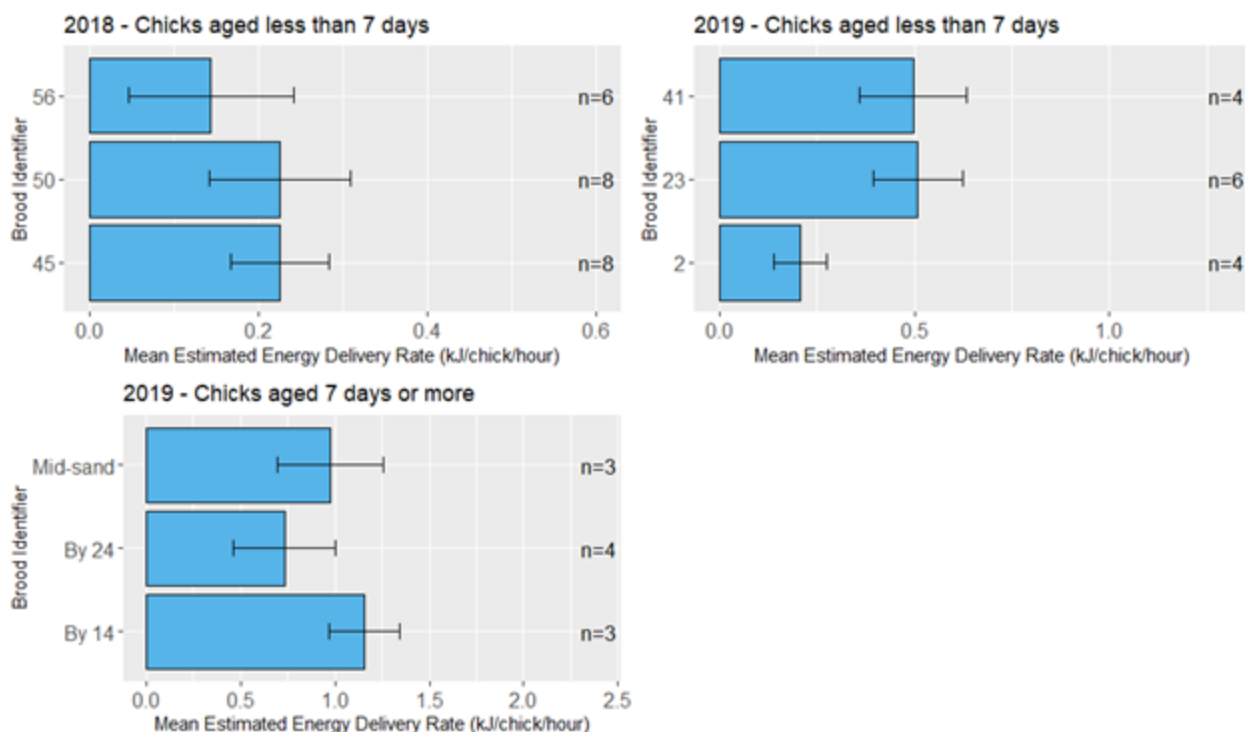


Figure A2. Comparisons between broods in mean estimated energy delivery (kJ/chick/hour). Bars indicate standard error of means.

Variation in mean size of prey items

Welch's ANOVA was used to compare the mean estimated size of prey items brought to chicks in different broods. Separate tests were carried out for Sandeels and Clupeids. No significant difference between broods was found in the mean size of Sandeels or Clupeids brought to chicks in any year or age category (Table A3, Figure A3).

Table A3. Results of Welch's ANOVA to compare size of prey items content of prey items between different chick broods. Broods with low numbers of data points or where there was a risk of replication were excluded from the analysis. See Figure A3 for details of the broods compared and sample sizes.

Year	Age of chicks	Prey Type	F-value _{df}	p
2018	Under 7 days	Sandeel	4.5 _{3, 4.9}	0.07
		Clupeid	1.00 _{1, 6.6}	0.35
2019	Under 7 days	Sandeel	3.06 _{3, 12.6}	0.07
		Clupeid	0.78 _{2, 8.1}	0.49
	7 days or over	Sandeel	0.03 _{1, 67.6}	0.85
		Clupeid	0.08 _{2, 25.9}	0.78

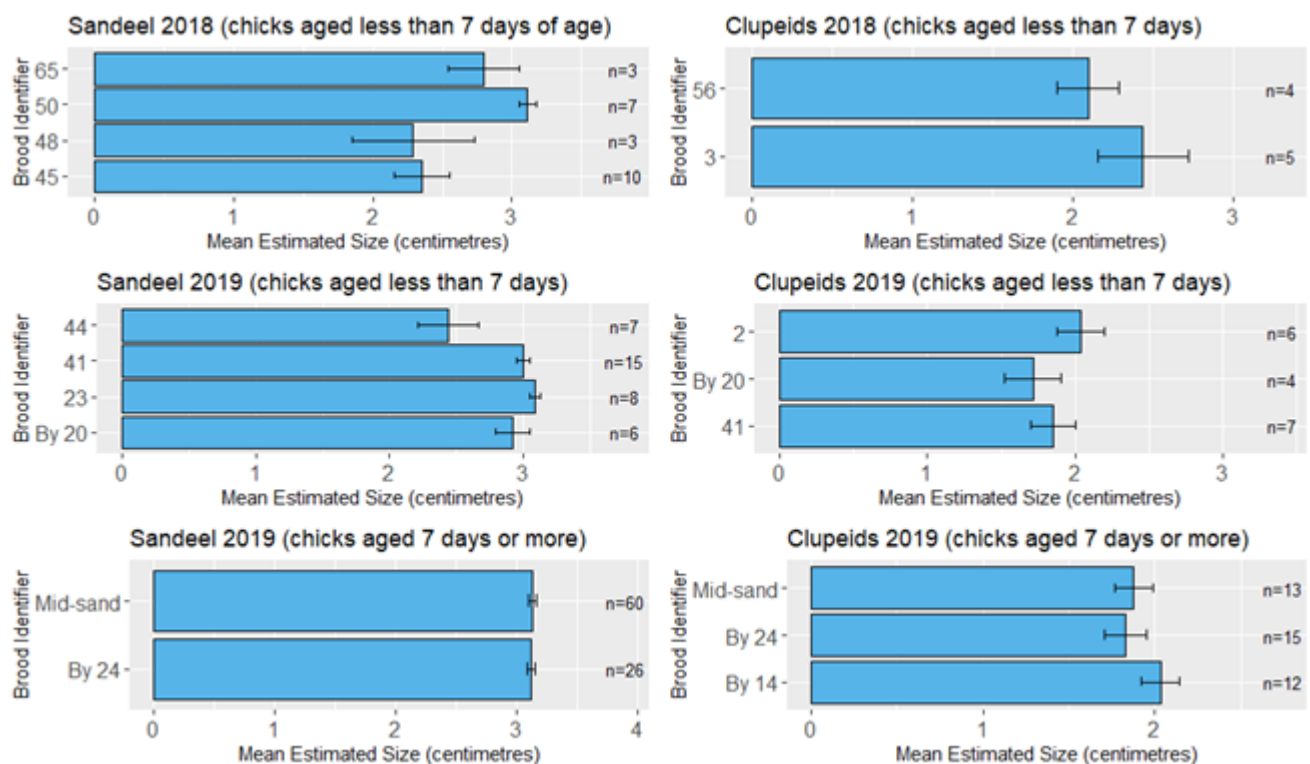


Figure A3. Comparison of mean prey size in centimetres between broods. Bars represent standard error of means.

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