Breeding Ecology of Arctic Tern (*Sterna paradisaea*) and Common Tern (*Sterna hirundo*)

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All illustrations and photographs are by Laura C Morris

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Abstract

Seabird breeding populations have been experiencing change over the last 40 years with low reproductive success being associated with poor foraging conditions. A comparison of the breeding ecology of Arctic and Common Terns showed significant differences in reproductive strategy and output associated with differences in their sensitivities to changing conditions. Both clutch size and productivity were consistently lower in Arctic Terns than Common Terns. Chicks of both species hatched asynchronously with mortality increasing down the brood hierarchy. Younger sibling survival was impacted both by seasonal conditions and by elder sibling survival, although to varying degrees depending on species and hatching order. Arctic Terns foraged at a higher rate but on less energy rich prey and on a less varied diet. Both species increased provisioning and decreased parental attendance at the nest as chicks grew older, corresponding with the changes in chicks' thermoregulatory abilities and energy requirements. Provisioning of chicks was primarily increased by selection of higher energy prey rather than through increased provisioning rate. Diurnal rhythms in either provisioning rate or diet were seen in both species, primarily associated with changing behaviour of prey fish. Temperature and precipitation affected provisioning, but adults maintained energy delivery to chicks. Increase in wind speed negatively impacted chick provisioning despite increased foraging effort. Chick mortality was linked to weather and feeding conditions, with high mortality linked to windy conditions and low provisioning. Yearly differences in productivity and chick mortality were associated with provisioning, and low parental attendance indicated poor foraging conditions. The reproductive output of both species is sensitive to declining foraging conditions and increased severity of weather conditions. The data implies that the sensitivity of Arctic Terns is greater than that of Common Terns, and that conditions around Coquet Island are sub-optimal for Arctic Tern breeding.

Contents

List of Tables

List of Figures

Acronyms

BTO – British Trust for Ornithology

IPCC – Intergovernmental Panel on Climate Change

RSPB – The Royal Society for the Protection of Birds

Abbreviations

AIC – Akaike Information Criterion

AICc – Corrected AIC

Dev – Deviance explained by the model compared to the null model

h – Hour

kJ – Kilojoules

km – Kilometres

mm – Millimetres

n – number of cases

NAO – North Atlantic Oscillation

p – P-value of statistical test, 0.05 taken as level of significance

PA – Parental attendance at the nest site

Para – Model parameters

rel.LL – Relative log likelihood

SD – Standard deviation

SE – Standard error

SST – Sea surface temperature

wi – AIC weights

a-chick – First hatched chick

b-chick – Second hatched chick

c-chick – Third hatched chick

*– represents $0.01<p<0.05$

**– represents $p<0.01$

•– represents $0.1<p<0.05$

Chapter 1. Recent Changes in the Marine Environment and Implications for Seabird Breeding Success

1.1 Introduction

Seabird breeding populations have been experiencing change over the last 40 years, with a decline in key indicators of breeding success. Adult birds have been observed abandoning eggs, chicks and nest sites and changes in adult behaviour have been recorded (Mavor et al. 2005; Wanless et al. 2005; Ashbrook et al. 2008), including increased aggression towards the chicks of other birds. High chick mortality has been seen throughout the United Kingdom, with some formerly productive breeding colonies experiencing complete failure (Monaghan et al. 1989; Uttley 1992; Mavor et al 2004). Protection from harvesting and measures to protect fish stocks have resulted in some recovery (Barrett & Krasnov 1996), but declines in population, breeding pairs, productivity and recruitment are still widespread.

Seabird productivity is influenced by a combination of biotic and abiotic factors, and high rates of chick mortality have been associated not just with low food availability and quality (Barrett et. al 1987; Monaghan et al. 1989; Wanless et al. 2005) but also with poor weather conditions (Dunn 1975; Becker & Spetch 1991; Riz et al. 2005). The current trend in climate change is for an increase in temperature, including sea surface temperature (SST) (Pachauri & Reisinger 2007) and this is impacting prey fish recruitment (Arnott & Ruxton 2002; Planque & Fredou 1999), distribution (Cortten 2001; Brander et al. 2003) and quality (Johnston et al. 1998; Imsland et al. 2005). If this trend continues, its impact on forage fish will increase as will the effect on seabird breeding populations, whose numbers will decline over time.

1.2 Climate change

The Intergovernmental Panel on Climate Change (IPCC) reported an average increase in global surface temperature (which includes sea surface temperature, SST) of 0.74ºC between 1906 to 2005 and suggested that the average temperature in the Northern Hemisphere is increasing at the fastest rate observed in the last 1300 years (Pachauri & Reisinger 2007). Incidences of heavy rainfall have increased by 2 to 4% and cloud

cover has increased by 2% over the same period. The Northern Hemisphere is experiencing relatively rapidly warming and increasingly extreme weather patterns. The majority of this change has been attributed to human activity and increases in the levels of the greenhouse gases (Crowley 2000; Pachauri & Reisinger 2007).

Marine climatic conditions are heavily influenced by natural phenomena such El Nino, La Nina and the North Atlantic Oscillation (NAO). The NAO arises from an alteration in the pressure gradient between the atmospheric high pressure zone over the Azores and the atmospheric low pressure zone over Iceland. The strength of the NAO index (the difference between the high and low pressures) has an effect on meteorological events such as the severity, frequency and trajectory of winter storms, wind speed and direction, precipitation levels, summer weather and SST (Fromentin & Planque 1996; Pauly and Becker 1996; Otterson et al. 2001). The fluctuations in the NAO have been linked with changes in fish distribution, recruitment and biomass (Fromentin & Planque 1996; MacKenzi & Köster 2004; Lehodey et al. 2006) and adult seabird survival and reproductive effort (Thompson & Ollason 2001; Frederiksen et al. 2004b; Favero & Becker 2006; Lavers et al. 2008).

The NAO experiences decadal variation and can be influenced by the natural changes in stratospheric ozone, tropospheric sulphates, volcanic aerosols and solar radiation. However, the increase in the NAO index over the last half century lies outside the range for simulated natural fluctuations (Gillet et al. 2003), and this increase has been linked to external forcing and the effect of climate change (Pachauri & Reisinger 2007) and increased greenhouse gases (Hoerling 2001; Gillet et al 2003).

1.3 Impact on the marine ecosystem

The main impact of climate change and changes in the NAO index on the marine ecosystem is through changing SST. Warmer SST has been negatively correlated with fish recruitment in the Northern Hemisphere (Arnott & Ruxton 2002; Planque & Fredou 1999; Lehodey et al. 2006), especially in the southern limits of their range. Low recruitment may be a result of low viability of eggs and young with increased SST associated with low rates of growth and development (Johnston et al. 1998; Kjellman & Eloranta 2002; Imsland et al. 2005).

Changing SST can cause fish populations to shift their range; a warming of waters not only forces cool water species further north in their range (Corten 2001; Brander et al. 2003) but can also lead to warm water species migrating into areas which were previously too cold for them (Stebbing et al. 2002; Brander et al. 2003; Kirby et al. 2006; Fleisher et al. 2007). These alien species may harm local ecosystems through competition for resources (reviewed in Streftaris et al 2005) and/or because they prove unsuitable prey for established predators (Wanless 2007).

An example is the sudden influx of Atlantic Snake Pipefish (*Entelurus aequoreus*) into the North Sea. Prior to 2002, the Snake Pipefish was very rarely recorded in U.K. waters (Harris et al. 2007). The increase in SST has not only allowed these fish to increase their geographic range, but also lengthened their breeding time, decreased incubation and increased larval growth rates. These factors have led to increased numbers of adults in areas where they were not previously found (Kirby et al. 2006). By 2004, Snake Pipefish were appearing in the diets of seabirds foraging the North Sea, but were found to be a poor prey, with reports of chicks struggling to digest the long, rigid body structure and of catastrophic breeding failures associated with high proportions of Snake Pipefish in the diet of chicks (Mavor et al. 2006, ibid 2007; Harris et al. 2007; Wanless 2007).

Changes in SST have also been linked with changes in the timing of seabird breeding (Tomita et al. 2008), breeding success (Frederikesen et al. 2004a) and provisioning behaviour (Weimerskirch et al. 2001; Peck et al. 2004; Quillfeldt et al. 2007). The impact is usually indirect, through the effect of SST on prey availability and quality.

Seabirds require a suitable and abundant prey species in order to raise chicks successfully. Fluctuations in breeding success have been closely linked to diet (Monaghan et al 1989; Baird 1990; Hamer et al. 1991; Barrett & Krasnov 1996; Wanless et al. 2005; Romano et al. 2006) and the rate of chick provisioning (Barrett et al. 1987; Croxall et al. 1999; Buber 2004).

The most frequent cause of chick death is starvation (Langham 1972; Quillfeldt 2001; Buber et al. 2004); chicks require a steady supply of food throughout the nestling period in order to fledge successfully. Parents can increase their foraging effort to mitigate the impact of low prey availability (Uttley 1992; Monaghan 1996; Suryan et al. 2000; Piatt

et al. 2007), but this is often insufficient to maintain provisioning rates. Low provisioning rates cause reduced growth rates (Barrett et al. 1987; Croxall et al. 1999; Buber et al. 2004) and lower fledging mass (Osterblom et al. 2001; Weimerskich et al. 2001), resulting in higher chick mortality, lower productivity and lower recruitment into the population.

Seabirds prefer certain prey species and an enforced switch in diet away from these species is associated with reduced productivity (Baird 1990; Massias & Becker 1990; Barrett & Krasnov 1996; Suryan et al. 1999; Romano et al. 2006). Different prey species have different lipid and energy contents (Hislop et al. 1991; Ball et al. 2007) and a change in diet can have a significant effect on the rate of energy delivery to chicks (Anthony et al. 2000). In addition, the size and/or structure of the alternative prey may not be suitable for chicks (Syryan et al. 1999; Wanless 2007). There is great variation both geographically and temporally in the lipid content of prey fish (Hisplop et al 1991; Anthony et al. 2000; Diamond & Devlin 2003; Wanless et al. 2005). Declining breeding success has also been associated with poor quality prey fish (Diamond & Devlin 2003; Wanless et al. 2005; Osterblom et al. 2006).

If changing SST results in migration or low recruitment of preferred prey species, and decline in their quality, the predictable result is reduced breeding success. This is likely to be increasingly the case if the current trend in climate change continues and the SST continues to rise. Close monitoring of the impact of these and other changes on seabird breeding success is therefore necessary.

1.4 Monitoring change

The effects of the evolving changes in the marine environment on the marine ecosystem need to be assessed. However, these ecosystems are very complex and lack suitable indicators for direct measurement. Their status can, however, be represented using proxy measurements (Boyde and Murry (2001). International fisheries data can be used to assess fish stocks through catch statistics; however, this has limited value since stock biomass is a poor indicator of recruitment into a population (Arnott and Ruxton 2002). Another option is to use a more easily monitored indicator species as a proxy for changes in the marine ecosystem.

The population size of a species can be a good indicator of long term environmental trends, but it does not reflect the short term changes unless they are extreme (Barrett and Krasnov 1996). During breeding, animals are under great physical stress as a result of the need to provision both themselves and offspring, and show rapid, relatively easily monitored changes in provisioning behaviour and reproductive output, even in response to small changes (Baird 1990; Broader & Pearcy 1992; Barrett & Krasnov 1996; Croxall et al. 1999; Boyde & Murray 2001; Furness 2007). Breeding success can therefore be used as an indicator of what is occurring in the food chain below the species.

Seabirds have been shown to be good bio indicators of conditions in the marine environment. Breeding success is known to reflect changes in foraging and provisioning conditions (Monaghan et al. 1989; Hamer et al. 1991; Suddaby & Ratcliff et al. 1997; Diamond & Devlin 2003; Wanless et al. 2005). Seabird diet and foraging rates have been shown to correlate with quantitative data from commercial fishing catches (Frank 1992; Montevecchi & Myers 1995; Diamond & Devlin 2003; Furness 2007) and can also provide indications for fish that are not readily or normally caught commercially (Barrett & Krasnov 1996; Barrett 2002).

Sensitivity to changes in the environment depends on a number of factors. Furness and Tasker (2000) developed a breeding bird sensitivity index for 25 species of seabird, using body size, energy cost of foraging, foraging range, foraging technique, daily time budget and dependence on certain types of prey. The index found seabirds that were small, surface feeders with a high dependence on one type of prey, limited foraging ranges and limited time available to increase foraging effort to be highly vulnerable to change. Black-legged Kittiwake (*Rissa Tridactyla*) and the Tern species (*Sterna*) were categorised as the most vulnerable to changes in prey availability.

1.5 Justification for and aims of the study

Climate change and the resulting increases in SST and the severity of weather phenomena (Hoerling 2001; Pachauri & Reisinger 2007; Gillet et al 2003) have already shown an impact on the marine ecosystem. Changing marine conditions are having a direct impact on marine species populations and breeding success. If current trends in climate change continue, the impact on the marine environment is likely to grow. It is

therefore important that the links between seabird breeding success and prey availability and weather conditions are well understood.

Seabirds are often used as indicators species with foraging and productivity showing close links with changes in the marine environment. Small, surface-feeding seabirds with limited foraging ranges are especially useful as bio-monitors because of their high sensitivity to change (Monaghan 1996; Croxall et al. 1999; Furness & Tasker 2000). In Furness & Taskers' (2000) sensitivity index, Arctic Terns (*Sterna paradisaea*) scored 22 and Common Terns (*S. hirundo*) 20 out of a maximum sensitivity score of 24, ranking them as the most sensitive and fourth most sensitive seabird species breeding in the U.K. Their high ranking reflects their limited foraging ranges, with most foraging occurring within a few kilometers of the breeding colony (Pearson 1968; del Hoyo 1996), the fact that their foraging is limited to the top few centimeters of the water column (Taylor 1983; Stienen et al. 2001), and their heavy reliance on Sandeels (*Ammodytes sps*) (Pearson 1968; Frank 1992; Monaghan 1992; Robinson et al. 2001).

Arctic and Common Terns are morphologically and physiologically similar members of the Sternidae family (Table 1.1). However, Arctic Terns are generally lighter built with narrower wings and longer tail streamers (Figure 1.1) and have shorter legs and a smaller beak to skull ratio (Figure 1.2) than do Common Terns. Both are piscivorous, feeding predominantly on small fish caught via shallow plunge or dip dives from the wing not pursuit dives limiting the depth to which they can forage within the water column.

	Arctic Tern	Common Tern
Length	34cm	33cm
Weight	104g	128g
Wingspan	80cm	88cm

Table 1.1 General biometrics of adult Arctic and Common Terns (Robinson 2005)

Figure 1.1 Arctic Tern (left) and Common Tern (right) in flight, showing the narrower wings and longer tail streamers of the Arctic Tern compared to the Common Tern.

Figure 1.2 Arctic Tern (left) and Common Tern (right) on the ground showing, the shorter legs and smaller, finer beak of the Arctic Tern compared to the Common Tern.

Both species have circumpolar breeding ranges throughout America, Asia and Europe and breed sympatrically throughout much of their ranges, although Arctic Terns breeding range extends further north into the Arctic while Common Terns breeding range extends further south (Birdlife International 2012). Arctic Terns are almost exclusively marine habitat breeders while Common Terns will also breed around fresh water lakes and in estuarine habitats. Both Arctic and Common Terns are almost exclusively colonial breeders, laying one clutch per breeding season. Arctic Terns typically lay clutches of one or two eggs and Common Terns clutches of two or three

eggs. Incubation lasts between 20 and 24 days for Arctic Terns and between 21 and 22 days for Common Terns. Incubation commences with the first egg, resulting in asynchronous hatching of the chicks. Both species hatch semi-precocial (Nice 1962) chicks which fledge when aged between 21 and 24 days for Arctic Terns and between 22 and 28 days for Common Terns (Delaceaux & Niestle 1990; Robinson 2005).

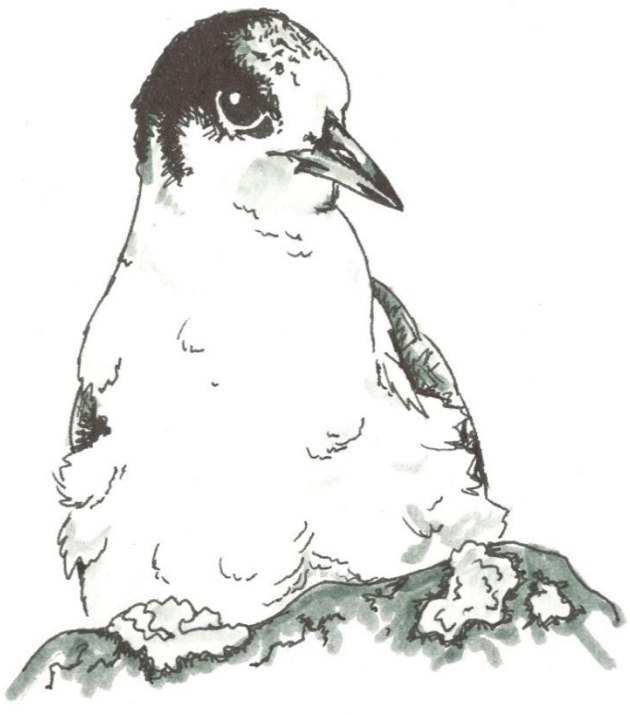
Both species are listed as 'Species of Least Concern' by the International Union for Conservation of Nature, with global populations of approximately 2 million Arctic Terns and between 1.6 and 4.6 million Common Terns (Birdlife International 2012). Results of the Seabird 2000 census put British breeding populations at 52,000 pairs of Arctic Tern and 10,000 pairs of Common Tern, a population decline of 31% for Arctic Tern and 15% for Common Tern since 1984 (Mitchell et al. 2004). As a result of localised breeding population decline, both species have 'amber' conservation status in the U.K. (Robinson 2005). Reduced breeding success, especially among Arctic Tern colonies, has been reported at various colonies around the British Isles in recent years, with some previously well-established colonies experiencing complete reproductive failure (e.g. Mavor et al. 2004 but see all reports).

The aim of this study is to provide a comprehensive description and comparison of the breeding and foraging behaviour of these two species when in close proximity at a well-established site and to investigate the impact of feeding conditions and weather on productivity and chick survival.

These data will allow a detailed understanding the general breeding ecology of Arctic and Common Terns and of the relationships among clutch size, productivity and foraging behaviour. Inter-seasonal differences in parental attendance and provisioning behaviour will be used to explain differences in productivity and chick mortality and to highlight areas of particular sensitivity.

The study of chick mortality in relation to hatching order, siblings and degree of asynchrony will enable assumptions to be made about the purpose and effects of asynchrony. Examination of the impact of weather and provisioning conditions on chick mortality throughout the nestling period will show which factors exert most influence on an individual chick's likelihood of fledging and will highlight areas of particular sensitivity.

With this study, we hope to explain differences in the sensitivity of each species to changing conditions, understand the relationship between provisioning behaviour and reproductive output, isolate warning signals for a poor year, and show how the sensitivity of a chick to the factors that influence its survival changes throughout its development. Indirectly, the study will identify factors that may serve as indicators or confirmation of ecological change.



Chapter 2. General Methodology

2.1 Study site

Data were collected during the 2006, 2007, 2008, 2009 and 2010 breeding seasons on Coquet Island, NE England, 55º 20' N, 1º 32' W, NU293046 (Figure 2.1). The island lies some 2 km east of the mouth of the Coquet River. It is a designated Site of Special Scientific Interest and a Special Protected Area under European Law for aggregations of breeding seabirds, with over 35,000 birds regularly breeding there. The island is owned by the Duke of Northumberland and managed by the Royal Society for the Protection of Birds (RSPB) as a reserve and nature sanctuary; no public access is allowed.

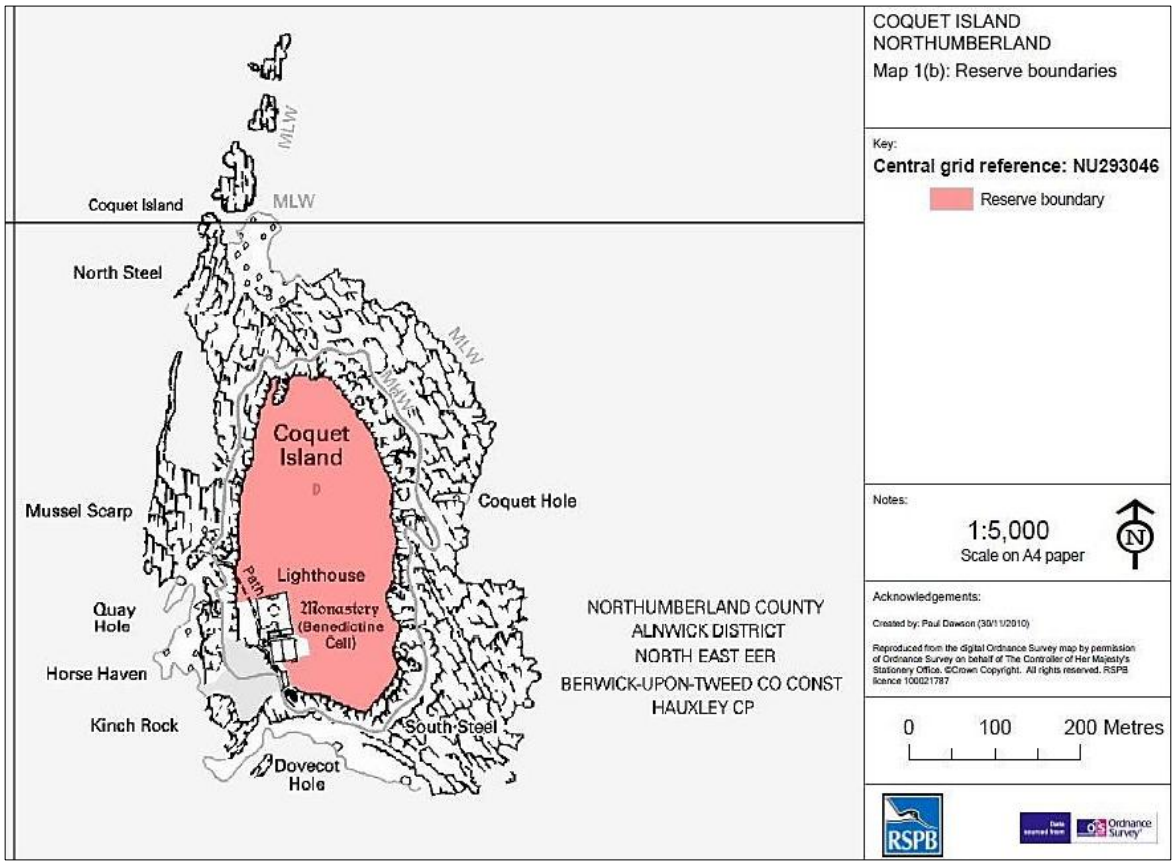


Figure 2.1 Map of Coquet Island, showing boundary of the RSPB reserve, mean high water line (MHW) and mean low water line (MLW), reproduced courtesy of the RSPB.

Large breeding colonies of both Arctic and Common Tern are present on the island, occupying largely segregated nesting areas although some overlap occurs. Average yearly breeding pair population during the study period was 1141 ± 122 Arctic Terns and 1212 ± 121 Common Terns (RSPB Coquet Island Annual Reports for 2006 through

2010). The study sites for each species were located within a central, low-overlap area of the colony, close to the lighthouse.

2.2 Study nests

2.2.1 Enclosures

Approximately two weeks after the first egg is laid, a sample of 30 nests of each species was randomly selected within the chosen study area. These were enclosed, with between one and three nests in each enclosure. A minimum distance of 45cm was left between nest and netting and a minimum of 5m of netting was used per enclosure. The netting was cut to approximated 40cm in height, stabilised using bamboo canes, and secured to the ground using metal pegs. Chicken wire was used in 2006 but this was abandoned in favour of heavy-filament plastic garden mesh (Gardman, 19mm mesh) from 2007, after chicks were seen with abrasions on their foreheads thought to be caused by the wire. Each nest was marked with an individual number-flagged bamboo pole to allow for identification during enclosure checks and observations.

Once enclosures were erected, nests were observed from a distance in order to minimize disturbance and ensure parents returned and brooded eggs. Vegetation within the enclosures was controlled throughout the season by hand pulling so as to leave patches for shelter but ensure enclosures were not overrun. RSPB staff place numerous 'chick shelters' (small wooden huts or plastic piping) around the colony, so each study nest was provided with a shelter.

2.2.2 Clutch size, hatching success and productivity

Maximum egg counts were used for clutch size. Hatch date was taken as the day a chick fully emerged from the egg. Eggs which started to pip but whose chicks failed to completely emerge were recorded as failed. Enclosures and nearby areas were checked every one or two days (weather permitting) to record newly hatched chicks and any dead or missing chicks giving age of chick accurate to a minimum of 2 days. Chicks missing from enclosures on 2 or more consecutive enclosure checks were recorded as dead if they were younger than 15 days unless they were found alive outside their enclosure. Uniquely-numbered rings enabled identification, see 2.2.3.

Productivity was recorded as number of chicks fledged per pair. A chick was considered successfully fledged if it was not found during enclosure searches on at least 2

consecutive occasions once it was over 22 days old, and not recovered dead before the age of 30 days. Weekly or bi-monthly searches of the whole island for chick corpses were carried out in conjunction with RSPB monitoring work. Chicks recovered dead away from the nesting area were counted as fledged if they were over 30 days old.

2.2.3 Chick identification

Soon after hatching, chicks from enclosed nests were ringed using uniquely numbered British Trust for Ornithology (BTO) metal rings so as to permit individual identification. For each chick, hatch day, hatching order (first hatched, a-chick; second hatched, b-chick; third hatched, c-chick) and outcome (fledged or died) were recorded, as were brood size, age difference between siblings and siblings outcome. From 2007, date of death and age at death were also recorded.

2.3 Provisioning and parental attendance

2.3.1 Observations

Hides were erected centrally within each colony with good views of the enclosed nests. Once chicks started to hatch, between 4 and 10 of the enclosed nests were observed from the hides for between 2 and 3 hours at a time. Observations began once at least 4 nests containing chicks could be observed concurrently and continued for as long as 4 or more nests contained chicks or until all observation had been made. Observations were conducted between 0500 - 0759, 0800 - 1059, 1100 - 1359, 1400 - 1659, 1700 - 1959 and 2000 - 2159 at each stage of the tidal cycle (high, ebbing, low and flooding tide) for both species. This gave a total of 136 hours of observation, split into 48 observation blocks, each season.

Because of the short breeding season and cyclical nature of tides, observations were not conducted at random, but a concerted effort was made to ensure that observations at particular times of day or states of the tide were spread throughout the season. Observations of the two species were paired wherever possible. For example, a 0500-0759 high tide observation of Arctic Terns would be followed the next day by one of Common Terns. Observations were not started if weather conditions were too severe (heavy rain), so as not to disturb brooding adults off their chicks but, once started, were not abandoned due to bad weather. Any observation which had to be cancelled was rescheduled at the first opportunity.

2.3.2 Provisioning

Adult birds were observed returning to the nest site. Return trips were classed as provisioning trips when the adult returned to the nest area with prey and attempted to feed prey to a chick, whether or not the chick was seen to eat the food.

Fish size was measured in 'beaks', with each beak length corresponding to approximately 35mm (Figure 2.2, Figure 2.3, Figure 2.4). All observations were carried out by the same observer, thereby reducing variability, and were calibrated using fish recovered from the colony.

Whenever possible, fish species was identified. In-field identification between the two Sandeel species (*Ammodytes marinus*; *A. tobianus*) and between the two Clupeid species (*Clupea harengus; Spratus spratus*) was not possible so these species were not disaggregated and treated. Fish measuring less than 20mm generally could not be accurately identified at distance so were grouped together as 'small fish'.

Energy values of Sandeel and Clupeid were calculated from their lengths using the equations detailed by Wanless et al. (2005)

$$\text{kJ Sandeel} = 0.0081 \times \text{Length (cm)}^{3.427}$$
$$\text{kJ Clupeid (Sprat)} = 0.0096 \times \text{Length (cm)}^{3.845}$$

The result was necessarily an approximation, given the margin of error in the estimation of prey length and the considerable variation in the energy value of fish of similar size (Wanless et al. 2005; Hislop 1991), but it gave an indication of the potential energy values available from the prey.

Provisioning rate per nest was recorded as number of provisioning trips per hour and calculated energy values of Sandeel and Clupeid were used to give estimated energy delivery rate ($kJ.h^{-1}$) and energy per feed. Per chick provisioning rate and energy delivery rate were calculated from the per-nest data divided by number of chicks in the nest at the time of observation.

Figure 2.2 Common Tern returning to the nest with Clupeid approximately 2.5 ‘beaks’ or 90mm in length

Figure 2.3 Arctic Tern carrying a Sandeel approximately 1.5 ‘beaks’ or 50mm in length

Figure 2.4 Common Tern carrying Sandeel approximately 2 ‘beaks’ or 70mm in length

2.3.3 Parental Attendance

Parental attendance was recorded as the time in minutes that at least one adult was present at the nest site (no distinction was made between individuals) during the hour. No distinction was made between adults actively brooding or simply spending time at the nest site engaging in other activities.

2.4 Data sources

2.4.1 Study data

All data used in the study were collected by the author except as indicated below.

2.4 2 RSPB clutch size and productivity data

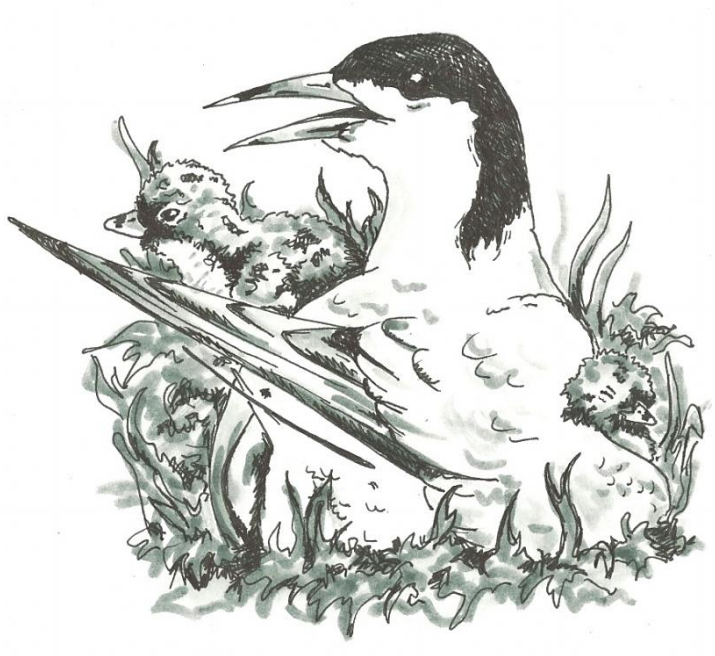
Additional data dating back to 1992 on yearly average clutch size and 1991 for yearly average productivity for the two species were available through the RSPB (see RSPB Coquet Island Annual Reports for 1991 through 2010 for methodology).

2.4.3 Weather conditions

Daily weather observations were obtained from Boulmer weather station (55º 25' N, 1º 34' W, NU265145), located on the mainland approximately 10km North-north-west of Coquet Island, for mean daily temperature (˚C), mean daily wind speed ($km.h^{-1}$) and daily precipitation (mm).

2.5 Permissions and licensing

All work was carried out with permission from the RSPB and with clearance from Natural England. All ringing was carried out by Laura Claire Morris under licence (BTO restricted 'C' licence for ringing Tern chicks).



Chapter 3. Differences in clutch size, hatching success and provisioning, and their effects on productivity

3.1 Abstract

Clutch size is limited by the ability of the adults to produce and incubate eggs and their ability to successfully raise chicks to fledging. A comparison of clutch size, hatching success, productivity, and provisioning behaviour of Arctic and Common Terns was conducted between 2006 and 2010 on Coquet Island in order to ascertain the factors limiting the clutch sizes of the two species. Arctic Terns laid smaller clutches than Common Terns and showed much less plasticity (both overall and between seasons), but correlation between yearly clutch sizes of the two species suggests both were influenced by conditions at or near the breeding colony. Arctic Tern 3-egg clutches were associated with lower hatching success than Common Tern 3-egg clutches, although complete failure was comparable between the species. Therefore, incubating ability was not felt to be a constraining factor; rather, Arctic Terns seem quicker to abandon incubation in favour of chick provisioning. Arctic Tern productivity was significantly lower than Common Tern productivity, although yearly means were highly correlated. Provisioning behaviour was significantly different between species, with Arctic Terns foraging at a higher rate but yielding prey of lower energy. As a result, Arctic Tern chicks received less total energy than those of Common Terns. It is suggested that the ability to provision chicks explains why Arctic Tern clutch size is largely limited to 2 eggs, as the already high provisioning rate of Arctic Terns restricts their ability to increase foraging effort further with an increased number of chicks. Common Terns, however, modify their clutch size in response to conditions at the time of laying.

3.2 Introduction

Why birds lay the number of eggs they do is a question many scientists have tried to answer (e.g. Lack 1954; Nisbet 1973; Slagsvold 1982; Slagsvold 1984). Current thinking is that the optimal clutch size should be such to maximise reproductive output throughout the reproductive life of the breeder (e.g. Charnov & Krebbs 1974). Clutches

should thus be limited to a size that does not negatively impact adult fitness in a way that reduces potential future breeding output.

There are major interspecies variations in clutch size between taxa and orders, with a range from 1 to over 14 eggs, but the modal inter-species clutch size tends to be 2, with the mean at just under 3 (2.8) eggs (Jetz et al. 2008). There is a general trend for clutches to increase in size with distance from the equator, especially in the Northern Hemisphere (Lack 1954; Young 1994; Dunn et al. 2000; Cardillo 2002; Evans et al. 2009; Westneat et al. 2009), and for clutch size to decline throughout the breeding season (Crick et al. 1993; Young 1994; Suddaby & Ratcliffe 1997; Evan et al. 2009; Westneat et al. 2009; Gladbach et al. 2010; Descamps et al. 2011).

The ability of a female to produce eggs is controlled by her energy reserves and limited to the level that ensures that she does not die or abandon during incubation (Winkler & Walters 1983). The correlation between female body condition and reproductive effort has been well documented, with female body mass being associated with variations in the onset of breeding and of clutch size (Erikstad et al. 1993; Gladbach et al. 2010; Descamps et al. 2011). The resting metabolic rate of passerine species increases by around 27% during egg laying (Nilsson and Raberg 2001) and the cost of egg production is significant; in studies where females are forced to lay larger clutches they exhibit a decline in fitness (Visser & Lessells 2001; Kalmback et al. 2004), a decline in future reproductive effort (Nager et al 2001; Kalmback et al. 2004), reduced quality of chicks (Monaghan et al 1995), and reduced investment in chick rearing (Heany & Monaghan 1995; Monaghan et al 1998). Yearly changes in body mass at the time of laying are associated with differences in clutch size (Gladbach et al. 2010), therefore yearly variation in clutch size can be considered as a response to conditions at the time of laying.

Clutch size should be limited by female body condition to ensure that the cost of producing surplus eggs does not negatively affect parental ability to successfully incubate and raise offspring, and does not negatively impact subsequent breeding efforts. Larger clutches can incur greater costs of incubation and can reduce the incubation efficiency. The impact of artificially enlarging clutch sizes by giving parent birds ‘free’ eggs (i.e. no cost incurred from egg production) has been shown to negatively impact female body condition (Visser & Lessells 2001; Hanssen et al. 2005),

suggesting increased costs associated with incubating larger clutches. Conversely, when the costs of incubation are reduced then parents fledge more chicks and have better subsequent breeding efforts (Reid et al. 2000).

Several studies have shown that artificially enlarging clutch size reduces the percentage hatching success of the clutch (Slagsvold 1982; Reid et al. 2000; Kim et al. 2010). Larger clutch sizes can result in sub-optimal incubation leading to failed eggs or to decreased chick quality at the time of hatching (Reid et al. 2000; Larson et al. 2003).

The classical theory on optimal clutch size suggests that this is one that produces the most fledged young. Thus clutch size is limited by the costs of parental behaviour (as determined by the environment) and the ability to successfully feed chicks (Lack 1954). However, more current theories on clutch size (e.g. Charnov & Krebbs 1974) suggest that the optimal clutch size is one that optimises the cost efficiency between yearly productivity and likelihood of adults surviving to breed again, so as to give maximum lifetime reproductive output. Raising chicks is a costly activity to parents and both males and females lose body mass during this period with adults often abandoning the breeding effort if body mass falls below a threshold level (Monaghan et al. 1989; Wedeln & Becker 1996; Moe et al. 2002). More effort is invested in feeding larger broods, so brood size should be limited by parental ability to provision chicks successfully without negatively impacting their future breeding potential.

In addition chicks need to be of high enough quality to survive post fledging and be recruited into the breeding population. While larger clutches may result in more fledglings, these may be of poorer quality therefore show higher post fledging mortality. By laying smaller clutches, adults can invest more in individual chicks and may thereby increase the likelihood of producing viable fledglings.

Therefore, differences in clutch sizes of similar species breeding in the same area are explained by both the physical parameters of the species (ability to produce and incubate eggs) and differences in the costs associated with raising chicks (ability to forage successfully). Intra-species variations, however, depend on lay date, female body condition and feeding conditions at the time of laying as a proxy for potential feeding conditions during the chick rearing period.

Arctic and Common Terns are migratory species returning to a colonial breeding area to lay a single clutch of eggs. The chicks of both species are semi-precocial and reliant on the parent birds for feeding (Fjeldsa 1977). The aim of this study was to compare the clutches of these two species at the same breeding site (Coquet Island) over a number of years in order to establish how clutch size changes within the season and how it relates to productivity. Hatching success, inter-seasonal differences and provisioning behaviour were investigated as factors which may explain differences in the observed clutch sizes between the two species.

3.3 Methodology and Analysis

3.3.1 Methodology

See Chapter 2, sections 2.1, 2.3.1, 2.3.2, 2.4.1.

3.3.2 Analysis

All data were tested for normality using the Kolmogorov-Smirnov test testing the null hypothesis of normal distribution and found to be non-normally distributed. Transformation of data was attempted but found to be ineffective for data normalisation, therefore non-parametric statistics were used. All analysis was undertaken using IBM SPSS Statistics, version 19.

Overall differences in clutch size (eggs.pair^{-1}), hatching success (percentage of eggs laid which successfully hatched) and productivity (chicks fledged.pair^{-1}) were analysed between species and between years using Pearson's Chi-Squared test with Z-test used to compared differences in column proportions (Bonferroni adjusted p-value for multiple comparisons across groups). Kruskall-Wallis test was used to compare productivity depending on clutch size (adjusted p-value), and Mann-Whitney U test was used to compare productivity between the species depending on clutch size. Species differences in yearly mean colony clutch size between 1992 and 2010 and productivity between 1991 and 2010 were analysed using Mann-Whitney U test. Spearman's Rho was used to correlate mean yearly clutch sizes and yearly mean productivity between the species.

Species comparisons of provisioning rate per hour (feed.nest^{-1}.h^{-1}, feed.chick^{-1}.h^{-1}), rate of estimated energy delivery per hour (kJ.nest^{-1}.h^{-1}, kJ.chick^{-1}.h^{-1}) and estimated energy per feed (kJ.feed^{-1}) were made using Mann-Whitney U analysis.

3.4 Results

3.4.1 Clutch size

Clutch sizes of both species ranged from 1 to 3 eggs, with Arctic Tern modal clutch size being 2 eggs and that of Common Terns 3 eggs (Figure 3.1). There was a significant difference in clutch size between the two species (Pearson's Chi-Squared, n=300, χ^2=61.415, df=2, p<0.001). Z-test analysis of column proportions showed that 1 and 2 egg clutches were significantly more likely to be laid by Arctic Terns while a significantly higher proportion of 3 egg clutches was laid by Common Terns.

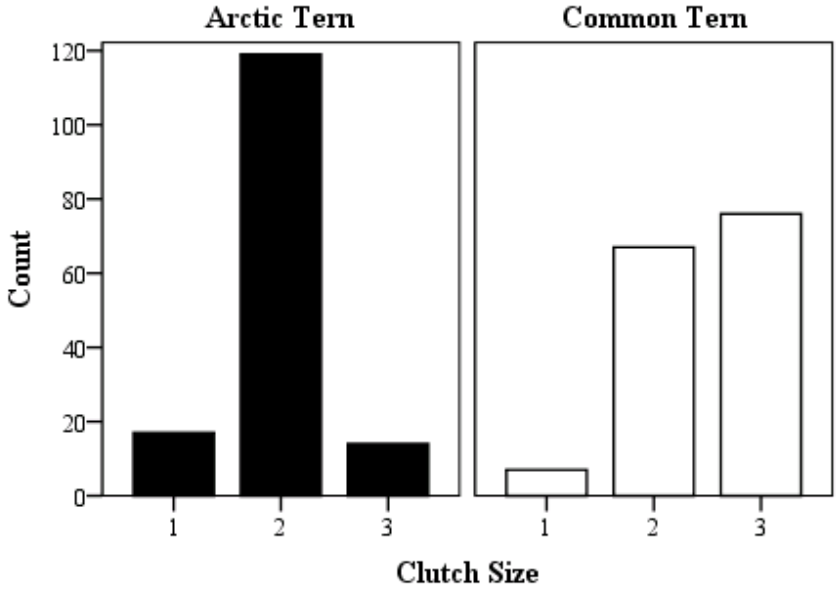


Figure 3.1 Distribution of clutch sizes (egg.pair^{-1}) from 150 Arctic Tern and 150 Common Tern nests.

The RSPB data for mean yearly clutch size between 1992 and 2010 calculated for the whole colony averaged 1.86±0.14 eggs per pair of Arctic Terns and 2.51±0.24 eggs per pair of Common Terns (mean ± SD). Mean clutch size was significantly different between the species (Mann-Whitney U, n=38, Z=5.126, p<0.001), with Common Terns generally having a larger yearly clutch size than Arctic Terns.

Between 2006 and 2010, year had no significant effect on Arctic Tern (Pearson's Chi-Squared, n=150, df=8, χ^2=14.580, p=0.068) but a significant effect on Common Tern clutch size (n=150, df=8, χ^2=38.268, p<0.001). Z-test analysis of column proportions showed that the proportion of Common Tern clutches containing 1 egg was similar between years but 2-egg clutches were more likely in 2006 and 2009 than in 2007 and

2010 and 3-egg clutches more likely in 2007 and 2009 than in 2006 and 2008 ($p<0.05$), (Figure. 3.2).

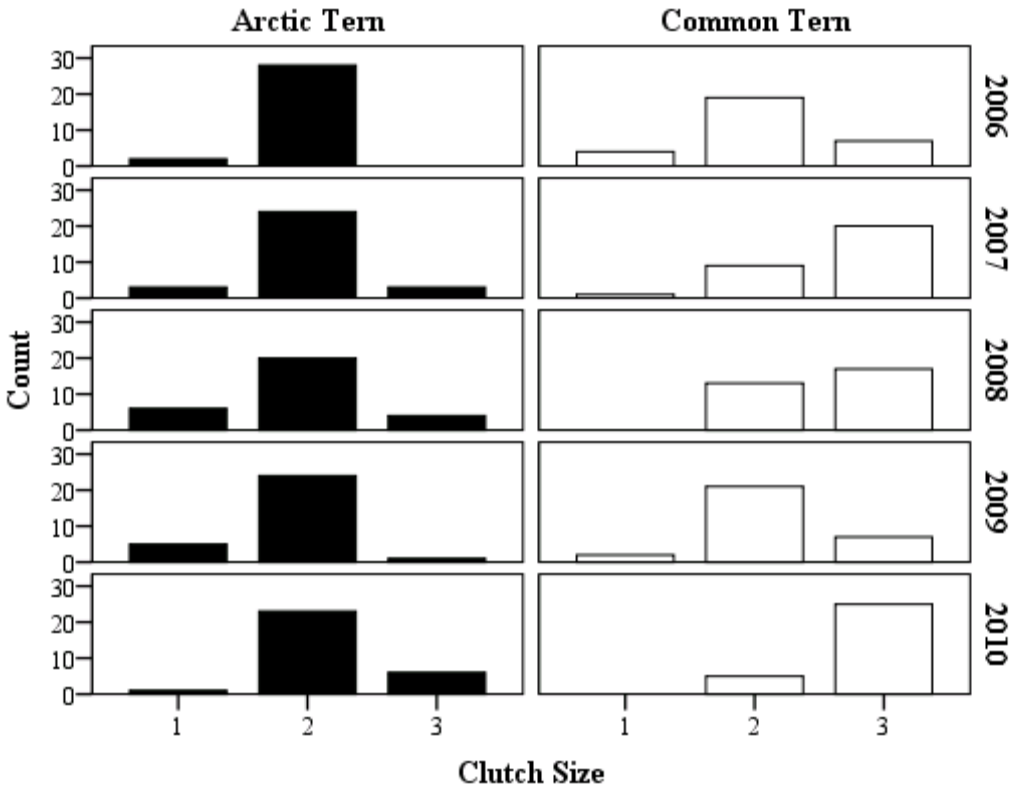


Figure 3.2 Yearly distribution of clutch size (egg.pair^{-1}) from a yearly sample of 30 Arctic Tern nests and 30 Common Tern nests sampled between 2006 and 2010.

Analysis of the correlation between yearly mean clutch size between 1992 and 2010 (RSPB data) showed a significant positive correlation between clutch sizes of the two species (Spearman's rho, n=19, Rho= 0.697, p=0.001, Figure 3.3), although Arctic Tern clutch size was always smaller than Common Tern clutch size and showed a subdued response to yearly variation compared to that of Common Terns (Figure 3.3).

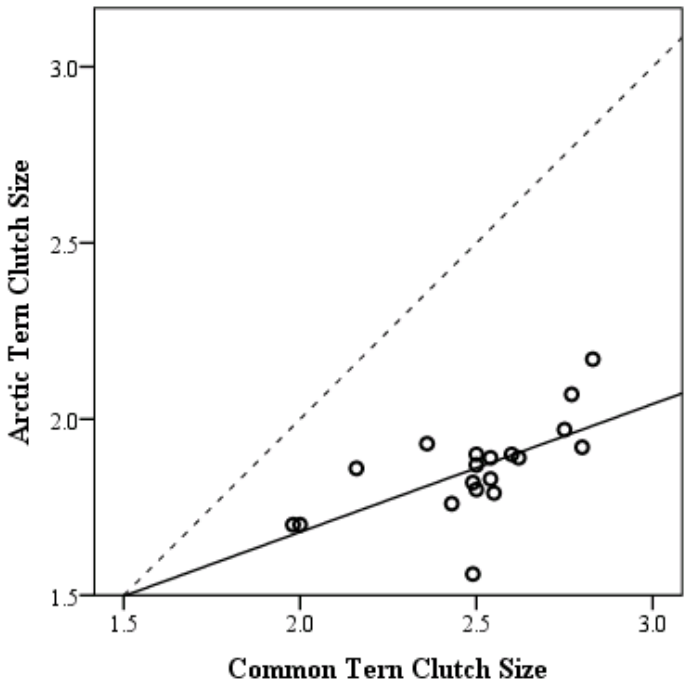


Figure 3.3 Mean clutch size (eggs.pair^{-1}) of Common Terns plotted against mean clutch size of Arctic Terns (1992 and 2010). Lines indicate the relationship between Arctic and Common Terns (solid line, R^2=0.412) and the line expected if clutch sizes of the two species were comparable between years (y=x, dotted line).

3.4.2 Hatching success

Of the 300 nests observed, 11 Arctic Tern and 6 Common Tern nests failed to hatch any chicks. These nests were included in productivity studies as all nests had been watched after erection of enclosures to ensure that both adults returned to the nest and brooded the eggs. The failure of nests was therefore not considered to be associated with human disturbance arising from the study.

The per-clutch percentage of eggs hatched from eggs laid (hatching success) ranged from 0% to 100% for both species. There was no difference in proportion of eggs hatched between Arctic and Common Terns (Pearson's Chi-squared, n=300, χ^2=3.712, df=3, p=0.294), with the majority of nests hatching all eggs successfully (Figure 3.4).

Pearson's Chi-squared test showed that hatching success was comparable between species when comparing clutches 2-eggs (n=189, df=2, χ^2=0.186, p=0.911) but not for 3-egg clutches (n=90, df=2, χ^2=6.227, p=0.044). Hatching success was almost significantly lower for Arctic Tern 1-egg clutches (n=25, df=1, χ^2 =0.002, p=0.062) . While the proportions of these clutches that failed completely (hatching success = 0%)

were comparable, Arctic Terns were significantly more likely to hatch only 2 out of 3 eggs and significantly less likely to hatch all 3 eggs than were Common Terns.

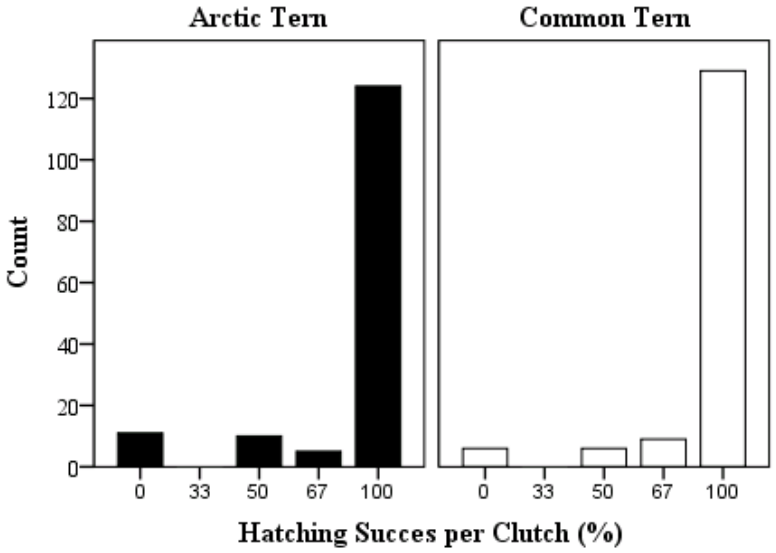


Figure 3.4 Distribution of hatching success (per clutch) of 150 Arctic Tern and 150 Common Tern clutches.

There was no difference in hatching success between years for either Arctic Terns (Pearson's Chi-squared, n=150, df=12, χ^2=16.172, p=0.184) or Common Terns (n=150, df=12, χ^2=17.429, p=0.134).

3.4.3 Productivity

Between 2006 and 2010, productivity per nest ranged from 0 to 2 for Arctic Terns and 0 to 3 from Common Terns, with modal productivity being 1 for both species. Pearson's Chi-squared analysis showed a significant difference between species (Pearson's Chi-Squared, n=300, χ^2=14.756, df=3, p=0.002). Z-test analysis of column proportions showed that a higher proportion of nests yielding a productivity of 0 belonged to Arctic Terns and that a higher proportion of nests yielding a productivity of 2 belonged to Common Terns ($p<0.05$) (Figure 3.5).

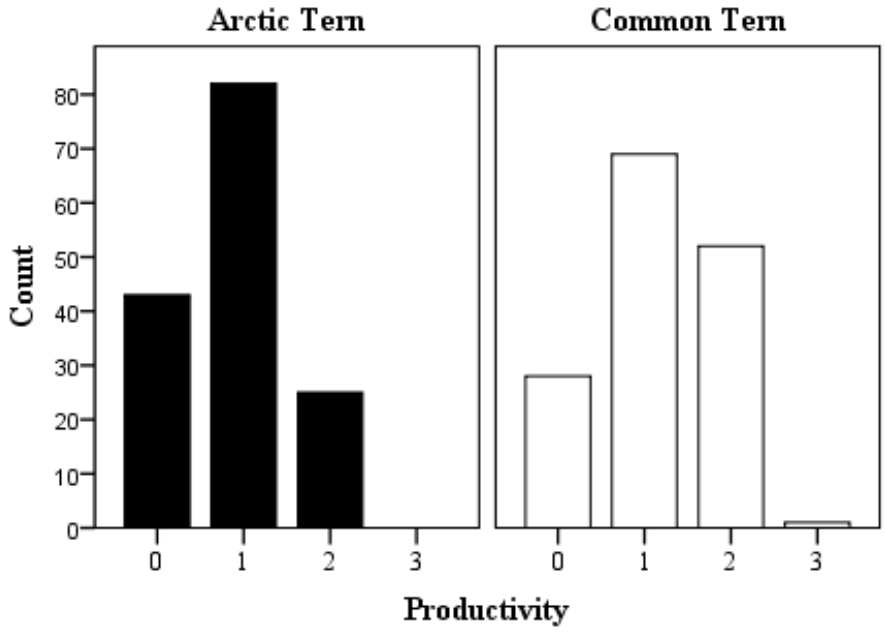


Figure 3.5 Distribution of productivity (chicks fledged.nest^{-1}) from 150 Arctic Tern and 150 Common Tern nests.

The RSPB mean yearly productivity data between 1991 and 2010 for the whole colony averaged at 0.857±0.334 chicks fledged per pair of Arctic Terns and 1.199±0.463 chicks fledged per pair of Common Terns (mean ± SD). Productivity was significantly different between the species (Mann-Whitney U, n=41, Z=2.348, p=0.019), with Common Terns generally having higher yearly productivity than Arctic Terns.

Clutch size had a significant effect on Arctic Tern productivity (Kruskall-Wallis, n=150, df = 2, χ^2=11.431, p=0.003) but not on that of Common Terns (n=150, df= 2, χ^2=3.572, p=0.168). Arctic Tern productivity was similar between 1 and 3-egg clutches (Z=1.296) and 2 and 3-egg clutches (Z=1.321) but significantly different between 1- and 2-egg clutches (Z=3.243, p=0.008) (Figure 3.6). Productivity was comparable between the species for 1-egg clutches (Mann-Whitney U, n=24, Z=1.319, p=0.260) and 2-egg clutches (n=186, Z=1.759, P=0.079) but significantly different for 3-egg clutches (n=90, Z=2.436, p=0.015).

Between 1991 and 2010, yearly mean productivity was not related to yearly mean clutch size for either Arctic Terns (Spearman's Rho, n=19, Rho=-0.065, p=0.793) or Common Terns (n=19, Rho=-0.180, p=0.462).

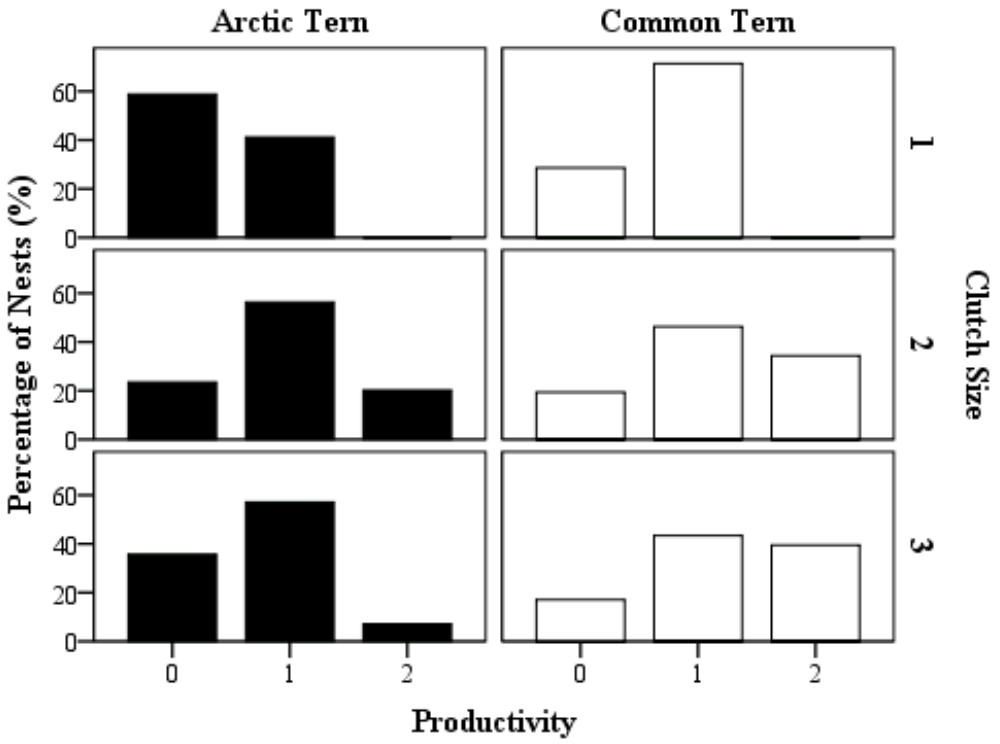


Figure 3.6 Distribution of productivity (chicks fledged.nest^{-1}) of Arctic and Common Tern nests (% of nests) depending on clutch size.

Productivity was significantly different between 2006 and 2010 for both Arctic Terns (Pearson's Chi-squared, n=150, df=8, χ^2=53.311, p<0.001) and Common Terns (n=150, df=12, χ^2=29.920, p=0.003) (Figure 3.7). Z-test analysis of Arctic Tern nests showed that the highest proportion of failed nests (productivity=0) occurred in 2008 and the highest proportion of nests fledging 2 chicks occurred in 2007 and 2009 (p<0.05). Z-test analysis of Common Tern nests showed that a higher proportion of nests fledged 1 chick in 2008 than in 2009, and that the proportion of nests fledging 2 chicks was lower in 2008 than all other years, and lower in 2006 than all years other than 2008 (p<0.05).

Analysis of the correlation between yearly mean productivity between 1991 and 2010 (RSPB data) showed a significant positive correlation between productivities of the two species (Spearman's rho, n=20, Rho= 0.703, p<0.001). Although Arctic Tern productivity was generally lower than Common Tern productivity, the yearly effect was similar between species (Figure 3.8).

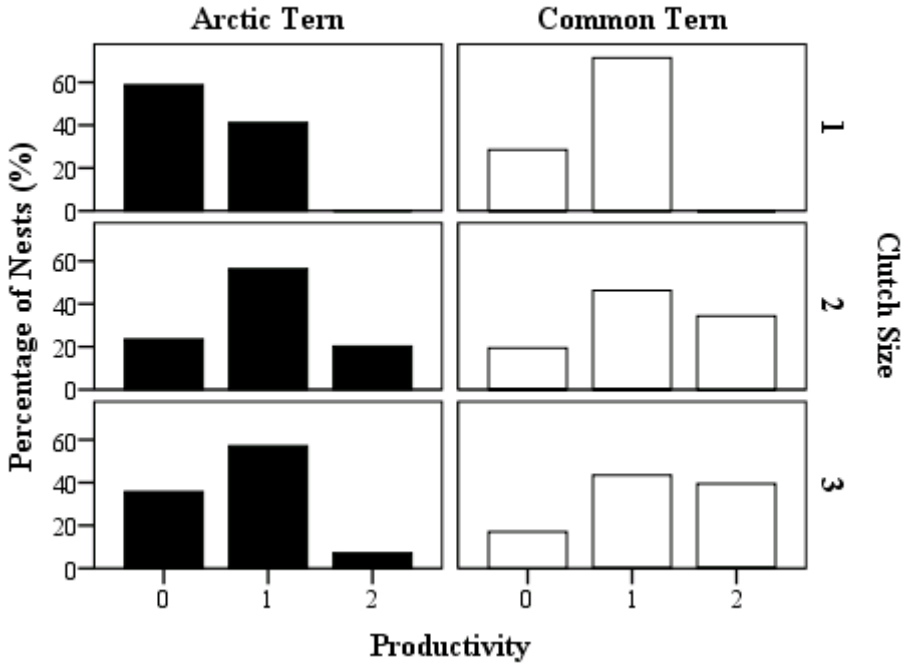


Figure 3.7 Yearly distribution of productivity (chicks fledged.nest^{-1}) from a yearly sample of 30 Arctic Tern and 30 Common Tern nests sampled between 2006 and 2010.

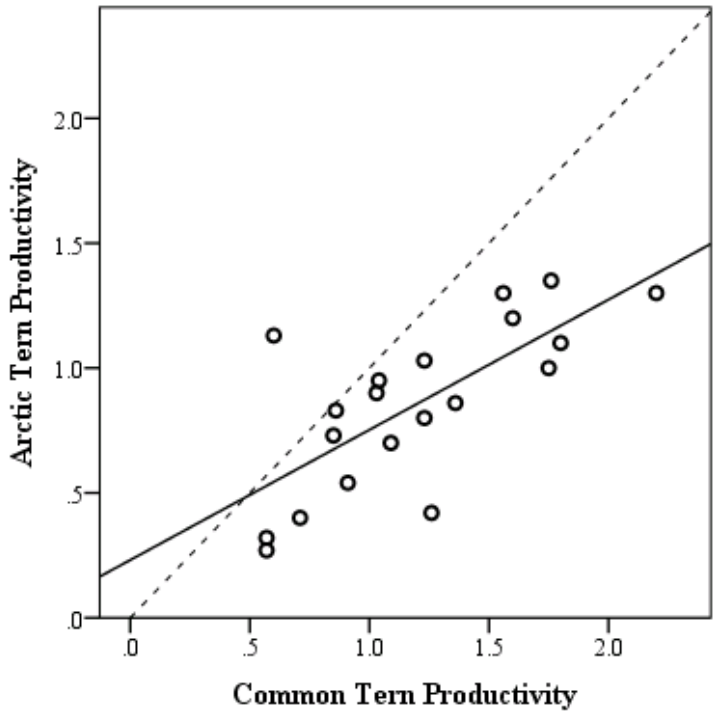


Figure 3.8 Mean yearly productivity (chicks fledged.pair^{-1}) of Common Terns plotted against mean yearly productivity of Arctic Terns between 1991 and 2010. Lines indicate relationship between Arctic and Common Terns (solid line, R^2=0.522) and the line expected if clutch sizes of the two species had been comparable between years (y=x, dotted line).

3.4.4 Provisioning behaviour

Mann-Whitney analysis of provisioning data showed that Arctic Terns returned to the nest area with food at a significantly faster rate than Common Terns, both per nest and per chick, but delivered significantly less estimated energy per hour, both per nest and per chick as well as per feed (Table 3.1, Figures 3.9, Figure 3.10, Figure 3.11).

	n	Z	p
Feed.nest^{-1}.h^{-1}	3502	5.337	<0.001
Feed.chick^{-1}.h^{-1}	3502	8.075	<0.001
kJ.nest^{-1}.h^{-1}	3484	4.684	<0.001
kJ.chick^{-1}.h^{-1}	3484	2.757	0.006
kJ.feed^{-1}	2906	12.076	<0.001

Table 3.1 Mann-Whitney analyses of differences in provisioning behaviour of Arctic and Common Terns comparing provisioning rate per nest (feed.nest^{-1}.h^{-1}) and per chick (feed.chick^{-1}.h^{-1}), rate of estimated energy delivery per nest (kJ.nest^{-1}.h^{-1}) and per chick (kJ.chick^{-1}.h^{-1}) and estimated energetic value per feed (kJ.feed^{-1})

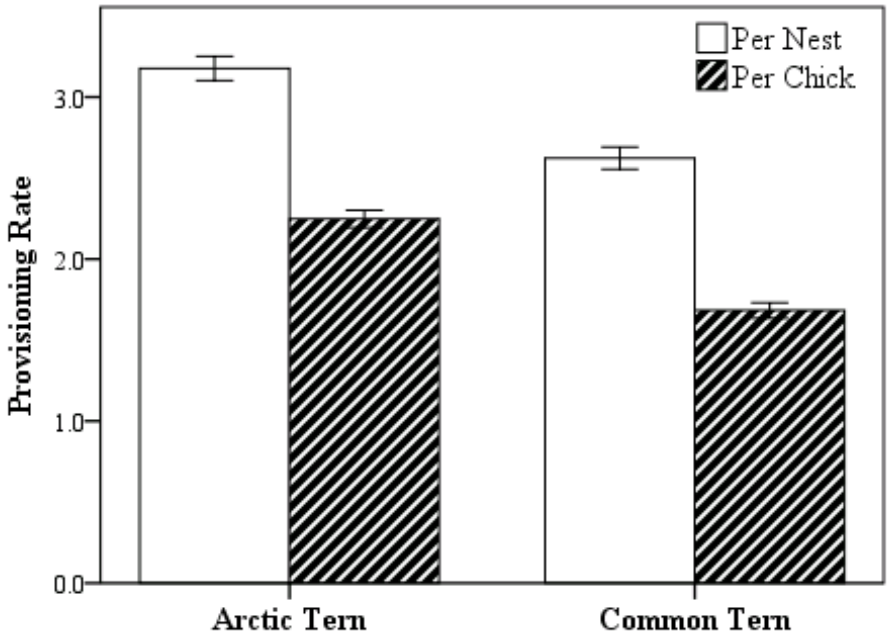


Figure 3.9 Arctic and Common Tern provisioning per nest (feed.nest^{-1}.h^{-1}) and per chick (feed.chick^{-1}.h^{-1}) ± SE.

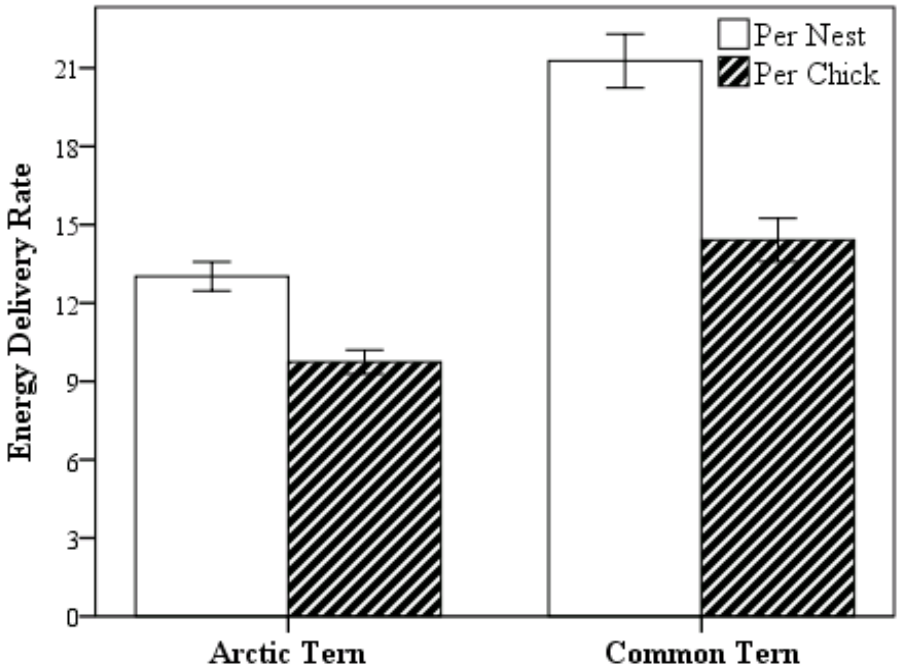


Figure 3.10 Arctic and Common Tern energy delivery per nest (kJ.nest^{-1}.h^{-1}) and per chick (kJ.chick^{-1}.h^{-1}) ± SE.

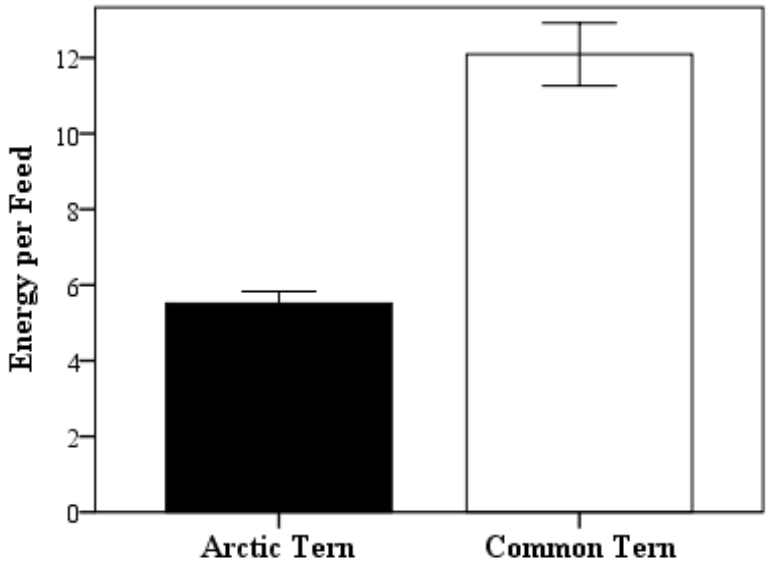


Figure 3.11 Arctic and Common Tern energy per feed (kJ.feed^{-1}) ± SE.

However once foraging rates were averaged by individual nests, feeds per nest were no longer significantly different between species although feeds per chick and energy per nest, chick and feed remained significantly different (Table 3.2)

	n	Z	p
Feed.nest^{-1}.h^{-1}	173	1.619	0.105
Feed.chick^{-1}.h^{-1}	173	2.172	0.030
kJ.nest^{-1}.h^{-1}	173	2.707	0.007
kJ.chick^{-1}.h^{-1}	173	2.453	0.014
kJ.feed^{-1}	173	4.567	0.001

Table 3.2 Mann-Whitney analyses of differences in provisioning behaviour of Arctic and Common Terns comparing per nest averages of provisioning rate per nest (feed.nest^{-1}.h^{-1}) and per chick (feed.chick^{-1}.h^{-1}), rate of estimated energy delivery per nest (kJ.nest^{-1}.h^{-1}) and per chick (kJ.chick^{-1}.h^{-1}) and estimated energetic value per feed (kJ.feed^{-1})

3.5 Discussion

This study supported previous findings on the clutch sizes of Arctic and Common Terns breeding on Coquet Island (Langham 1974; Monaghan et al. 1989; Uttley et al. 1989; Robinson et al. 2001) and showed that the clutches laid by Arctic Terns were on average smaller and showed less variation in size than did those of Common Terns. Both species laid between 1 and 3 eggs but Arctic Terns had a clear modal clutch size, with 79% of the 150 nests monitored containing 2-egg clutches. In contrast, Common Terns showed no clear modal clutch size, with similar percentages of nests containing 2-egg clutches (45%) and 3-egg clutches (51%). This difference in the plasticity of clutch size was also found when examining variation between years. While Arctic Tern clutch size did not vary between years, the clutch size of Common Terns did, and their modal clutch size varied from 2- and 3-eggs between years.

Variation in clutch size has been shown to be affected by female body condition and conditions at the breeding site at the time of laying (Murphey et al. 1984; Erikstad et al. 1993; Suddaby & Ratcliffe 1997; Gladbach et al. 2010; Descamps et al. 2011). Inter-seasonal differences in clutch size were observed for Common Terns between 2006 and 2010 but not for Arctic Terns. However, the average yearly clutch sizes of the two species (from 1992 through 2010, calculated from the whole colony) were closely correlated, indicating that both species are subject to seasonal effects on their clutch size. While the variation was less evident for Arctic Terns than for Common Terns, the yearly pattern in clutch size variation was similar (Figure 3.12). It was not possible to identify the factor(s) behind the yearly difference in clutch size as data on female body

weights and feeding conditions at the time of egg-laying were not available. However, the close correlation between the species suggests that whatever factors are influencing clutch size, they act on both species; this implies a link with conditions at the breeding ground rather than with conditions at the wintering site or during migration.

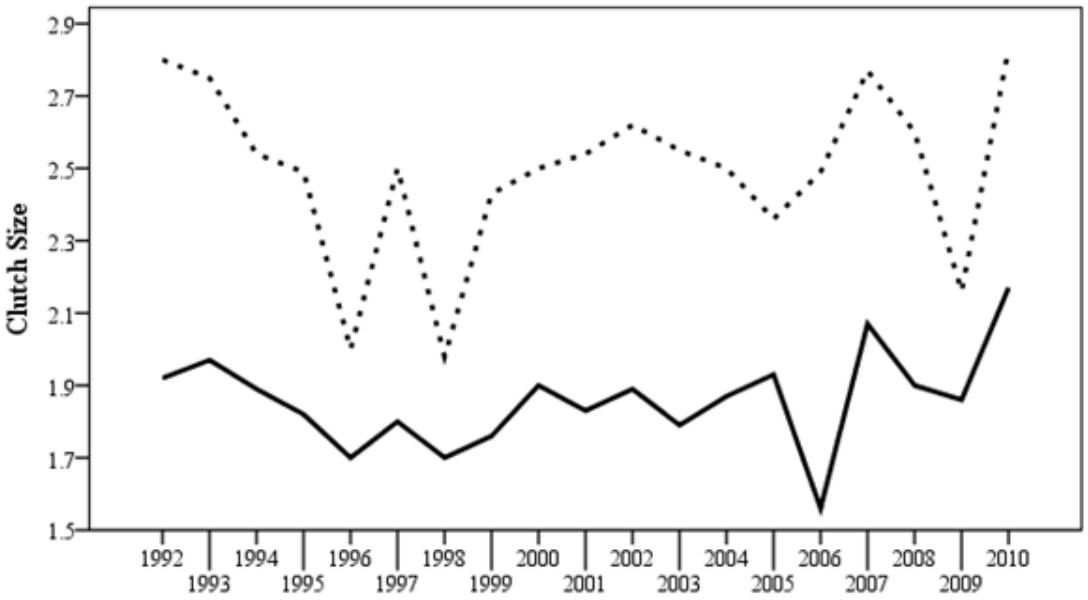


Figure 3.12 Average clutch size of Arctic (solid line) and Common Terns (dotted line) breeding on Coquet Island from 1992 through 2010.

While Arctic Tern productivity was significantly lower than that of Common Terns, the percentage of eggs laid by Arctic Terns that became fledged chicks was 45.2% and that for Common Terns was 49.7%. Therefore the breeding strategies of both species are similarly successful in terms of yield from investment (Mann-Whitney U, n=300, Z=1.158, p=0.247). What, then, are the constraining factors on clutch size?

The ability to brood eggs successfully has been shown to be a constraining factor on maximum clutch size (Slagsvold 1982; Reid et al. 2000; Larsen et al. 2003; Kim et al 2010). Both species hatched a similar percentage of the eggs laid (around 90%). However, Arctic Terns were less likely to successfully hatch 3 eggs than were Common Terns. The best reproductive strategy should maximise reproductive output while minimising investment. Failed eggs translate into wasted investment (both in terms of egg production and incubation effort). Arctic Tern 3 egg clutches were more likely to contain 'wasted' eggs, and therefore give a lower yield to investment ratio than 2-egg clutches. This should favour the production of 2-egg clutches over 3-egg clutches and is a potential reason for the prevalence of the smaller clutch size seen in Arctic Terns.

The higher failure rate of Arctic Tern 3-egg clutches could be due to reduced incubating success compared with that of Common Terns. While it is not possible to rule out this explanation, the rate of complete failure of 3-egg clutches was similar between Arctic and Common Terns. This suggests that incubation efficiency is not a major constraint. Hatching asynchrony is analysed in Chapter 4, but all Arctic Tern third chicks hatched within 3 days of the second chick, while hatching asynchrony between Common Tern second and third chicks was up to 5 days. Rather than brooding efficiency being a constraining factor, I propose that while Common Terns continue to incubate eggs in the nest, Arctic Terns abandon incubation in favour of chick provisioning. The differences in the foraging behaviour and parental attendance (Chapter 7) of the two species would indicate that Arctic Terns are under greater pressure to adequately provision chicks. This being the case, a single adult Arctic Terns may be unable to adequately provision two chicks once the second chick is over 3 days of age and the second adult abandons incubation to contribute to the foraging effort. In contrast, Common Terns appear to be able to maintain sufficient supply of food to young chicks without requiring both parents to forage and are therefore able to continue incubation of third eggs until hatching. Unfortunately insufficient data was collected to be able to compare Common Tern hatching success from 3 chick clutches between years, however one might expect higher rates of failure in years of poor overall feeding as provisioning pressures force both adults to forage and abandon incubation.

Clutch size had little link with productivity, with yearly clutch size having no correlation with yearly productivity and with similar numbers of chicks fledging from 2- or 3-egg clutches for both species. 1-egg clutches showed lower hatching success for both species and lower productivity for Arctic Terns. Small clutch sizes have been associated with younger, inexperienced birds (Sydman et al. 1991; Gonzales-Solis et al. 2004; Westneat et al. 2009; Limmer & Becker 2009; Limmer & Becker 2010) and poor condition of parents (Erikstad et al. 1993; Gonzales-Solis et al. 2004; Gladbach et al. 2010; Descamps et al. 2011). It is likely that this low success rate of single clutches was due to high abandonment or failure to incubate successfully due to poor quality parenting (although no data were collected to support this suggestion).

Provisioning behaviour of both species gives an indication that ability to successfully provision chicks may be a constraining factor for Arctic Terns. Both Arctic and

Common Tern chicks are completely reliant on parents for food throughout the pre-fledging period so their chances of survival are closely linked with the ability of parent birds to provide sufficient food during this time. Daily energy needs vary throughout the chick rearing period for both species, but Arctic Tern chick energy requirements are greater than those of Common Tern chicks of an equivalent age (Klassen et al. 1989).

Analysis of provisioning data showed that this was not reflected in the estimated energy being delivered to the nest. Common Terns foraged at a lower rate than Arctic Terns but on more energy rich prey (larger prey items and with a higher reliance on the more energy rich Clupeid, see Chapter 5) with Common Terns therefore returning to the nest with more 'estimated energy' per hour than Arctic Terns. Each foraging trip provided an Arctic Tern chick with approximately 4kJ of energy while for a Common Tern chick the figure was approximately 10kJ. In other words, Arctic Terns would have had to provision their chicks 2.5 times faster than Common Terns to provide the equivalent energy, but observed provisioning rates were only 1.3 times faster.

Foraging behaviours of the two species are compared in more detail later (Chapter 5). It appears Arctic Terns are either selecting quantity over quality, or have a preference for small prey, or are unable to utilise the feeding resources as successfully or efficiently as Common Terns. If there is a selection for quantity over quality, it still appears that conditions are suboptimal for Arctic Terns as they are failing to forage at a sufficient rate to compensate for the lower energy prey they are catching. If there is a bias in favour of smaller prey items by Arctic Terns, then there may be insufficient or inaccessible supply in the foraging areas around Coquet Island. The explanation of why there might be a difference in the ability of the two species to successfully exploit the foraging resources is complex, but Common Terns may favour different foraging areas which yield higher quality prey or may be able to exploit prey which are inaccessible to Arctic Terns.

The cornerstone of clutch-size theory is that clutch size is limited by parental ability to feed chicks (Lack 1954). Arctic Terns provisioned at a higher rate than Common Terns but with less yield for their effort, resulting in Arctic Tern chicks receiving less food despite their higher energy needs. Due to their already-high foraging effort, Arctic Terns may be unable to increase their provisioning rate enough to accommodate 3 chicks, thereby limiting clutch size (see Chapter 5 for provisioning in response to brood size).

While yearly productivity was not correlated with yearly clutch size, both species exhibited closely correlated yearly variations in productivity (Figure 3.13). Conditions during chick rearing impacted both species' ability to raise their chicks and affected yearly productivity. Poor feeding conditions are associated with poor breeding seasons (Barrett et al. 1987; Monaghan et al. 1989; Uttley et al. 1989; Croxall et al. 1999; Buber et al. 2004).

Common Terns showed a greater variation in productivity between years than did Arctic Terns but, with the exception of 2005, they maintained a higher productivity. Arctic Terns had years of very low reproductive output, with productivity of less than 1 chick per pair occurring in 12 years, and productivity falling below 0.5 on 4 occasions. This suggests high vulnerability to poor feeding conditions. It is proposed that Arctic Tern productivity is limited by ability to provision chicks even when conditions are favourable, while that of Common Terns is more limited by poor foraging conditions, and they are able to fledge more chicks when conditions are favourable. In poor years Arctic Terns appear less able to maintain productivity than Common Terns, suggesting that they are the more vulnerable to changing conditions.

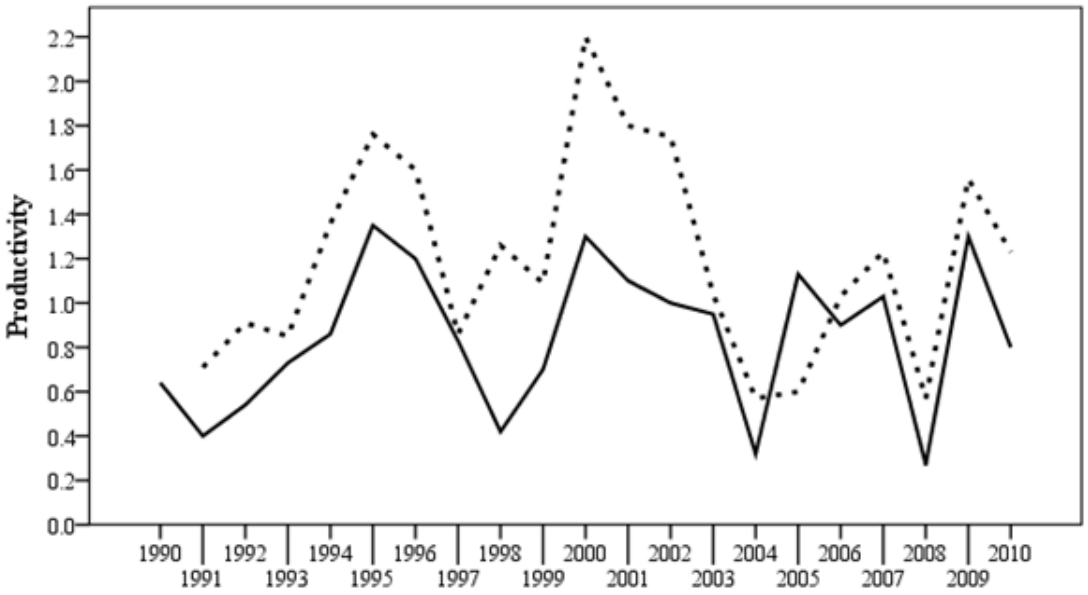


Figure 3.13 Average productivity of Arctic Terns (solid line) from 1990 and Common Terns (dotted line) from 1991 through 2010.

In conclusion, Arctic Terns laid fewer eggs and fledged fewer chicks than Common Terns. Hatching success and productivity were similar between species apart from

between 3-egg clutches, from which Arctic Terns both hatched and fledged fewer chicks than Common Terns. It is proposed that the low reproductive output from their 3-egg clutches was a result of Arctic Terns abandoning incubation in favour of chick provisioning prior to the third egg hatching. Provisioning behaviour of the two species was significantly different, with Arctic Terns provisioning chicks at a higher rate but on low energy prey resulting in lower energy delivery. It is suggested that their already high foraging effort may limit ability to provisioning larger broods and would make Arctic Terns more vulnerable to poor foraging conditions. Both species showed yearly variation in productivity but Common Terns maintained a higher reproductive output than Arctic Terns and appeared to show greater increase in productivity in good seasons. This suggests that for Common Terns the ability to provision chicks was not a limiting factor. It is proposed that, for Arctic Terns, clutch size is primarily limited by ability to provision chicks. For Common Terns, the high yearly variation in clutch size suggests that in certain years maternal condition affects egg production. The higher productivity would imply that when conditions were favourable, ability to provision chicks adequately was not a limiting factor.

Chapter 4. The effects of brood size, hatching order and timing on chick mortality

4.1 Abstract

Chick mortality is affected by the timing of hatching and by siblings. The effect of asynchronous hatching is the establishment of a brood hierarchy and increased mortality in younger siblings. Unlike a-chicks, the mortality rates of b-chicks of both Arctic and Common Terns showed high inter-annual variation. In some years, b-chick survival matched that of the a-chick, but in other years there was 100% mortality. This is evidence for brood reduction in response to reduced resources, with younger siblings failing to compete with elder siblings when resources were scarce. Younger siblings were also affected by elder sibling mortality, with the likelihood of survival increasing after the death of an elder sibling. This suggests that the presence of younger siblings in the nest acts as insurance in case of elder sibling mortality. No evidence was found to support the peak load hypothesis.

4.2 Introduction

Chick mortality can be caused by numerous factors, ranging from congenital defects to adverse weather conditions. However, the fixed factors such as timing of hatching (Hatchwell 1991; Sydman 1991; Moreno et al 1994; Nisbet et al. 1998) and a chick's place in the order of hatching within the brood (Langham 1974; Braun & Hunt 1983; Hunt & Evans 1997) can have a significant impact on the likelihood of a chick reaching fledging age.

Chicks hatched later in the season can be of poorer quality (smaller size or lower body mass) (Moreno et al. 1994), show higher mortality (Hatchwell 1991; Sydman 1991), and be less likely to be recruited into the breeding population (Daan et al. 1990; Tinbergen & Daan 1990; Cool et al 1994; Spear & Nur 1994; Dzus & Clark 1998). The timing of hatching clearly has a high impact on chick mortality and it is likely that a decline in productivity and an increase in chick mortality will occur as a season progresses.

Birds are either synchronous or asynchronous hatchers. In synchronous species brooding starts with the completion of the brood and all chicks hatch at about the same time. In asynchronous species, brooding starts once the first egg has been laid. As a result there is a delay, sometimes of several days, between the hatching of chicks within a single clutch. This often establishes a brood hierarchy, with the later-hatching chicks showing increased or complete mortality (Langham 1974; Braun & Hunt 1983; Hunt & Evans 1997). It is generally accepted that synchronous hatching is the ancestral norm with asynchronous hatching evolving later (Ricklefs 1965). Four main theories have been proposed to explain the evolutionary benefits of asynchronous hatching as a response to external pressures rather than physical constraints imposed by parental biology (although it is important to note that these hypotheses are not mutually exclusive).

1) Brood reduction hypothesis

The brood reduction hypothesis suggests that initial brood size should be such that if feeding conditions are good then all chicks could survive (e.g. Lack 1954; Howe 1976). However, if feeding conditions decline during the breeding season then the unequal competitive ability of the chicks within an asynchronous brood allows for easy removal of weaker, younger chicks without risk to healthier, older chicks (Ricklefs 1965; Litzow et al. 2002). It is expected to be advantageous where food supply is unreliable and unpredictable (Clark & Wilson 1981).

Brood reduction relies on the brood hierarchy established by asynchronous hatching to facilitate sibling removal. Several studies have found unequal resource allocation among chicks of an asynchronous brood, either through preferential feeding by parents (Braun & Hunt 1983; Fujioka 1985) or through the ability of elder siblings to dominate access to food, with younger siblings only accessing food when elder siblings are full (e.g. Braun & Hunt 1983; Hunt & Evans 1997; Smith et al. 2005). This results in increased mortality down the brood hierarchy, especially when resources are limited (Ricklefs 1965; Langham 1972; Braun & Hunt 1983; Amundson & Stokland 1988; Bollinger 1994; Hunt & Evans 1997; Smith et al. 2005). Brood reduction is often facultative, showing differing levels depending on resource availability.

2) Insurance egg/chick hypothesis

The insurance hypothesis suggests that the extra eggs are laid to act as an insurance policy against failure of primary eggs or chicks, with survival occurring only if something happens to an elder sibling (Braun & Hunt 1983; Evans 1997; Hunt & Evans 1997).

Forbes (1990) outlines three criteria needed for the insurance hypothesis to be effective:

1) Fairly high likelihood of primary egg or chick failure;
2) Small cost to parents to produce surplus offspring; and
3) The ability to easily remove the surplus offspring if they are not needed (as allowed by brood hierarchy and sibling competition).

Evans (1997) added an additional criterion:

4) Insurance offspring must be maintained in a viable condition during the high risk period for primary chicks.

In other words, the cost of producing and maintaining insurance chicks must be low and the risk of chick mortality high to make this a worthwhile strategy. If elder siblings survive, obligate brood reduction generally occurs.

Differing mortality rates should be observed depending on whether it is fluctuating food supply (therefore brood reduction) or parental ability (therefore insurance chicks) that limit chick survival. If brood reduction due to fluctuating food supply occurs, mortality of younger siblings should be less affected by sibling survival, instead mortality should show greater variation (both intra- and inter-yearly). However if productivity is limited by parental ability to provision a certain number of chicks, and surplus eggs/chicks act as an insurance policy against primary offspring failure, then younger sibling mortality should be influenced by elder sibling survival, and mortality should occur when chick energy demands are low, thereby reducing parental investment, and little yearly variation would be predicted.

3) Nest predation hypothesis

If predation risk is high and continuous throughout the breeding season, commencing incubation with the first egg lowers the time between egg production and fledging and thereby reduces the time exposed to predators (Hussell 1972, but see Clark & Wilson 1981).

There are no land based predators on Coquet Island and any predation pressures from large gull species (*Larus argentatus ,L. fuscus* and *L. marinus*), Black-headed Gulls (*Larus ridibundus*) or Corvids (*Corvus monedula* and *C. corone*) tend to be limited and restricted to the fringes of the main tern colony. While the nest predation hypothesis may have had an historical influence on the evolution of asynchrony in hatching, at this breeding site it is not considered to be currently relevant and is not further considered.

4) Peak load reduction hypothesis

Chicks show increased food demands with age and size (e.g. Langham 1972; Klassen et al. 1989). By hatching chicks asynchronously it is possible to either reduce the peak demand of a brood or reduce the duration of peak demand, and this is likely to be of greatest evolutionary benefit when parental foraging is limited (Hussell 1972, but see Clark& Wilson 1981).

Peak load hypothesis relies on the peak energy demands being too great for parents to be able to provision all chicks adequately their demands peak simultaneously. If this is the case, there should be a decrease in chick mortality with increasing degree of hatching asynchrony, as this reduces the pressures on parental foraging.

Arctic and Common Terns undertake asynchronous hatching, with broods of up to 3 chicks hatching over the course of several days. A comparison between chick mortality of the two species and the effects of hatching order, siblings and degree of asynchrony should enable interpretation of how asynchrony effects survival. Mortality is expected to increase down the brood hierarchy, with younger siblings showing higher mortality rates and dying at a younger age. If brood reduction is occurring then younger sibling mortality should show great variation between years; if the insurance hypothesis holds true, then younger sibling mortality will be significantly affected by elder sibling

survival. If hatching asynchrony reduces the peak load on parent birds, then the degree of asynchrony should affect nest productivity and chick survival.

4.3 Methodology and analysis

4.3.1 Methodology

See Chapter 2 section 2.2.

4.3.2 Analysis

For each season and species, the day the first study chick hatched was classed as day 1. This enabled analysis of distribution between species regardless of date within the breeding season. Hatch day and ages at death were tested for normality using Kolmogorov-Smirnov testing of the null hypothesis of normal distribution and were found to be non-normally distributed. All analysis was undertaken using IBM SPSS Statistics, version 19.

Differences in the hatch-day distribution between species were tested using Mann-Whitney U analysis, and differences between years compared using Kruskall-Wallis analysis with pair-wise comparisons (adjusted p-value). The correlation between productivity and hatch day was tested using Spearman's Rho correlation and the effect of hatch day on chick mortality was tested using binary Logistic Regression.

The effect of hatch day, hatching order and year on age at death was tested using Log Rank (Mantel-Cox) Kaplan-Meier survival analysis.

Differences in the proportions of chicks fledging and dying by species, hatching order and between years were analysed using Pearson's Chi-squared test, with Z-test of column proportions used to compare groups. Productivity and chick mortality depending on brood size was analysed using Pearson's Chi-squared test with Z-test of column proportions when appropriate.

Distribution of hatching asynchrony was compared between first, second and third chicks, and between species using Mann-Whitney U analysis. The effect of degree of asynchrony on chick mortality was analysed using binary logistic regression.

4.4 Results

4.4.1 Seasonal trends: hatch day

For the observed nests, all eggs hatched within 20 days of first egg of the year hatching for Arctic Terns and within 23 days for Common Terns, with peak hatching occurring 6 days after the first egg hatched (Figure 4.1).

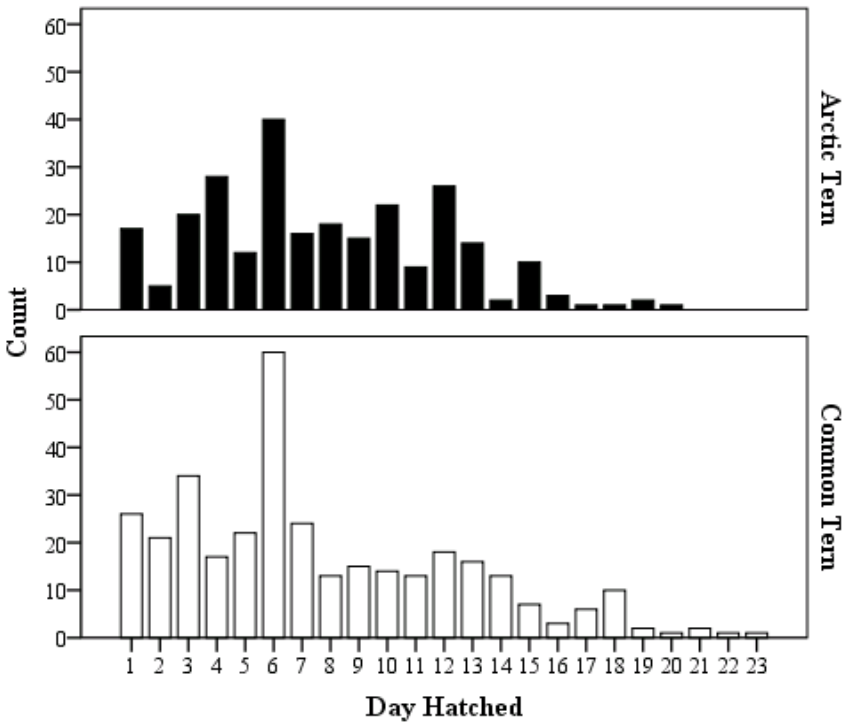


Figure 4.1 Distribution of hatching within the season of 262 Arctic Tern chicks and 340 Common Tern chicks hatched between 2006 and 2010 (from 150 nests of each species overall), day1 = day first chick of the season from the observed nests is seen to fully hatch.

Mann-Whitney U analysis of distribution of hatching showed no difference in the seasonal distribution of hatching between Arctic and Common Terns (Mann-Whitney U, n=601, Z=-0.994, p=0.320).

There was a significant difference in distribution of hatching between years for both Arctic Terns (Kruskall-Wallis, n=262, df=4, χ^2=16.837, p=0.002) and Common Terns (Kruskall-Wallis, n=340, df=4, χ^2=65,612, p<0.001). Pair-wise analysis showed that Arctic Tern distribution only differed between 2006 and 2010 (p=0.002) and Common Tern distribution differed between all years apart from 2006 and 2007 (p=0.115), 2006

and 2009 (p>0.999) and between 2007 and 2010 (p>0.999), with an almost significant difference between 2008 and 2010 (p=0.065), (Figure 4.2).

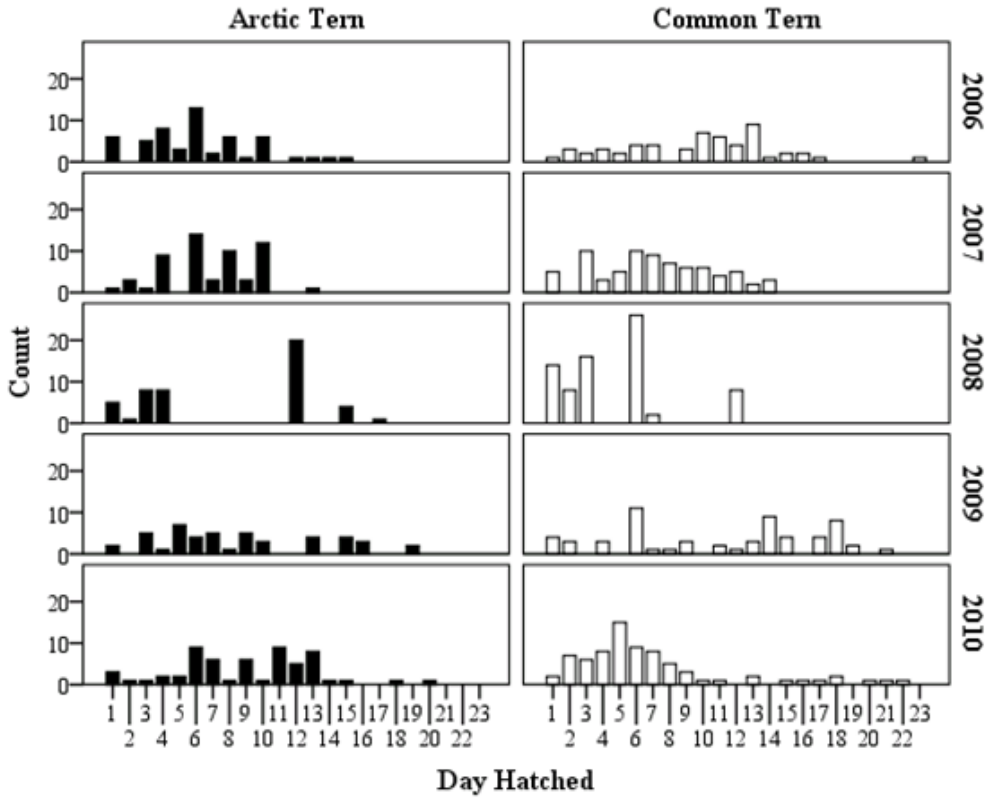


Figure 4.2 Distribution of Arctic and Common Tern chick hatching within the season for the years 2006 through 2010 (hatching days recorded from a different random sample of 30 nests of each species observed each year).

4.4.2 Seasonal Trends: mortality

There was no correlation between hatch day of first chick in the nest and productivity for either Arctic Terns (Spearman's Rho, n=138, Rho=-0.124, p=0.147) or Common Terns (n=144, Rho=-0.011, p=0.893).

Logistic regression of Arctic Tern chick survival to fledging (1=fledged, 0=died) as a dependant variable showed a significant increase in mortality of chicks hatching later in the season (hatch day as model predictor) (Table 4.1, Figure 4.3).

	β	SE	Walds	df	p	Exp(β)
Hatch Day	-0.086	0.031	7.781	1	0.005	0.917
Constant	0.682	0.269	6.415	1	0.011	1.977
			χ^2	df	p	
Omnibus test for model coefficients			8.086	1	0.004	

Model Summary: -2 log likelihood= 355.108. Cox & Snell R^2= 0.030. Nagelkerke R^2= 0.041.

Model Predictors: Outcome: 0=56.2% correct; 1=61.4% correct; overall=58.8% correct.

Table 4.1 Logistic regression of the effect of hatch day on the survival outcome of 247 Arctic Tern chicks (1=fledged, 0=died)

Logistic regression analysis of Common Tern chick survival to fledging (1=fledged, 0=died) did not demonstrate a significant relationship between chick mortality and time of hatching within a season (Table 4.2, Figure 4.3).

	B	SE	Walds	df	p	Exp(β)
Hatch Day	-0.25	0.022	1.300	1	0.254	0.975
Constant	0.248	0.202	1.497	1	0.221	1.281
			X^2	df	P	
Omnibus test for model coefficients			1.306	1	0.253	

Model Summary: -2 log likelihood= 468.409. Cox & Snell R^2= 0.004. Nagelkerke R^2= 0.005.

Model Predictors: Outcome: 0=32.7% correct; 1=69.5% correct; overall=51.6% correct.

Table 4.2 Logistic regression of the effect of hatch day on the survival outcome of 330 Common Tern chicks (1=fledged, 0=died)

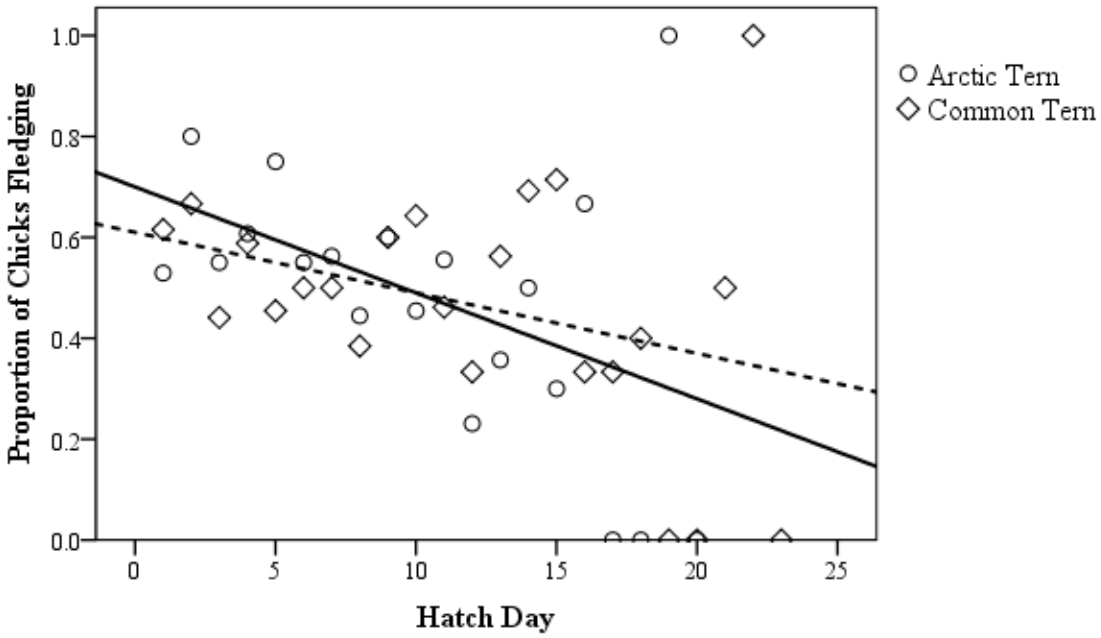


Figure 4.3 Mean proportion of Arctic and Common Tern chicks fledging depending on when they hatched within the season, lines show relationship between hatch day and proportion of chicks fledging (Arctic Tern: solid line; Common Tern: dotted line).

Age of death was significantly negatively correlated with hatch day for both Arctic Terns (Spearman's Rho, n=101, Rho=-0.467, p<0.001) and Common Terns (n=132, Rho=-0.308, p<0.001), (Figure 4.4).

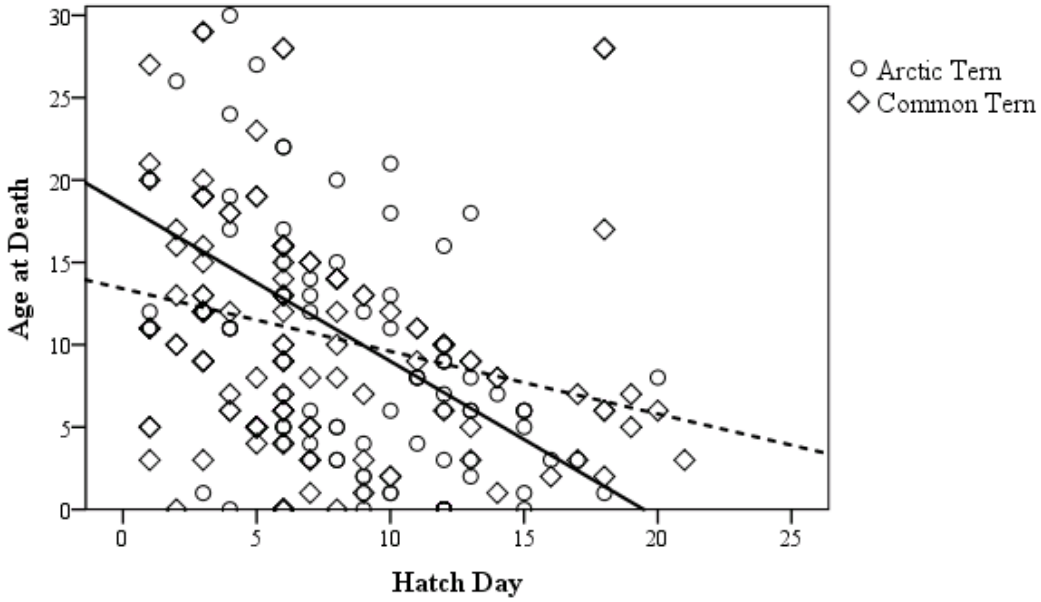


Figure 4.4 Arctic and Common Terns age at death in relation to when they hatched within the breeding season, lines show the negative relationship between hatch day and age of death (Arctic Tern: solid line; Common Tern: dotted line).

4.4.3 Hatching order and chick mortality

Hatching order had a significant effect on proportion of chicks dying or fledging for both Arctic Terns (Pearson's Chi-squared comparing a- and b-chicks only, n=252, df=1, χ^2=49.070, p<0.001) and Common Terns (comparing a-, b- and c-chicks, n=340, df=2, χ^2=98.095, p<0.001). Z-test of column proportions showed significantly lower mortality in Arctic Tern a-chicks than b-chicks, while mortality in Common Tern chicks decreased significantly down the brood hierarchy, with lowest mortality in a-chicks, then b-chicks and highest mortality in c-chicks (Figure 4.5).

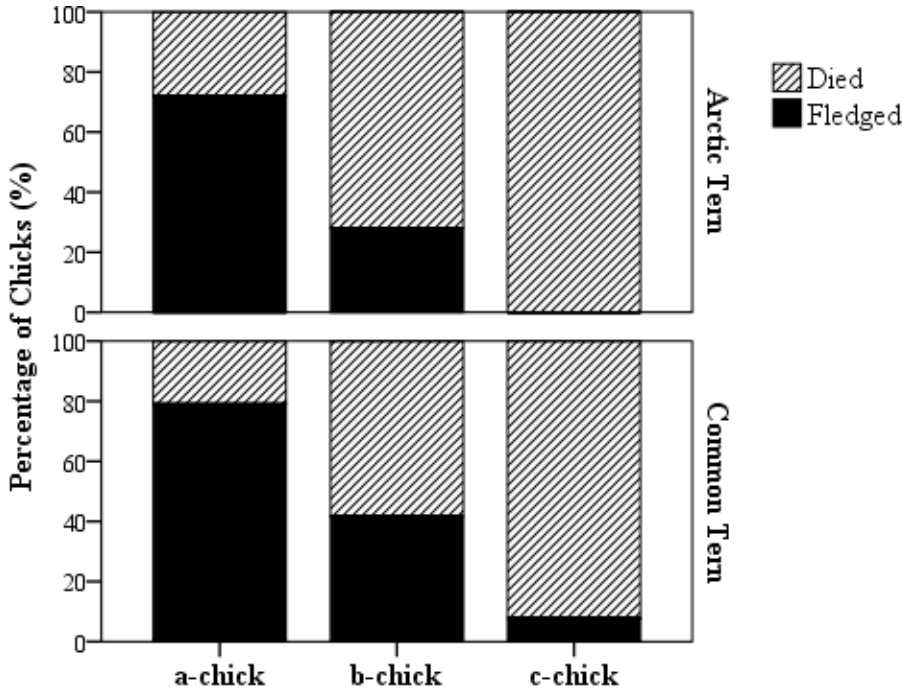


Figure 4.5 Percentage of chicks fledging or dying depending on hatching order for Arctic and Common Terns.

There was no difference between Arctic and Common Tern a-chick mortality (Pearson's Chi-squared, n=283, df=1, χ^2=2.002, p=0.157) but b-chick mortality was significantly more likely for Arctic than Common Terns (n=247, df=1, χ^2=5.160, p=0.023).

Kaplan-Meier survival analysis of Arctic Tern chick mortality showed an almost significant variation in distribution of age at death between a-chicks and b-chicks, with b-chick deaths occurring slightly more frequently at younger ages. Common Tern chick mortality varied in distribution between chicks of different hatching orders overall and between all pair-wise comparisons, with death occurring significantly younger further down the brood hierarchy (Table 4.3, Figure 4.6, Figure 4.7). Arctic Tern c-chick mortality was not analysed because of very low sample size (n=6).

		n	χ^2	df	p
Arctic Tern	a-chick *v.* b-chick	94	3.778	1	0.052
Common Tern	Overall	133	30.972	2	<0.001
	a-chick *v.* b-chick	85	8.931	1	0.003
	a-chick *v.* c-chick	71	18.784	1	<0.001
	b-chick *v.* c-chick	110	15.131	1	<0.001

Table 4.3 Kaplan-Meier survival analyses of pre-fledging ages at death for Arctic and Common Terns depending on hatching order

Kaplan-Meier survival analysis showed no significant inter-species variation in mortality distribution either overall or when comparing a-chick or b-chick mortality for Arctic and Common Terns (Table 4.4).

	n	χ^2	df	p
Total	217	0.505	1	0.477
a-chick	47	0.012	1	0.914
b-chick	118	2.858	1	0.091

Table 4.4 Kaplan-Meier survival analyses comparing pre-fledging ages at death of Arctic and Common Tern chicks overall and between a- and b-chicks

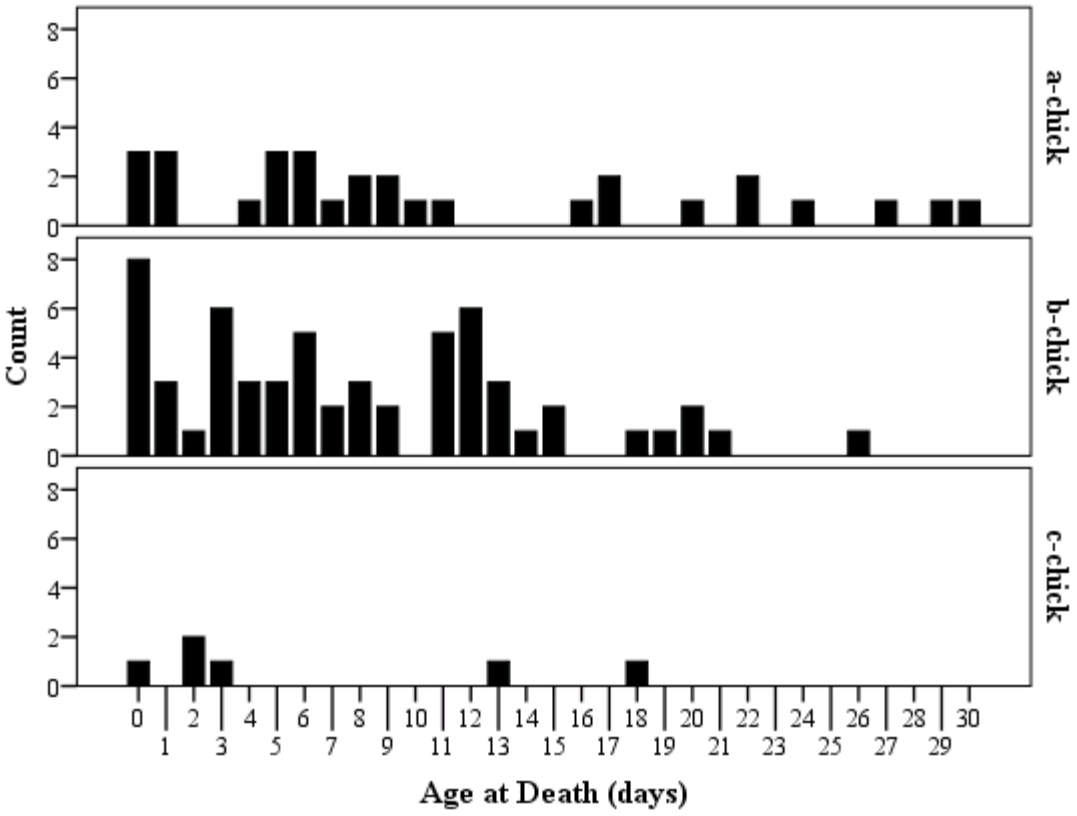


Figure 4.6 Distribution of age at death for Arctic Tern chicks depending on hatching order.

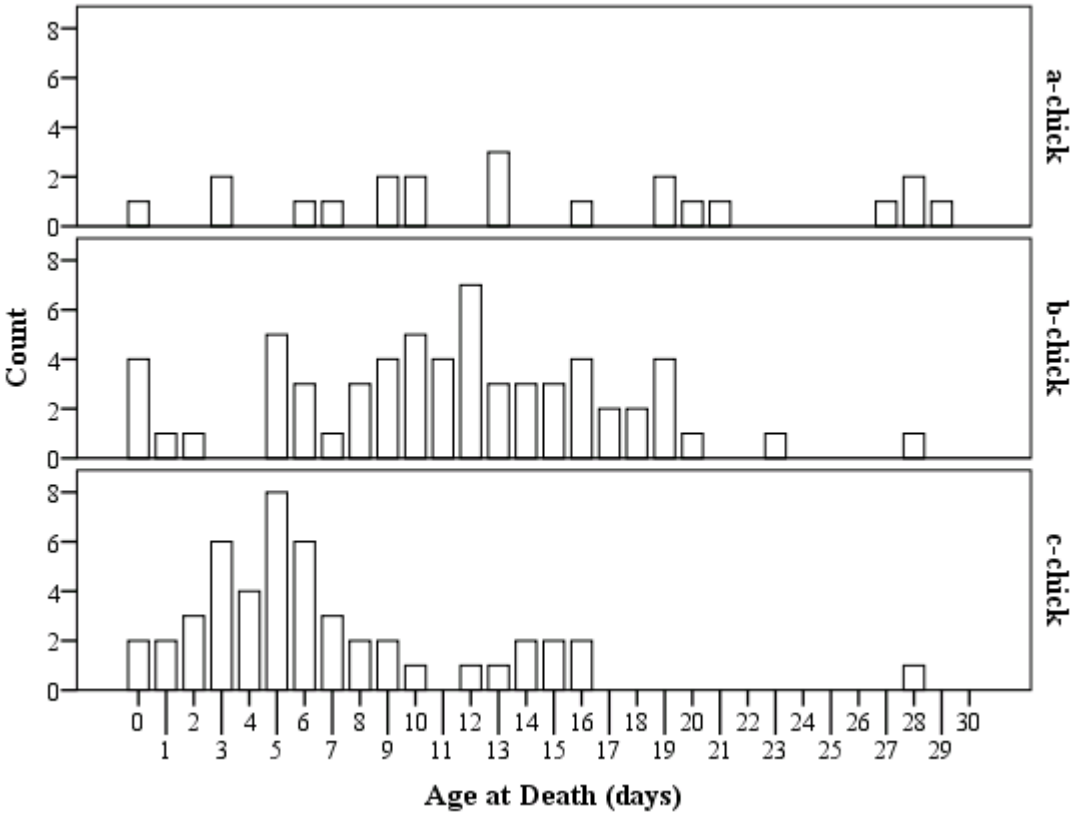


Figure 4.7 Distribution of age at death for Common Tern chicks depending on hatching order.

4.4.4 Effect of brood size

Brood size had no effect on productivity for either Arctic Terns (Pearson's Chi-squared, n=138, df=4, χ^2=7.380, p=0.117) or Common Terns (n=144, df=6, χ^2=9.629, p=0.141). Nor did brood size affect the proportion of a- or b-chicks dying (between brood sizes of 1, 2 or 3 for a-chicks and between brood sizes of 2 or 3 for b-chicks) for either Arctic or Common Terns (Table 4.5).

		n	χ^2	df	P
Arctic Tern	a-chick	138	1.475	2	0.478
	b-chick	115	0.680	1	0.409
Common Tern	a-chick	144	1.063	2	0.588
	b-chick	132	0.281	1	0.596

Table 4.5 Pearson's Chi-squared analysis of the effect of brood size on mortality of Arctic and Common Tern chicks depending on hatching order

Kaplan-Meier analysis of age at death showed an effect on brood size on Arctic Tern a-chicks, with single chicks dying at a younger age (all deaths occurred by the age of 10 days) than those from 2-chick broods. No effect of brood size was found for Arctic Tern b-chick or Common Tern a- or b-chicks (Table 4.6, Figure 4.5). Arctic Tern mortality between 1- and 2-chick broods and 3-chick broods was not analysed because of the small sample size for a-chick age at death (n=3) from 3-chick broods. No Common Tern a-chick age at death were recorded for 1-chick broods.

		n	χ^2	df	p
Arctic Tern	a-chick (1- *v.* 2-chick brood)	31	6.437	1	0.011
	b-chick (2- *v.* 3-chick brood)	60	0.950	1	0.330
Common Tern	a-chick (2- *v.* 3-chick brood)	23	0.049	1	0.824
	b-chick (2- *v.* 3-chick brood)	62	1.431	1	0.232

Table 4.6 Kaplan-Meier survival analyses of pre-fledging ages at death of Arctic and Common Tern chicks depending on brood size

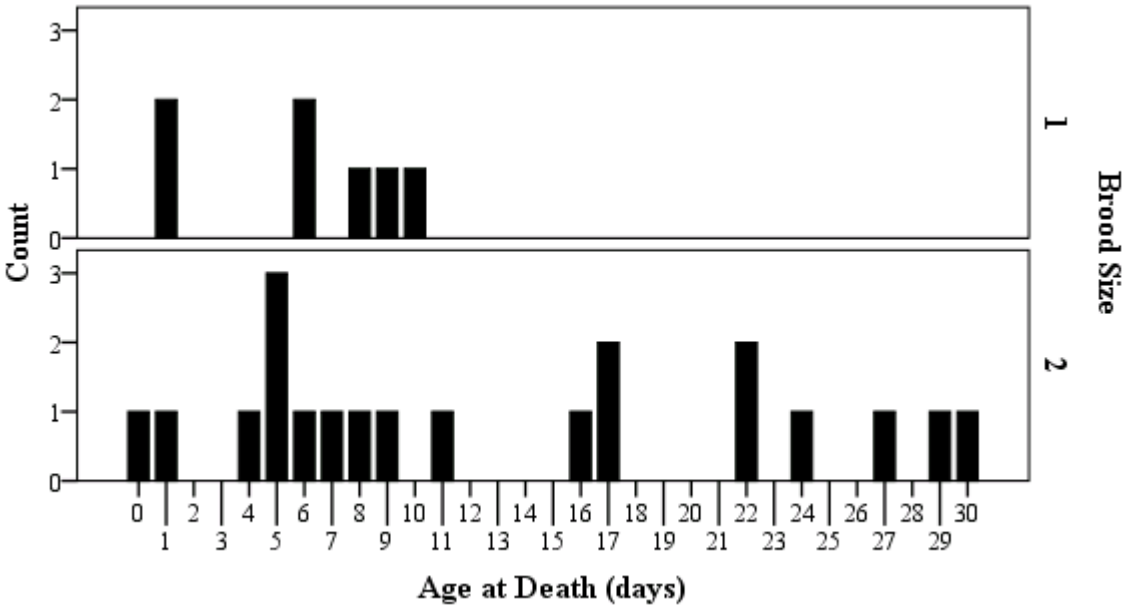


Figure 4.8 Distribution of Arctic Tern a-chick age at death depending on brood size.

4.4.5 Effect of younger siblings

Proportion of Arctic and Common a-chicks fledging or dying was not affected by b-chick mortality (Pearson's Chi-squared, Arctic Terns, n=88, df=1, χ^2=1.417, p=0.234; Common Terns, n=108, df=1, χ^2=1.786, p=0.181). If mortality of both b- and c-chicks was taken into account, then a significantly higher proportion of Common Tern a-chick survived when a younger sibling died (n=108, df=1, χ^2=3.904, p=0.048, Figure 4.9). Common Tern b-chick survival was significantly affected by c-chick mortality, with a significantly higher proportion of the b-chicks that fledged having outlived a younger sibling (n=52, df=1, χ^2=7.606, p=0.006, Figure 4.10). Because of the small sample size, mortality of Arctic Tern c-chicks was not analysed.

4.4.6 Effect of elder siblings

A significantly higher proportion of Arctic Tern b-chicks fledged if they had outlived their elder sibling (Pearson's Chi-squared, n=89, df=1, χ^2=7.180, p=0.007, Figure 4.11). Common Tern a-chick mortality had no effect on b-chick survival (n=109, df=1, χ^2=2.444, p=0.118). Common Tern c-chick survival was significantly affected by combined a- and b-chick mortality, with only c-chicks that outlived at least one elder sibling managing to fledge (n=55, df=1, χ^2=18.265, p<0.001, Figure 4.12).

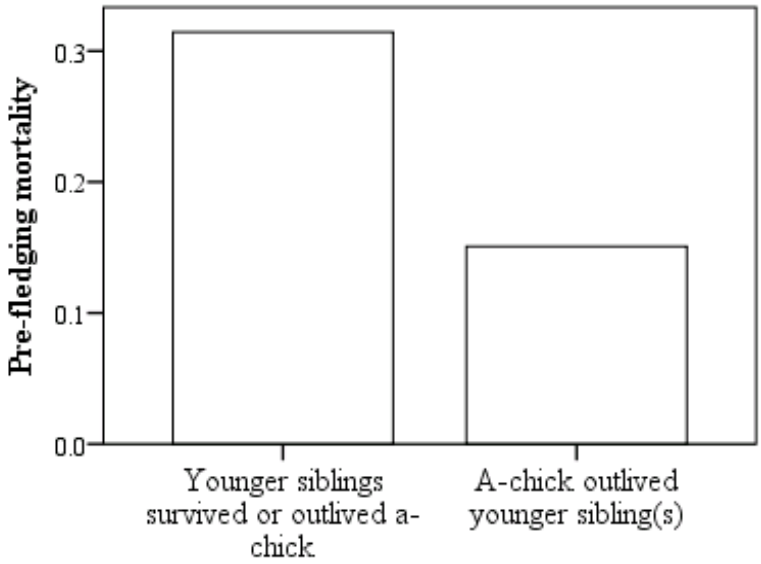


Figure 4.9 Proportion of Common Tern a-chicks who died prior to fledging depending on whether their younger sibling(s) survived (or survived longer than a-chick) or if a-chick outlived at least one younger sibling.

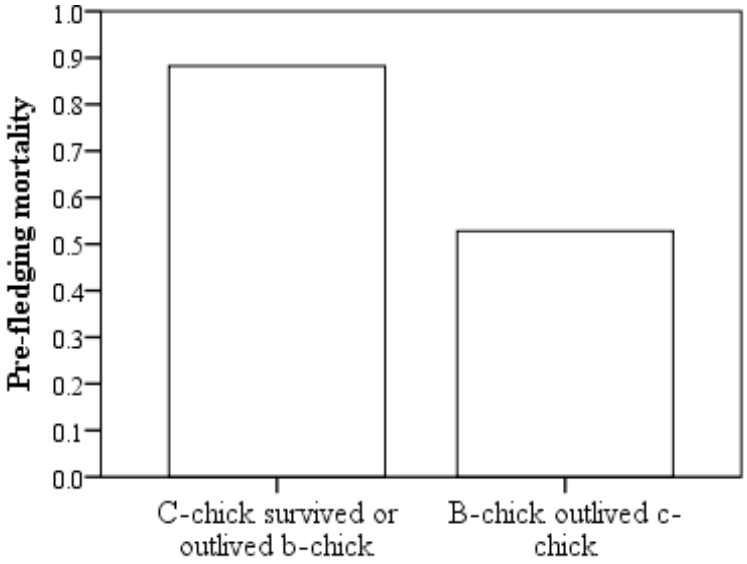


Figure 4.10 Proportion of Common Tern b-chicks who died prior to fledging depending on whether their younger sibling survived (or survived longer than b-chick) or if b-chick outlived it.

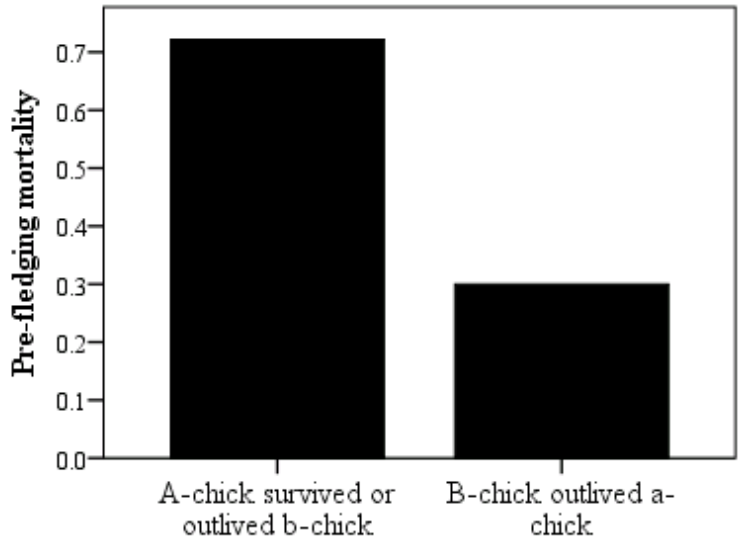


Figure 4.11 Proportion of Arctic Tern b-chicks who died prior to fledging depending on whether their elder sibling survived (or survived longer than b-chick) or if b-chicks outlived it.

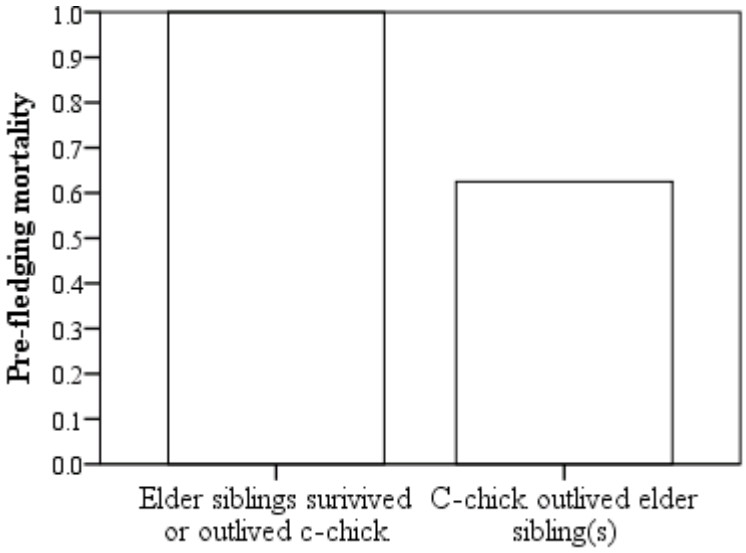


Figure 4.12 Proportion of Common Tern c-chicks who died prior to fledging depending on whether their elder siblings survived (or survived longer than c-chick) or if c-chicks outlived them.

4.4.6 Hatching asynchrony

Both species showed hatching asynchrony, with brood completion taking between 0 and 5 days for Arctic Terns and between 0 and 9 days from Common Terns. Hatching asynchrony between a- and b-chicks ranged between 0 and 4 days for both Arctic and Common Terns. Hatching asynchrony between b- and c-chicks ranged between 0 and 3 days for Arctic Terns and 0 and 6 days for Common Terns (Figure 4.13).

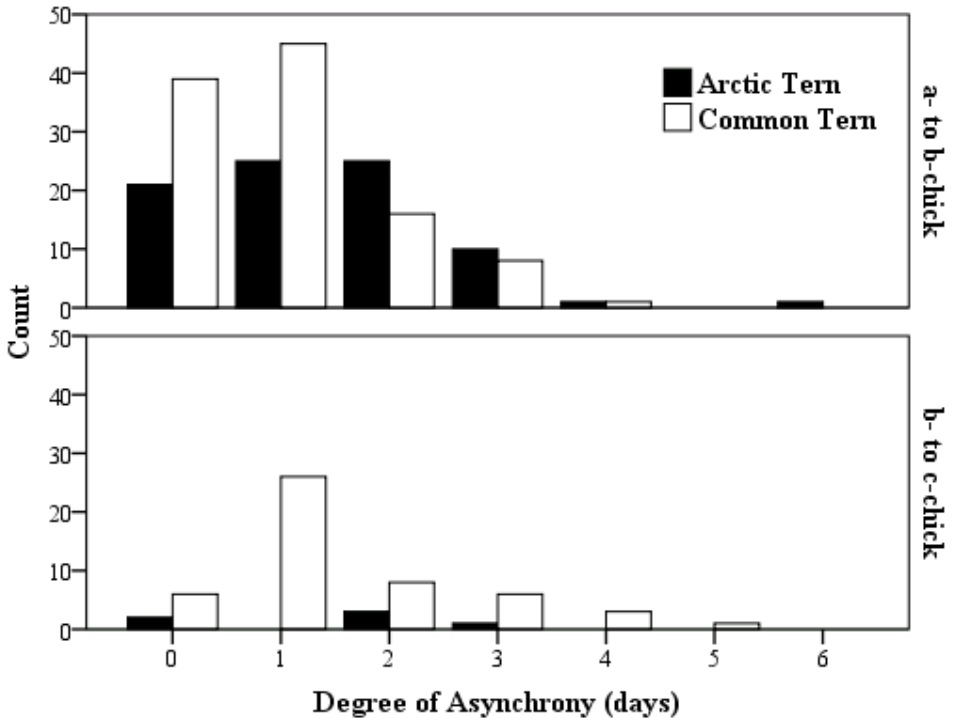


Figure 4.13 Distribution of hatching asynchrony between first and second chicks (a- to b-chick) and second and third chicks (b- to c-chick) for Arctic and Common Terns

There was no difference in the degree of Arctic Tern hatching asynchrony between a- and b-chicks with the degree of asynchrony between b- and c-chicks (Mann-Whitney U, n=113, Z=0.582, p=0.561). Common Terns showed a greater degree of asynchrony between b- and c-chicks than between a- and b-chicks (n=189, Z=3.085, p=0.001).

Arctic Terns took less time to completely hatch a clutch than did Common Terns (Mann-Whitney U, n=236, Z=2.325, p=0.020), while the degree of hatching asynchrony between a-and b-chicks (n=236, Z=1.825, p=0.068) and b- and c-chicks (n=66, Z=0.047, p=0.963) was comparable between species.

Logistic regression analysis showed no effect of increasing hatching asynchrony between first and second chick hatching on a- or b-chick mortality for either Arctic or Common Terns. Hatching asynchrony between second and third chicks had no effect on either b- or c-chick mortality for Common Terns (Table 4.7).

			β	S.E.	Wald	df	Sig.	Exp(β)
Arctic Tern	a-chick	a- to b-chick	-0.017	0.218	0.01	1	0.938	0.983
		Constant	1.060	0.394	7.240	1	0.007	2.886
	b-chick	a- to b-chick	-0.057	0.206	0.078	1	0.781	0.944
		Constant	-0.56	0.362	2.390	1	0.122	0.571
Common Tern	a-chick	a- to b-chick	-0.230	0.241	0.915	1	0.339	0.794
		Constant	1.554	0.351	19.630	1	0.001	4.731
	b-chick	a- to b-chick	0.072	0.206	0.122	1	0.727	1.075
		Constant	-0.384	0.279	1.895	1	0.169	0.681
	b-chick	b- to c-chick	0.173	0.251	0.474	1	0.491	1.189
		Constant	-0.76	0.494	2.369	1	0.124	0.468
	c-chick	b- to c-chick	-1.040	0.712	2.131	1	0.144	0.354
		Constant	-1.017	0.782	1.694	1	0.193	0.362

Table 4.7 Logistic regression of effect of length of hatching asynchrony on the mortality of Arctic and Common Tern chicks of different hatching order (1=fledged, 0=died)

4.4.7 Inter-annual variation

Year had a significant effect on Arctic Tern a-chick mortality, with a significantly higher proportion of a-chicks dying in 2008 than in all other years (Pearson's Chi-squared, n=139, df=4, χ^2=19.858, p=0.001 with Z-test for column proportions, Bonferroni adjusted p-value). Arctic Tern b-chick mortality was significantly different between years, with mortality equally high in 2006, 2008 and 2010, significantly lower 2007 and lowest in 2009 (n=115, df=4, χ^2=40.441, p<0.001). Year had a significant effect on Common Tern a-chick mortality, with highest proportion of chicks dying in 2008 and lowest in 2009 and 2010 (n=144, df=4, χ^2=10.583, p=0.032). Common Tern b-chick mortality was significantly affected by year, with lowest mortality seen in 2009 but otherwise comparable between years (n=132, df=4, χ^2=25.256, p<0.001), (Figure 4.14).

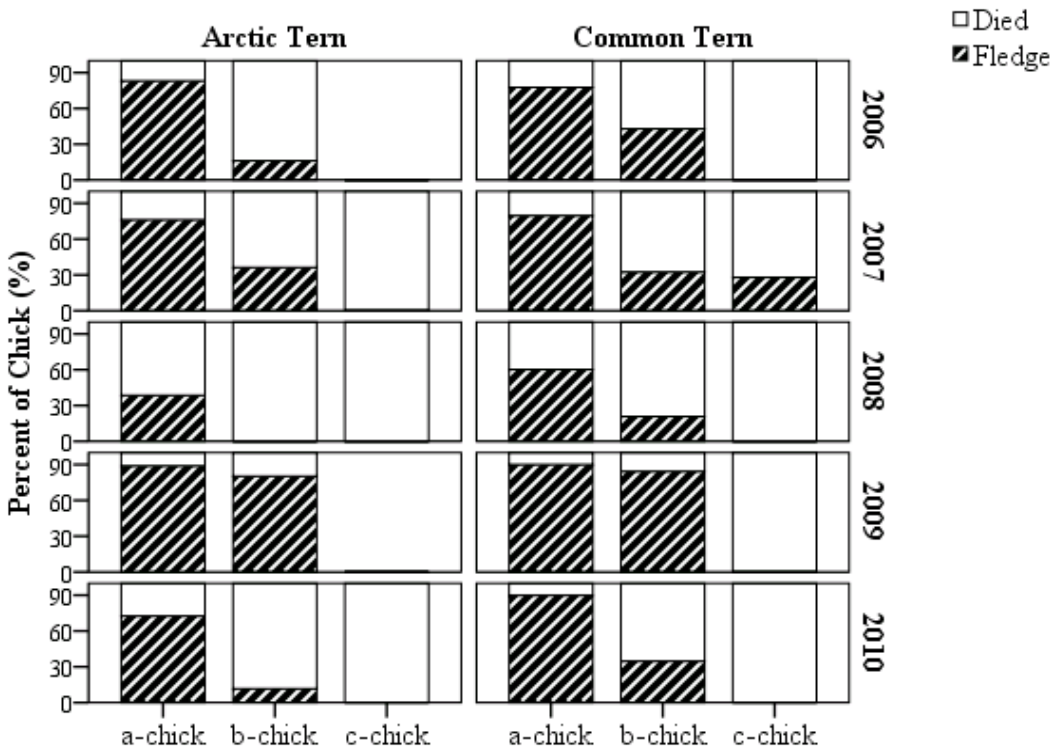


Figure 4.14 Proportion of Arctic and Common Tern chicks fledging or dying prior to fledging by hatching order depending on year.

Both Arctic and Common Tern b-chick mortlaity was always signifincantly lower than that of a-chicks apart from in 2009 when mortality was comparable (Table 4.8)

	Arctic Tern	Common Tern
2006	<0.001	0.014
2007	0.003	<0.001
2008	0.002	0.002
2009	0.350	0.415
2010	<0.001	<0.001

Figure 4.8 One-sided Fisher's exact test testing for differences in the number of chick fledging or dying depending on hatching order, split between years.

Kaplan-Meier analysis of differences in age of death between years showed no difference for Arctic Tern a- or b-chicks or Common Tern b-chicks. Common Tern a- and c-chick distribution of age at death varied significantly between years (Table 4.9). Common Tern a-chick deaths occurred at significantly younger ages in 2009 and 2010

than in 2007 and 2008. Common Tern c-chick deaths occurred at slightly older ages in 2007 than other years (Table 4.10, Figure 4.15, Figure 4.16).

		n	χ^2	df	p
Arctic Tern	a-chick	34	0.258	1	0.612
	b-chick	60	0.018	1	0.894
Common Tern	a-chick	23	5.517	1	0.019
	b-chick	62	0.704	1	0.401
	c-chick	48	10.073	1	0.002

Table 4.9 Kaplan-Meier survival analyses of pre-fledging ages at death of Arctic and Common Tern chicks depending on year

	a-chick				c-chick			
	n	χ^2	df	p	N	χ^2	df	p
2007 vs. 2008	17	0.491	1	0.483	25	6.882	1	0.009
2007 vs. 2009	9	9.715	1	0.002	19	0.198	1	0.657
2007 vs. 2010	9	7.398	1	0.007	30	12.977	1	<0.001
2008 vs. 2009	14	9.302	1	0.002	18	0.481	1	0.488
2008 vs. 2010	14	6.539	1	0.011	29	3.738	1	0.053
2009 vs. 2010	6	1.561	1	0.212	23	2.385	1	0.124

Table 4.10 Kaplan-Meier survival analyses of pre-fledging ages at death of a- and c-chick Common Terns

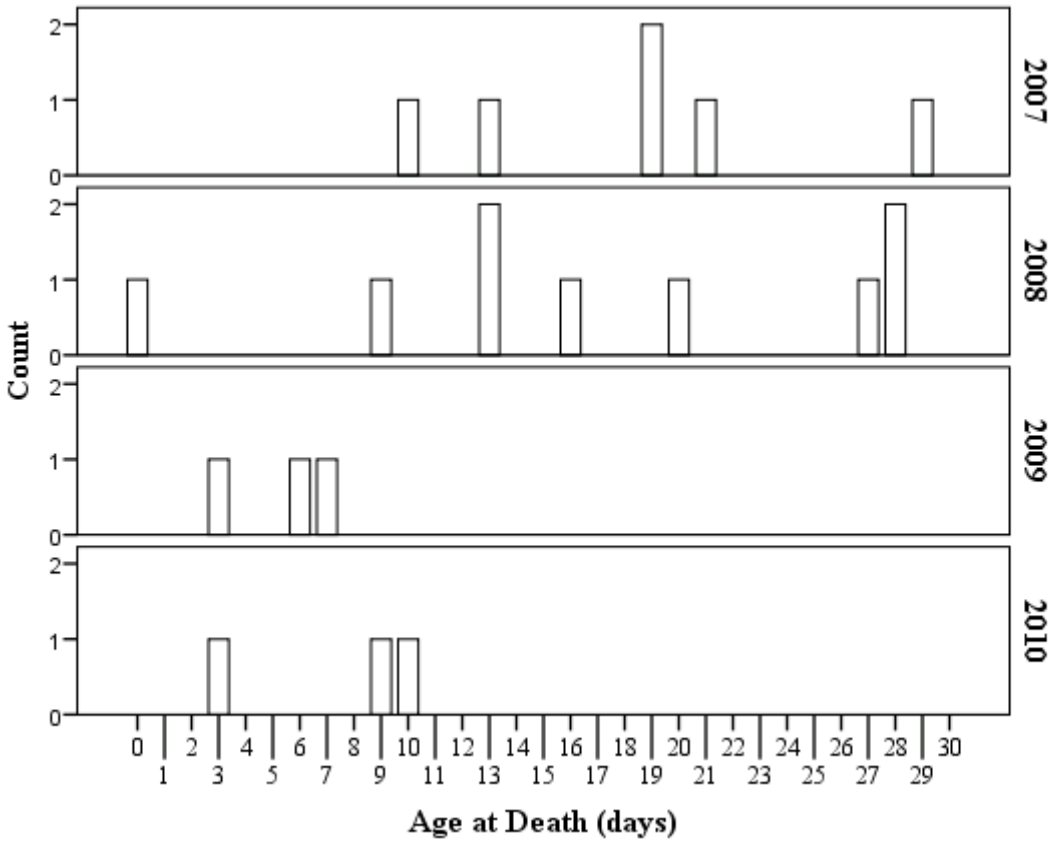


Figure 4.15 Distribution of 23 Common Tern a-chick ages at death, showing a significant effect of year (Kaplan-Meier, χ^2_{23}=5.517*).

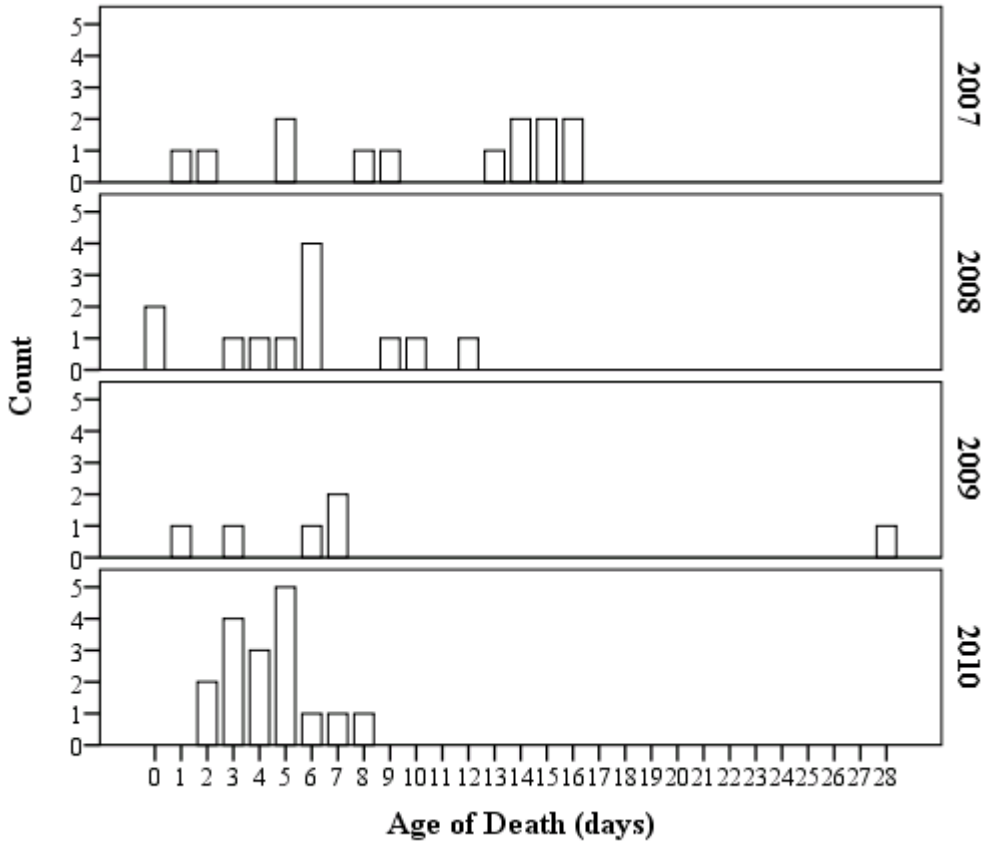


Figure 4.16 Distribution of 48 Common Tern c-chick ages at death showing a significant effect of year (Kaplan-Meier, χ^2_{48}=0.073**)

4.5 Discussion

Both Arctic and Common Terns exhibited similar patterns in hatching: the majority of hatching occurred within the first week (52% of Arctic Tern chicks and 60% of Common Tern chicks), peaked during this time and then steadily declined, with less than 10% of the chicks hatching 2 weeks after the first chick hatched. The distribution of hatching varied slightly between years, with some years showing more protracted hatching than others.

There was no effect of season on either Arctic Tern or Common Tern productivity or Common Tern chick mortality. These results differ from other studies which showed a decline in productivity and an increase in mortality as the season progressed (Hatchwell 1991; Sydman et al. 1991; Moreno et al 1997). However, Arctic Tern chick mortality did increase in chicks hatched later in the season and later-hatched chicks of both species died younger, showing that the timing of hatching affects chick mortality. Later breeding has been linked with poor quality or young parents (Sydman 1991). However, studies have shown that it is hatch day and parental investment rather than parental quality that influences chick condition and mortality (Hatchwell 1991; Verhults & Tinbergern 1991; Norris 1993; Moreno et al. 1997). It is possible that the longer migration of Arctic Terns means that they are more likely to abandon late chicks.

Overall, this study supports the findings of previous studies with regard to percentage mortality and age at death changing depending on hatching order (Langham 1974; Bollinger et al. 1990; Hunt & Evans 1997; Smith et al. 2005). Both species hatched more chicks than could usually be successfully raised to fledging, and second-hatched chicks showed significantly higher mortality (72% of Arctic and 56% of Common Tern chicks) than the 23% mortality seen in both species for chicks that hatched first. Common Tern third-hatched mortality was also significantly higher (92%) than both first- and second- hatched mortality, and all Arctic Tern third-hatched chicks failed to fledge.

Distribution of mortality also differed within the brood hierarchy. First-hatched chicks showed mortality fairly evenly distributed throughout the pre-fledging period, while the majority of younger siblings died at a younger age (Table 4.11). Interestingly, in years of very low first-hatched chick mortality, the age at death was correspondingly low (Common Terns 2009 and 2010). It is proposed that as these years corresponded with

good food supply, once chicks survived the high-risk early days the subsequent risk of mortality was very low.

	First Hatched	Second Hatched	Third Hatched
Arctic Tern	Within 22 days	Within 12 days	n/a
Common Tern	Within 27 days	Within 15 days	Within 8 days

Table 4.11 Showing time from hatching by when 75% of deaths had occurred for Arctic and Common Tern chicks depending on hatching order

Hatching order within the brood has an important effect on the likelihood of fledging and a brood hierarchy is established through asynchronous hatching. For asynchronous hatching to benefit reproductive output, surplus chicks must be able to be easily removed from the brood once it becomes apparent that they are negatively impacting elder siblings. The easiest way of removing chicks from the nest is by limiting their access to food.

Unequal allocation of resources within a hierarchical brood is known to occur either through preferential feeding of elder siblings by parent birds (Braun & Hunt 1983; Fujioka 1985; Anderson & Ricklefs 1992; Stienen et al. 2000; Ostreiher 2001) or through the comparative advantage of elder siblings in either direct competition for a food item or in their ability to access food first (first to reach parents) (Braun & Hunt 1983; Hunt & Evans 1997; Smith et al. 2005). Adequate food supply is crucial for chick development and successful fledging (Langham 1972; Becker& Specht 1991; Quillfeldt 2001; Buber et al. 2004) and if younger chicks' access to food is limited by older chicks, then death due to starvation is more likely. However, the majority of mortality recorded here (75%) occurred before the peak energy demands of the chicks are reached (Klassen et al 1989), suggesting that ability to provision chicks may not be a limiting factor.

Increased yearly variability of second-hatched chick survival rates compared to first-hatched indicates that brood reduction due to limited food supply occurred. Brood reduction occurs when food supply is such that parents can no longer adequately provide for all chicks in the brood. Brood hierarchy allows the removal of younger siblings so that elder siblings still receive sufficient food. The yearly patterns in chick mortality were similar between first- and second-hatched chicks but more exaggerated

in the second-hatched chicks. This indicates that second-hatched chicks are much more vulnerable to fluctuating resources, with 'good' or 'bad' years being reflected more closely in their mortality rates. Both chicks experience the same weather conditions and predation risks, and hatching order is unlikely to affect their impact.

Variability in feeding conditions will, however, result in higher second-hatched chick mortality in years of poor food supply, because of the comparative advantage of elder siblings, and in low mortality in years when food is plentiful. But the main premise behind brood reduction is that under optimal conditions all the chicks can fledge (Lack 1954; Howe 1976). In 2009, mortality was very low overall with only 15% of all Arctic Tern chicks and 22% of all Common Tern chicks failing to fledge, indicating highly favourable breeding conditions. In that year the proportion of chicks fledging and dying was comparable between first and second chicks. This suggests that mortality was not dictated by hatching order and access to resources but rather by external factors unrelated to parental ability to provision and therefore supports the brood reduction hypothesis.

Traditionally, the success of a breeding season has been measured in terms of overall productivity. However, the increased sensitivity to variable resources shown by younger siblings in asynchronous, brood reducing species may provide a more sensitive indicator, and younger sibling mortality could give a more accurate assessment of the 'quality' of a season than does overall productivity.

Arctic Terns showed higher yearly fluctuations in chick mortality than Common Terns. While Common Tern mortality of both first- and second-hatched chicks only altered when years were either extremely poor or extremely good, Arctic Tern second-hatched chick mortality was more variable. This increased sensitivity to seasonal differences may indicate a higher vulnerability of Arctic Terns to adverse conditions.

It is not only resource supply that affects younger sibling mortality: younger siblings show decreased mortality with the death of an elder sibling. Arctic Tern second-hatched and Common Tern third-hatched chicks both showed a decline in mortality when they outlived an elder sibling (while not significant, there also appears to be a decline in mortality for Common Tern second-hatched chicks with the death of first-hatched chicks [$p=0.118$]). Furthermore, the proportions surviving to fledging age then began to

resemble those of the chick above them in the brood hierarchy (Table 4.12). This was not a result of decreasing brood size, as brood size had no effect on mortality rates. Instead it appears that with the death of an elder sibling, the survivor moves up the brood hierarchy and obtains increased access to food supply. This suggests that younger siblings can act as 'insurance' against elder chick mortality and are maintained (at least initially) in sufficiently good condition to successfully 'take over' should the need arise.

		Mortality in:	
		Younger sibling when elder sibling died	Sibling above it in the hatching order
Arctic Tern	Second Hatched	30%	26%
Common	Second Hatched	29%	23%
Tern	Third hatched	63%	57%

Table 4.12 Comparing percentage mortality of younger siblings after the death of an elder sibling with the mortality of an elder sibling

Analysis of the impact of younger siblings on elder sibling survival showed a significant decline in Common Tern elder sibling survival when younger sibling(s) survived. This would support the theory that the establishment of a brood hierarchy is important to ensure that younger siblings can be removed before they negatively impact elder siblings. If the hierarchy fails and one or more younger siblings survive, then their presence in the nest means elder siblings may no longer receive a sufficient proportion of the resources, with fitness suffering and mortality increasing as a result. However, the data is open to different interpretation. It is possible that in nests where the younger siblings survive they do so because of a lack of fitness (and therefore increased likelihood of mortality) in the elder siblings, i.e. survival is still dictated by the elder siblings. How younger sibling presence in the nest impacts elder chick survival once resources become a limiting factor is an often overlooked aspect of asynchronous hatching, and warrants further investigation, e.g. through experiments manipulating the number of siblings surviving within a brood.

Resource-driven brood reduction and the use of younger chicks as insurance in case of elder sibling mortality are not mutually exclusive. The impact of both resources and siblings on younger chick mortality indicates that Arctic and Common Terns are using

asynchrony both to aid brood reduction and to use younger siblings are insurance chicks. There is evidence that the survival of second-hatched chicks of both species is linked to food supply and to elder-sibling survival. However, Common Terns are more likely to fledge 2 chicks than Arctic Terns (Chapter 3), and mortality of second-hatched chicks was higher in Arctic in than Common Terns, and occurred at a younger age. While both showed a decline in mortality with the death of the elder sibling, the decline was not significant for Common Terns. It is proposed that Common Tern second-hatched chick survival is controlled predominantly by resource availability and brood reduction while Arctic Tern b-chicks act as insurance chicks as well as being effected by variable resources.

Unlike second-hatched chicks, Common Tern third-hatched chicks showed very low survival rates (8%) and survival was very strongly linked with the death of an elder sibling. It is proposed that unless conditions are very favourable, Common Tern third-hatched chicks exist solely as replacements for elder siblings. If both elder siblings survive, mortality occurs at an early age (80% of mortality occurred within the first 10 days after hatching), ensuring low energy investment in unneeded chicks. The role of Arctic Tern third-hatched chicks is unclear. They are a relatively rare occurrence, with only 6% of observed nests hatching three chicks and all of these chicks failing to fledge. It is possible that third eggs are laid as insurance against failure of primary eggs, but no reproductive benefit of larger clutch sizes was found (Chapter 3).

Another suggested benefit of asynchronous hatching is that it reduces the peak energy demands of the brood and so makes provisioning easier (peak load hypothesis). However these data do not provide evidence to support the hypothesis, as the degree of hatching asynchrony did not affect the reproductive output of the nest or individual chick mortality rates, and the majority of younger sibling mortality occurs before the peak in energy demands is reached (Klassen et al. 1989). The impact of asynchrony was considered in terms of a linear relationship; it is likely that there is an ‘optimal’ degree of asynchrony which minimises the total energy demands of the brood while still ensuring younger chick survival under favourable conditions and not overly prolonging the chick rearing period.

A benefit of asynchrony not previously discussed here is that of enabling chicks to be spread across the season. Non-migratory species or those that migrate short distances

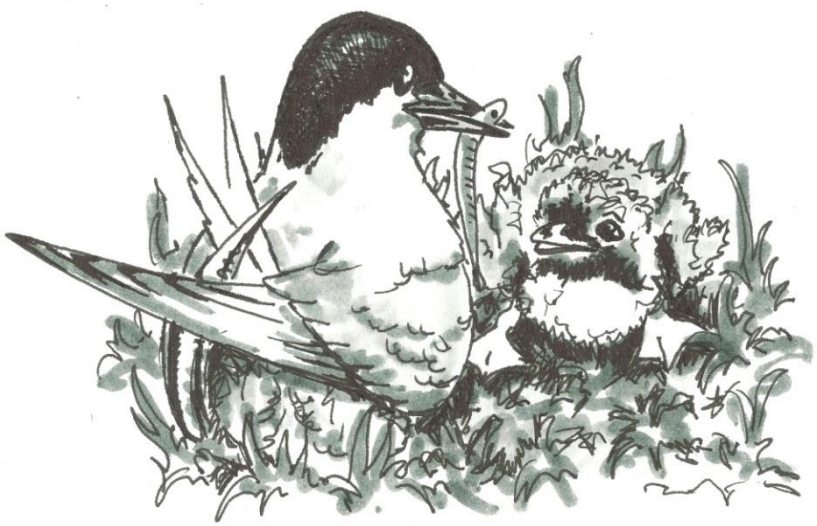
have a greater ability to modify the timing of their breeding to suit conditions (Crick & Sparks 1999; Dunn & Winkler 1999; Sanz 2002). Long distance migrators such as these terns have little opportunity to adjust the timing of breeding because of the limited window in which to raise their chicks between migrations. By hatching chicks asynchronously over a span of days, birds in effect increase their breeding period and thereby reduce the risk of 'missing' the optimum breeding time. This could prove especially valuable for species feeding on highly variable resources such as Sandeel whose population not only experiences a seasonal pattern but is also highly mobile.

While the degree of asynchrony was not found to affect survival rates of chicks, it is likely to reinforce the effects of the brood hierarchy. Asynchrony between first and second chicks was greater in Arctic Terns than in Common Terns, and greater between Common Tern second and third chicks than first and second chicks. This is consistent with the higher percentage mortality seen in the younger chicks. A larger age difference would increase the effect of the brood hierarchy and facilitate removal of surplus chicks. It is suggested that when brood reduction occurs due to insufficient resources, the age difference between chicks should be small compared to that when chicks act primarily as insurance. If chicks' survival depends on resources, they need to be able to compete with elder siblings when conditions are favourable. Reduced degree of asynchrony allows younger siblings a better chance of survival. However, if younger siblings only survive if an elder sibling dies, then they need to be rapidly and easily removed from the nest before they become a drain on resources. Increased age difference between siblings will magnify the effects of the brood hierarchy and ensure that a younger sibling fails to compete with an elder sibling.

So far only methods of facilitating chick removal have been discussed; however, Common Terns have been shown to alter the sex ratio of third laid eggs in favour of female chicks (Howe 1976; Fletcher & Hamer 2004). Female offspring have been shown to have higher survival rates than their male equivalents (Sayce & Hunt 1987; Fletcher & Hamer 2004; Gonzales-Solis et al. 2005; Rotkowska & Cichon 2005). By increasing the viability of third hatched chicks, females are increasing the chances that these chicks will survive in good condition should an older sibling perish. However, should the presence of these chicks become detrimental to the fitness of the brood, their removal is still facilitated by the establishment of the brood hierarchy.

The evolutionary benefit of asynchronous hatching is that, while it is beneficial to have larger broods to maximise productivity, it is better to fledge fewer chicks of higher quality that are more likely to survive to be recruited into the population than more chicks of lower quality that may not survive post-fledging. By hatching chicks asynchronously and so establishing a brood hierarchy, the younger chicks can be removed when they become a drain on limited resources, thereby increasing the likelihood that those chicks which fledge are of high quality.

In conclusion, both Arctic and Common Terns hatched more chicks than they could usually successfully fledge. Hatching asynchrony resulted in the establishment of a brood hierarchy, with increased mortality down the brood. The brood hierarchy enables the easy removal of younger siblings should conditions be unfavourable or should they be no longer needed. However, the two species are using slightly different strategies. Arctic Tern second-hatched and Common Tern third-hatched chicks act as insurance in case of elder sibling(s). Resource-driven brood reduction is predominantly controlling Common Tern second-hatched chick mortality, although it also affects Arctic Tern second-hatched chicks. Mortality of second-hatched chicks showed increased yearly variability compared to that of first–hatched chicks because the brood hierarchy limited their access to resources. It is proposed that secondary chick survival could be used as a more sensitive assessment of a season's 'quality' than nest productivity.



Chapter 5. The effects of age and number of chicks on provisioning and chick diet, and variations between species and year

5.1 Abstract

Arctic and Common Tern chicks are entirely dependent on their parents for food. Adults of both species provisioned their chicks predominantly with Sandeel, with Clupeid being the second most common prey species. Arctic Terns provisioned chicks at a faster rate but on lower energy prey (both size and species) than Common Terns and showed a greater reliance on Sandeel. Both species increased the amount of food delivered to the nest as their chicks got older. This was achieved primarily by increasing the rate of energy delivery, by selecting more energy rich prey (both by size and species) and by slightly increasing their foraging effort. Food delivery increased with increased brood size, but both species appeared to maintain feeding rate and energy delivery per chick by increasing foraging effort. Yearly variability in foraging behaviour was pronounced, with differences in rate of energy delivery linked with yearly differences in size and species in diet. Poor foraging years were associated with poor breeding years, with low productivity and high mortality of chicks.

5.2 Introduction

Semi-precocial chicks such as Tern chicks do not feed themselves and are completely reliant on parents for food (Nice 1962). Parent birds need to provision chicks with sufficient food to meet the chicks energy requirements and with the appropriate type and size of prey to ensure breeding success.

As a chick grows its energy requirements and expenditure increase, at least initially (Ricklefs & White 1981; Klassen et al. 1989; Drent et al. 1992; Gabrielsen et al. 1992; Konarzweski et al. 1993; Klassen 1994; Schekkerman & Visser 2001). To accommodate the increased demands of a chick, parents increase the amount of energy delivered to the nest (Langham 1972; Massias & Becker 1990; Drent et al. 1992; Gabrielsen et al. 1992; Konarzweski et al. 1993; Robinson et al. 2001). Parents can increase energy delivery by increasing feeding rate, and a higher rate of food delivery is often associated with increased age of chick (Johnson & Best 1982; Barrett et al. 1987;

Emms & Verbeck 1991; Goodbred & Holmes 1996; Robinson & Hamer 2000; Robinson et al. 2001). Alternatively, parents can augment energy delivery by selecting higher energy prey, either through larger prey items (Emms & Verbeck 1991; Stienen et al. 2001) with higher energy content (Hislop et al. 1991; Ball et al. 2007) or by selecting more energy rich prey species (Casaux et al. 2008).

The energy needs of the brood are a function of the number of chicks in the brood. More chicks require more food, and increased provisioning rate is often associated with larger broods (Pearson 1968; Langham 1972; Johnson & Best 1982; Anderson & Ricklefs 1992; Meyer et al. 1997; Wright et al. 1998; Robinson & Hamer 2000; Anderson et al. 2005). While brood provisioning rate increases with brood size, provisioning per chick usually declines, indicating limits on clutch size due to provisioning ability (Pearson 1968; Johnson & Best 1982; Laiolo et al. 1998; Robinson & Hamer 2000).

Whatever the energy needs of the chicks, parents are limited in what they can provide by food is availability. Fish quantity and distribution vary greatly between years (Rindorf et al 2000; Arnott & Ruxton 2002; Perry et al. 2005; Furness 2007; Malzahn & Boersma 2007). Changes in availability and quality of prey species are often reflected in what the adult birds bring back to the chicks (Frank 1992; Montevecchi & Myers 1995; Diamond & Devlin 2003; Wanless et al. 2005; Furness 2007). While adults can sometimes compensate for shortage of forage fish by increasing foraging effort (Uttley 1992; Hamer et al. 1991; ibid. 1993; Monaghan et al. 1994; Monaghan 1996; Suryan et al. 2000; Wanless et al. 2005; Piatt et al. 2007; Ronconi & Burger 2008) or, if an option, by switching prey species (Murphy et al. 1984; Hamer et al. 1993; Frick & Becker 1995; Croxall et al. 1999; Suryan et al. 2000; Kato et al. 2001; Barrent 2002; Casaux et al. 2008), breeding success often declines when forage fish are scarce.

Low productivity and/or low chick growth rates have been associated with low provisioning rates (Barrett et al. 1987; Croxall et al. 1999; Weimershich et al. 2001; Buber et al. 2004), scarcity of primary prey species in diet (Monaghan et al. 1989; Hamer et al 1991, ibid. 1993; Syndman et al. 1991; Barrett & Krasnov 1996; Suddaby & Ratcliffe 1997; Furness 2007), low quality of prey (Golet et al. 2000; Diamon & Devlin 2003; Wanless et al. 2005; Osterblom et al. 2006; Romano et al. 2006), or high proportion of alternative prey in the diet (Murphy et al. 1984; Baird 1990; Massias & Becker 1990; Kato et al. 2001; Romano et al. 2006).

Arctic and Common Terns have limited foraging ranges while at the breeding colony and they feed predominantly on surface-available prey and tend to rely heavily on Sandeel (Pearson 1968; Frank 1992; Monaghan 1992; Furness & Tasker 2000; Robinson et al. 2001). These factors combine to increase their vulnerability to fluctuations in prey availability and distribution (Monaghan 1996; Croxall et al. 1999; Furness & Tasker 2000). Observing the provisioning behaviour of syntopically breeding birds over five consecutive breeding seasons (2006 through 2010) will enable species differences and the effect of age and number of chick to be assessed from a large data set. Data on yearly provisioning and how this related to yearly productivity both within and between species will facilitate a better understanding of their population dynamics in relation to fluctuations in the marine environment.

5.3 Methodology and analysis

5.3.1 Methodology

See Chapter 2, sections 2.3.1 and 2.3.2.

5.3.2 Analysis

Data were tested for normality using one sample Kolmorgorov-Smirnof test and found to be non-normally distributed. Transformation of data was attempted but found to be ineffective for data normalisation. Analyses using Generalized Linear Models (GLMs) were attempted but models showed poor fit. Although GLMs would provide powerful tools for analysing the data, a more-sophisticated approach to modelling the underlying data distributions is required but is beyond the scope of this thesis. All analysis was undertaken using IBM SPSS Statistics, version 19.

Therefore, provisioning data and diet data were analysed using Kruskall-Wallis test across multiple groups (with pair-wise analysis for comparisons between groups, adjusted p-value) and Mann-Whitney U test across two groups. Differences between species in overall size of prey were analysed using Mann-Whitney U test, while differences in proportions of prey of different size categories were analysed using Pearson's Chi-Squared test with Z-test of column proportions used for comparison between groups (Bonferroni-adjusted p-value).

Analysis of the effect of brood size was split by age category of eldest chick in the brood to take account of the increasing provisioning needs of chicks with age increasing the impact of different brood sizes (Langham 1972).

5.4 Results

5.4.1 Species provisioning

General provisioning behaviour of Arctic and Common Terns was analysed in chapter 3 and is summarised in Table 5.1.

	Mean ± SD				Mann-Whitney U Test
	n	Arctic Tern	n	Common Tern	(Z)
Feed.nest^{-1}.h^{-1}	1870	3.2 ± 3.2	1597	2.6 ± 2.8	5.337**
Feed.chick^{-1}.h^{-1}	1870	2.25 ± 2.34	1597	1.68 ± 1.91	4.684**
kJ.nest^{-1}.h^{-1}	1856	13.0 ± 24.1	1597	21.3 ± 41.3	8.075**
kJ.chick^{-1}.h^{-1}	1856	9.74 ± 20.00	1585	14.42 ± 33.23	2.757**
kJ.feed^{-1}	1562	5.52 ± 12.57	1331	12.09 ± 30.34	12.076**

Table 5.1 Mean provisioning rate (feed.h^{-1}) and rate of estimated energy delivery (kJ.h^{-1}) per nest and per chick and estimated energy value per feed (kJ.feed^{-1}) ± SD for Arctic and Common Terns

5.4.2 Species diet

Arctic Terns were observed making 5,384 food deliveries to the nest site (1,870 nest observations). Common terns were observed making 4,531 food deliveries to the nest site (1,597 observations).

Both species were recorded provisioning their chicks with Sandeel (*Ammondytes sps*), Clupeid (Sprat, *Spratus spratus,* Herring,*Clupea harengus*), small fish of less than 20mm in length (various species, too small to identify), Pipefish (*Entelurus sps*), Shrimp (*Crangon sps*), Squid, Lumpsuckers (*Cyclopterus sps*), Polychaete Worms, Three-spined Stickleback (*Gasterosteus acukeatus*), Lesser Weever (*Echiichtys vipera*), Blenny (*Parablennius sps*) and small Flounder species (*Pleuronechdae*). All species that made up 0.5% or less of the proportion of fish brought back to the nest were grouped together for analysis as 'Other' (Table 5.2).

	Arctic Tern		Common Tern	
	Percentage (%)	Listed in analysis as	Percentage (%)	Listed in analysis as
Sandeel	82.84	Sandeel (Se)	70.91	Sandeel (Se)
Clupeid	11.90	Clupeid (Cl)	23.54	Clupeid (Cl)
Small fish	3.86	Small fish (Sm)	3.50	Small fish (Sm)
Pipefish	<0.1	Other*	1.40	Pipefish (Pf)
Shrimp	0.74	Shrimp (Sh)	0.49	Other†
Squid	0.14	Other	0.14	Other
Lumpsucker	0.24	Other	<0.01	Other
Polychaete Worm	0.24	Other	0.01	Other
Stickleback	<0.1	Other	<0.01	Other
Weever	<0.1	Other	<0.01	Other
Blenny	<0.1	Other	<0.01	Other
Flounder	<0.1	Other	<0.01	Other

*Other=0.66% of Arctic Tern prey brought to the nest
†Other=0.64% of Common Tern prey brought to the nest

Table 5.2 Complete list of prey species observed being brought to the nest by Arctic and Common Terns showing percentage of diet by species

Arctic Terns brought significantly different proportions of the different prey species to the nest (Kruskall-Wallis, n=7.825, χ^2=5,178.615, df=4, p<0.001), with Sandeel being the most common prey item, followed by Clupeid, then small fish, Shrimp and 'Other' prey species (Table 4.3, Figure 5.1). Common Terns also brought significantly different proportions of the different prey species (n=6.690, χ^2=408.994, df=4, p<0.001), with their most common prey item being Sandeel, followed by Clupeid, then small fish, Pipefish and 'Other'.

	Arctic Tern				Common Tern			
	Cp	Sm	Sh	Other	Cp	Sm	Pf	Other
Se	48.50**	56.30**	59.65**	59.48**	29.65**	45.89**	47.58**	48.29**
Cp		7.800**	11.15**	10.91**		16.24**	17.93**	18.64**
Sm			3.350**	3.181*			1.689	2.399
Sh				0.169				0.710

Table 5.3 Standardized test statistic from pair-wise analysis (adjusted p-value) from Kruskall-Wallis test of differences in proportions of different prey species brought to the nest by Arctic and Common Terns

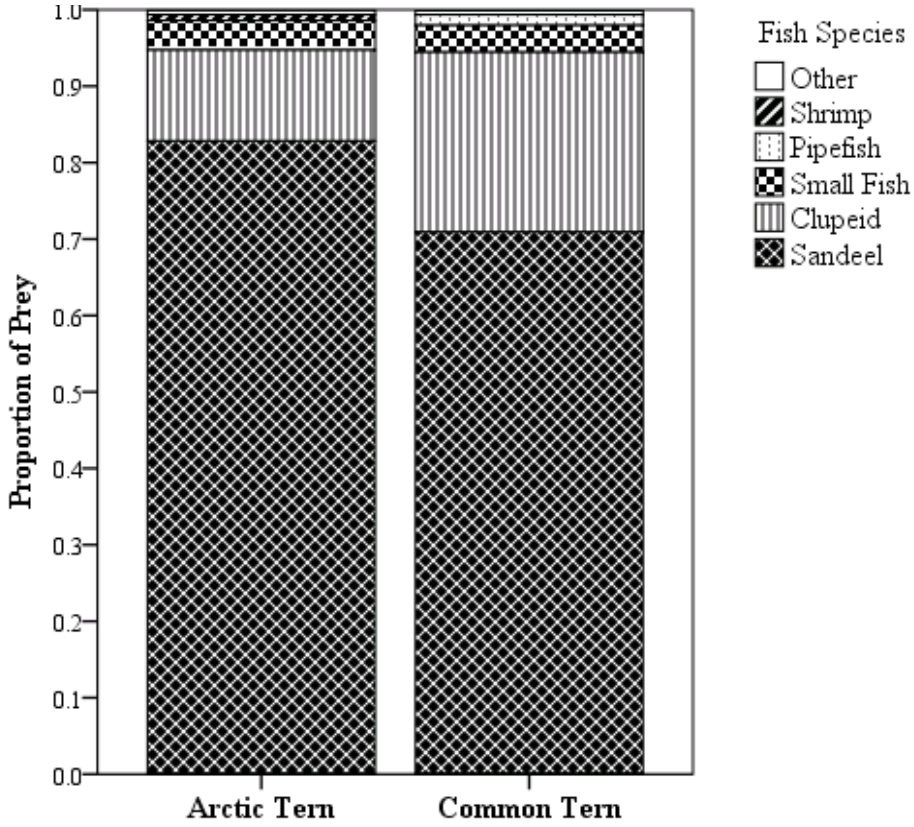


Figure 5.1 Proportions of different prey species brought to the nest by Arctic and Common Terns. Both species provision chicks predominantly with Sandeel and a significantly smaller proportion of Clupeid.

Sandeel made up a larger proportion of prey brought back to the nest by Arctic Terns than by Common Terns (Mann-Whitney U, n=2903, Z=7.982, p<0.001), and that Clupeid made up a larger proportion of prey brought back to the nest by Common Terns than by Arctic Terns (n=2903, Z=9.119, p<0.001). Proportions of small fish and 'Other' were found to be similar for both species (Small fish, n=2903, Z=1.661, p=0.097; Other, n=2903, Z=0.820, p=0.412) (Figure 5.1).

Arctic Terns brought 5385 Sandeels to the nest site ranging in size from 25 to 120mm (mean ± SD = 53±10mm). Z test of column proportions showed a significant difference in the number of Sandeel of different sizes brought to the nest, with the largest number being in the medium size group (40 to 69mm), the next highest proportion being small sized (<40mm), followed by large (70 to 99mm), with only 0.3% of Sandeel brought to the nest being greater than 100mm (very large). Common Terns brought 3614 Sandeel to the nest site, ranging in size from 25 to 160mm (mean ± SD =57±13). Z test of column proportions showed a significant difference in the number of Sandeel of different sizes brought the nest, with the highest proportion being medium sized, followed by large sized, and with only 1.8% of fish brought to the nest very large sized and 1.1% small sized (Figure 5.2).

Arctic Terns brought 454 Clupeid to the nest site, ranging in size from 40 to 140mm (mean ± SD = 65±18mm). Common Terns brought 708 Clupeid to the nest site, ranging in size from 40 to 160mm (mean ± SD = 73±23mm). Z test of column proportion showed that both species brought predominantly medium sized fish, with no small fish and equal proportions of large and very large sized fish (Figure 5.2).

Arctic Terns brought significantly smaller Sandeel (Mann-Whitney U, n=8999, Z=15.233, p<0.001) and significantly smaller Clupeid (n=1162, Z=5.546, p<0.001) to the nest than did Common Terns. Proportions of prey of different size groups differed between Arctic and Common Terns for both Sandeel (Pearson's Chi-squared, n=8999, χ^2=378.521, df=3, p<0.001) and Clupeid (n=1162, χ^2=19.570, df=2, p<0.001). Z test of column proportions showed that Arctic Terns brought in a higher proportion of Sandeel less than 40mm in length than did Common Terns, a similar proportion of Sandeel between 40 to 69mm in length, and less Sandeel between 70 to99mm and over 100mm. Arctic Terns brought in a higher proportion of Clupeid between 40 and 69mm in length than did Common Terns but less between 70 to 99mm and over 100mm.

0.3% of Sandeel brought to the nest by Arctic Terns were over 100mm in length and 1.1% of Sandeel brought to the nest by Common Terns were less than 40mm and 1.8% over 100mm. These groups were not further analysed because of their small sample size.

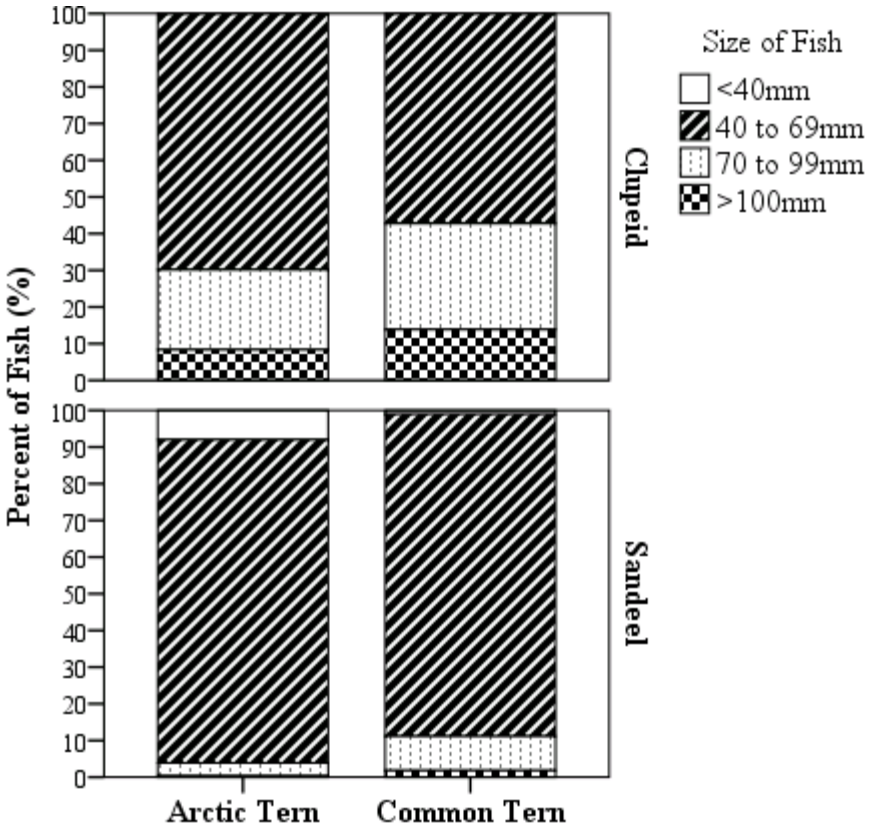


Figure 5.2 Different size groups of Sandeel and Clupeid brought to the nest, by Arctic and Common Terns.

5.4.3 Chick age and provisioning behaviour

Kruskall-Wallis analysis of age group of chicks and provisioning behaviour showed that age had a significant effect on feeds per chick per hour, energy per chick per hour and energy per feed for both Arctic and Common Terns (Table 5.4; Figure 5.3; Figure 5.4; Figure 5.5).

	Arctic Tern				Common Tern			
	n	χ^2	df	p	n	χ^2	df	p
Feed.chick^{-1}.h^{-1}	1870	26.940	5	<0.001	1597	19.488	5	<0.001
kJ.chick^{-1}.h^{-1}	1856	39.227	5	<0.001	1585	65.818	5	<0.001
kJ.feed^{-1}	1562	60.316	5	<0.001	1331	153.282	5	<0.001

Table 5.4 Kruskall-Wallis analysis of the effect of age of eldest chick on provisioning rate (feed.chick^{-1}.h^{-1}), energy delivery rate (kJ.chick^{-1}.h^{-1}) and energy per feed (kJ.feed^{-1}) for both Arctic and Common Terns

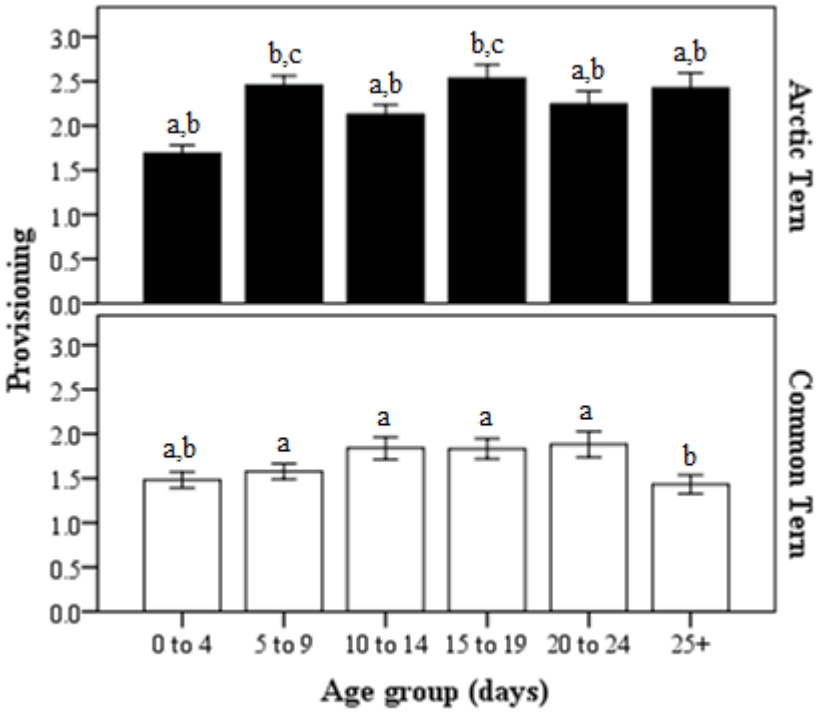


Figure 5.3 Provisioning trips (feed.chick^{-1}.h^{-1}) depending on the age of the eldest chick in the nest ± SE. Columns with the same letter are not significantly different from each other ($p<0.05$).

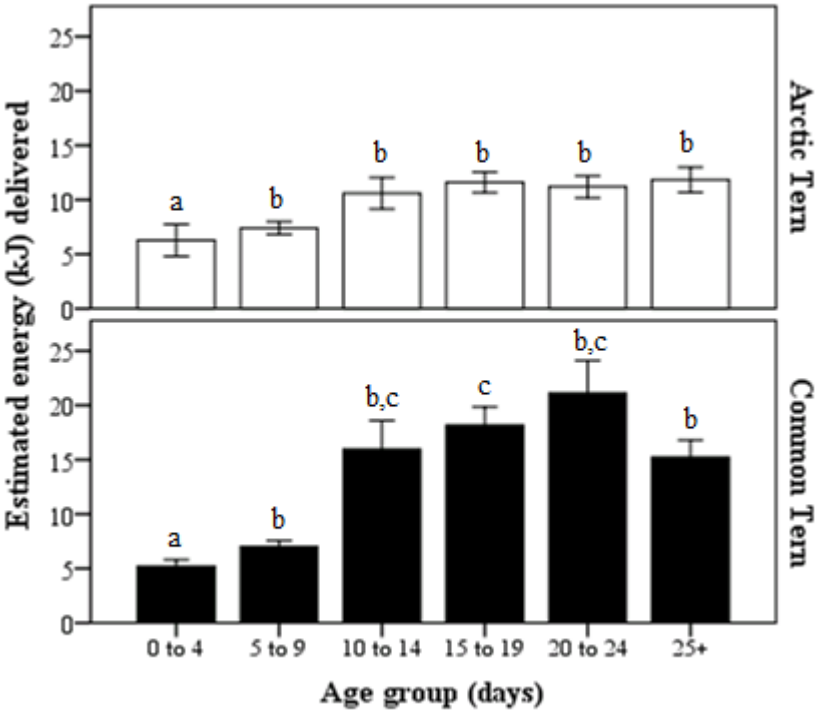


Figure 5.4 Estimated energy delivery rate (kJ.chick^{-1}.h^{-1}) depending on the age of the eldest chick in the nest ± SE. Columns with the same letter are not significantly different from each other ($p<0.05$).

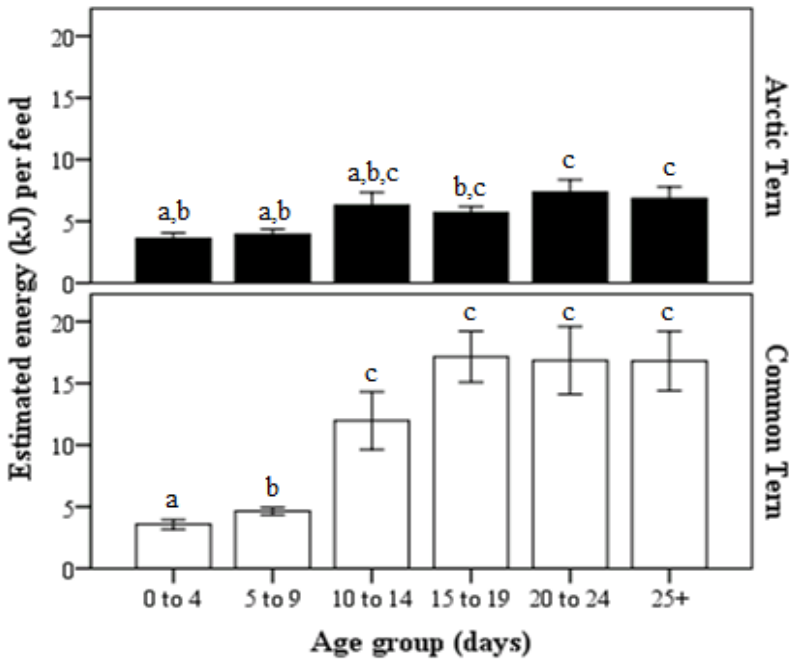


Figure 5.5 Estimated energy per feed (kJ.feed^{-1}) depending on the age of the eldest chick in the nest ± SE. Columns with the same letter are not significantly different from each other ($p<0.05$).

5.4.4 Chick age and diet

Spearman's rho correlation of age of eldest chick in the nest with proportion of different prey items brought to the nest demonstrated a moderate significant negative correlation between proportion of Sandeel and age of chick for both species and a significant positive correlation between age and proportion of Clupeid, although this was weak for Arctic Terns. Proportions of small fish and 'Other' increased with age of chick for Common Terns but not for Arctic Terns. Proportion of Shrimp increased with age of chick for Arctic Terns and proportion of Pipefish increased with age of chick for Common Terns (Table 5.5, Figure 5.6).

	Arctic Tern			Common Tern		
	n	Spearman's rho	p	n	Spearman's rho	p
Sandeel	1565	-0.125	<0.001	1336	-0.299	<0.001
Clupeid	1565	0.090	<0.001	1336	0.205	<0.001
Small fish	1565	0.035	0.162	1336	0.138	<0.001
Shrimp	1565	0.097	<0.001			
Pipefish				1336	0.017	<0.001
Other	1565	0.045	0.077	1336	0.056	0.042

Table 5.5 Spearman's rho correlation of age of eldest chick in the nest with proportion of Sandeel, Clupeid, Small Fish, Shrimp (Arctic Terns only), Pipefish (Common Terns only) and 'Other' brought to the nest by Arctic and Common Terns

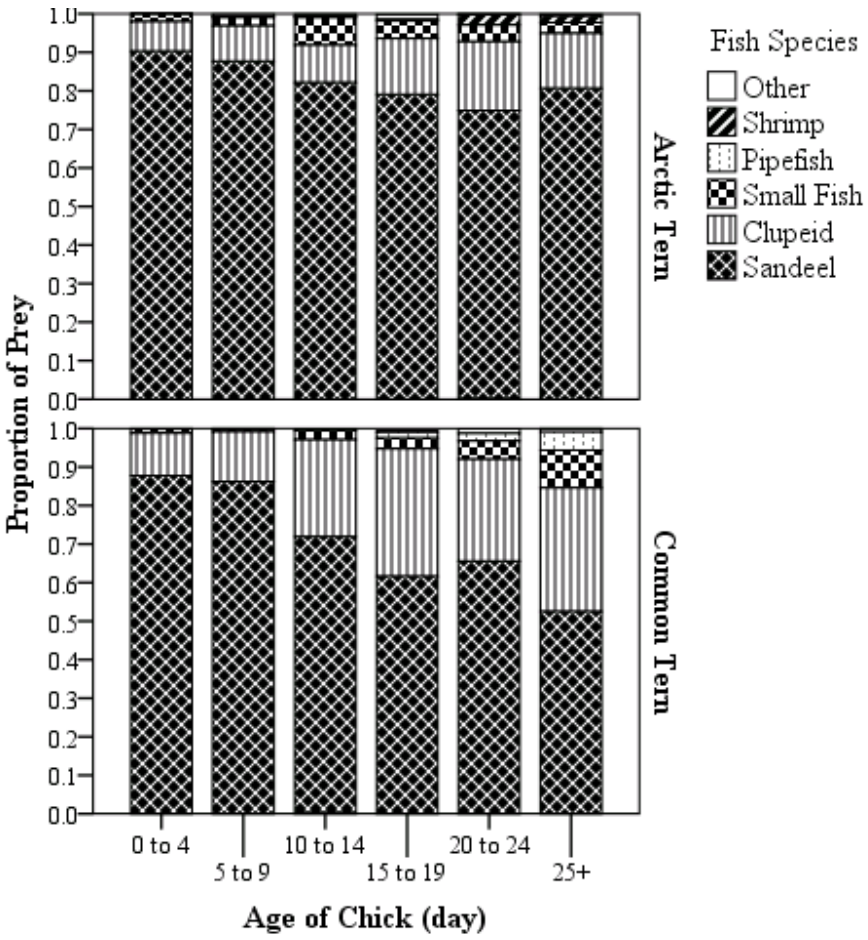


Figure 5.6 Proportion of different fish species brought to the nest by Arctic and Common Tern depending on the age of the eldest chick in the nest.

Age of eldest chick had a significant effect on the proportion of different sized Sandeel brought to the nest by Arctic Terns (Pearson's Chi-Squared, n=5352, χ^2=314.971, df=10, p<0.001) and Common Terns (n=3491, χ^2=70.017, df=5, p<0.001). Age of eldest chick had a significant effect on the proportions of different sized Clupeid brought to the nest by Arctic Terns (Pearson's Chi-Squared, n=452, χ^2=36.826, df=10, p<0.001) and Common Terns (n=703, χ^2=76.169, df=10, p<0.001) (Figure 5.7).

Percentage of total fish of each size caught fed to chicks depending on age of oldest chick is shown in Table 5.6 with subscript letters denoting significant differences between values (Z test of column proportions, p<0.05).

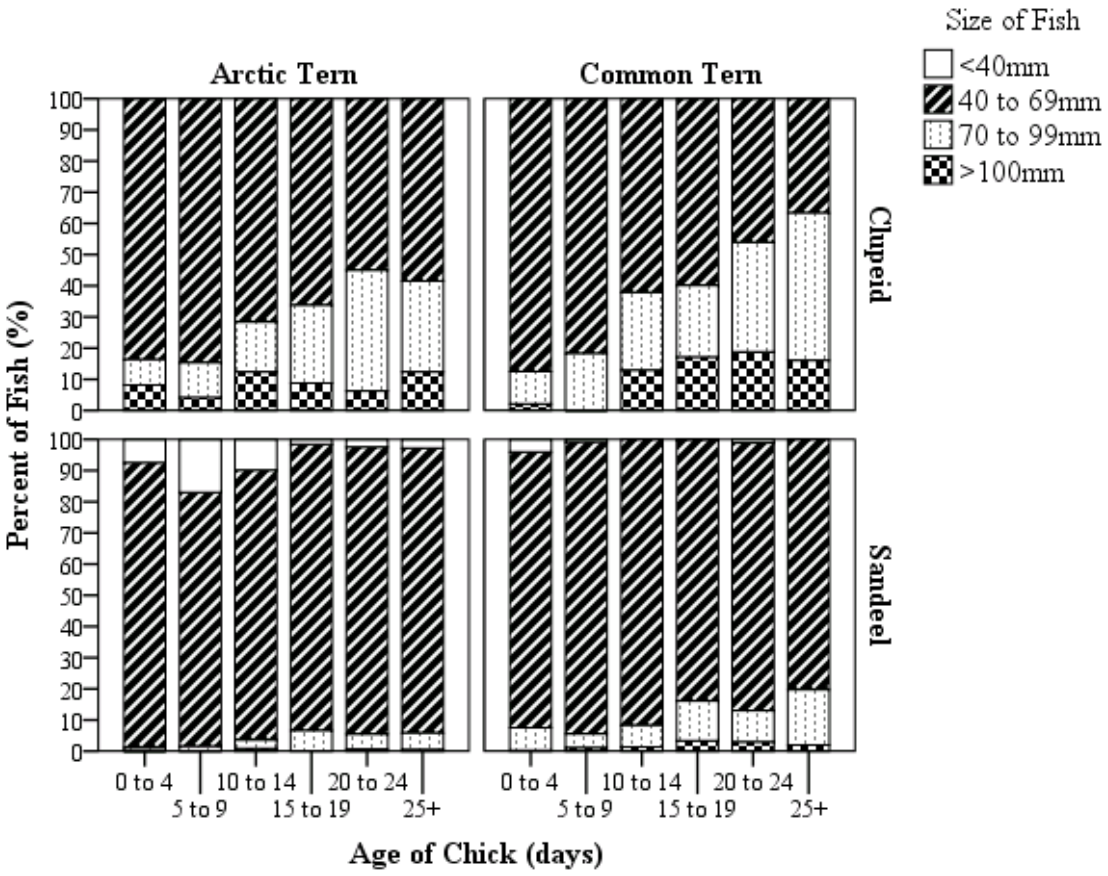


Figure 5.7 Percentage of Sandeel and Clupeid of different sizes brought to the nest by Arctic and Common Tern depending on age of eldest chick,

			0 to 4	5 to 9	10 to 14	15 to 19	20 to 24	25+
Arctic Tern	Sandeel	<40mm	11.3_{a}	53.7_{b}	22.2_{a}	3.5_{c}	4.6_{c}	4.6_{c}
		40 to 69mm	$12.5_{a,b}$	23.3_{c}	17.6_{b}	17.6_{a}	15.4_{a}	$13.5_{a,b}$
		70 to 99mm	3.7_{a}	10.6_{a}	$14.3_{a,b}$	31.2_{b}	20.1_{b}	20.1_{b}
	Clupeid	40 to 69mm	12.9_{a}	26.2_{a}	$18.3_{a,b}$	$16.7_{a,b}$	13.9_{b}	12.0_{b}
		70 to 99mm	4.0_{a}	$11.1_{a,b}$	13.1_{b}	$20.2_{b,c}$	31.3_{c}	$19.2_{a,b,c}$
		>100mm	10.5_{a}	10.5_{a}	26.3_{a}	18.4_{a}	13.2_{a}	21.1_{a}
Common tern	Sandeel	40 to 69mm	16.3_{a}	$19.2_{a,b}$	$19.2_{b,c}$	17.7_{d}	$16.6_{c,d}$	10.4_{d}
		70 to 99mm	$12.7_{a,b}$	8.6_{a}	13.6_{a}	$25.4_{b,c}$	18.3_{b}	21.5_{c}
		>100mm	1.5_{a}	$10.8_{a,b}$	$13.8_{a,b}$	33.8_{b}	27.7_{b}	$12.3_{a,b}$
	Clupeid	40 to 69mm	10.4_{a}	$14.3_{a,b}$	$20.2_{b,c}$	26.9_{c}	$15.8_{c,d}$	11.9_{d}
		70 to 99mm	2.4_{a}	$3.9_{a,b}$	$16.1_{a,b}$	$20.5_{a,b}$	$23.9_{b,c}$	30.2_{c}
		>100mm	1.0_{a}	1.0_{a}	$17.3_{a,b}$	31.6_{b}	$26.5_{a,b}$	$21.4_{a,b}$

Table 5.6 Percentage of total fish of each size caught fed to chicks of each age group

5.4.5 Brood size and provisioning behaviour

Provisioning rate per nest was found to be significantly different depending on brood size for both species through all age groups (Table 5.7, Figure 5.8).

	Arctic Tern				Common Tern			
Kruskall-Wallis	n	χ^2	d.f.	p	n	χ^2	d.f.	p
0 to 4 days	284	8.898	2	0.012	236	23.875	2	<0.001
5 to 9 days	368	15.765	2	<0.001	237	39.343	2	<0.001
10 to 14 days	340	35.710	2	<0.001	238	24.243	2	<0.001
15 to 19 days	297	35.354	2	<0.001	308	35.603	2	<0.001
Mann-Whitney U	n	Z		p	n	Z		p
20 to 24 days	288	5.550		<0.001	309	4.085		<0.001
25 days and older	293	2.804		0.001	278	2.860		0.004

Table 5.7 Kruskall-Wallis (between broods of 1-, 2- and 3-chicks) and Mann-Whitney U (between brood of 1- and 2-chicks) analysis of the effect of Arctic and Common Tern brood size on provisioning rate (feed.nest^{-1}.h^{-1}) for different age groups of eldest chick

Kruskall-Wallis and Mann-Whitney U analyses showed that provisioning rate per chick varied depending on brood size for Arctic Terns but not for Common Terns. (Table 5.8, Figure 5.8).

	Arctic Tern				Common Tern			
Kruskall-Wallis	n	χ^2	d.f.	p	n	χ^2	d.f.	p
0 to 4 days	284	11.235	2	0.004	236	5.482	2	0.065
5 to 9 days	368	5.974	2	0.051	237	1.701	2	0.427
10 to 14 days	340	6.108	2	0.047	238	1.065	2	0.587
15 to 19 days	297	0.312	2	0.856	308	3.756	2	0.153
Mann-Whitney U	n	Z		p	n	Z		p
20 to 24 days	288	1.156		0.248	309	1.028		0.304
25 days and older	293	0.997		0.319	275	1.494		0.135

Table 5.8 Kruskall-Wallis (between broods of 1-, 2- and 3-chicks) and Mann-Whitney U (between broods of 1- and 2-chicks) analysis of the effect of brood size on Arctic and Common Tern provisioning rate per chick (feed.chick^{-1}.h^{-1}) for different age groups of eldest chick

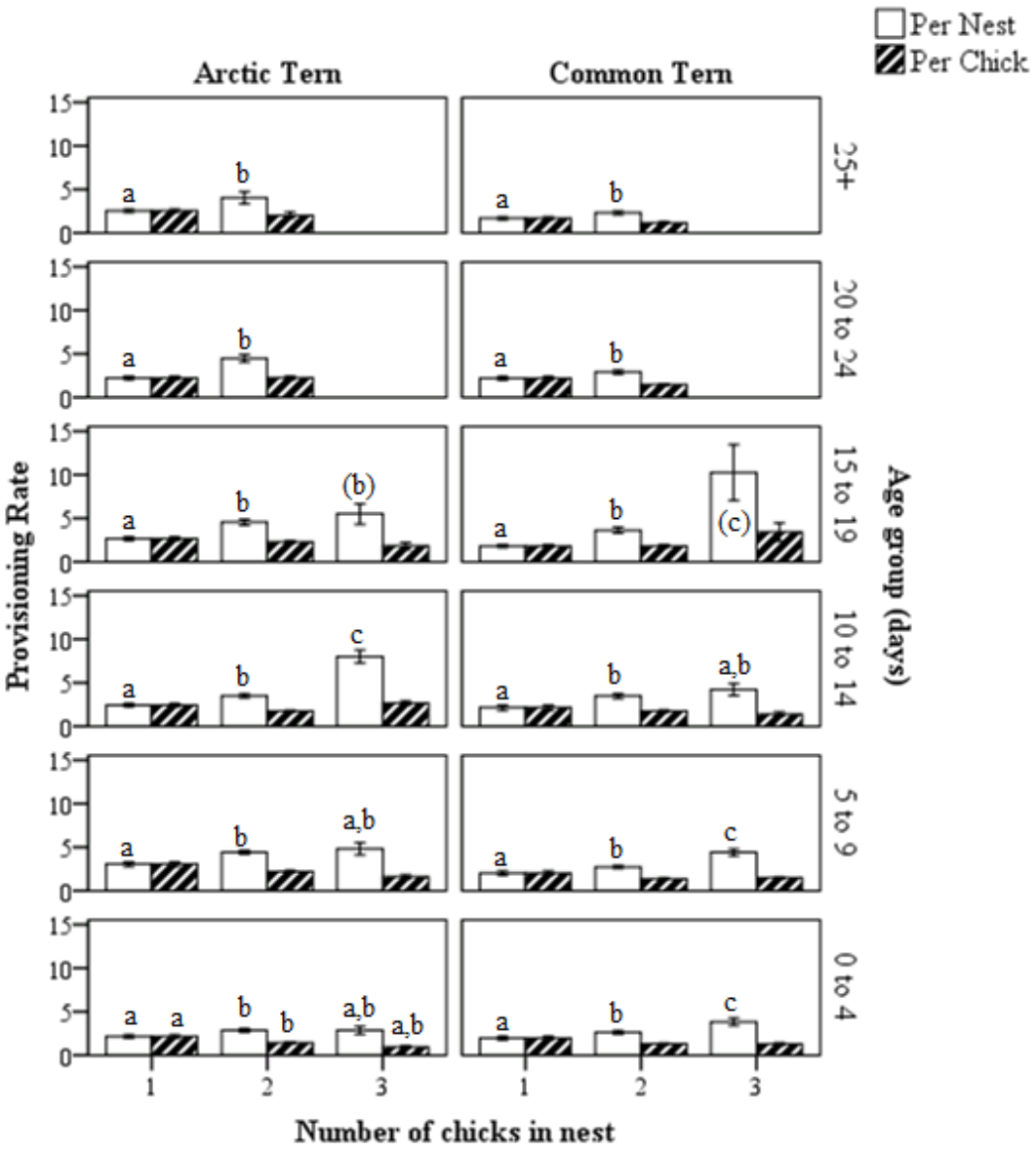


Figure 5.8 Provisioning rate (feeds.h^{-1}) ±SE per nest and per chick depending on brood size and age group for Arctic and Common Terns Columns with the same letter are not significantly different from each other ($p<0.05$).

Energy delivery rate per nest was found to be significantly different depending on brood size for both species (Table 5.9, Figure 5.9).

Rate of estimated energy delivery per chick varied depending on brood size only for Arctic Terns, with eldest chicks aged between 0 and 4 days (although pair-wise analysis did not show any significant difference between broods: 1 vs. 2 Z=22.164•; 1vs. 3 Z=1.981; 2 vs. 3 Z=1.055). For Common Terns it varied overall and for nests containing eldest chicks aged between 10 to14 days (although pair-wise analysis

showed no significant difference between broods: 1 vs.2 Z=2.363•; 1 vs.3 Z=0.771; 2 vs. 3 Z=2.275•) and between 15 to 19 days (Table 5.10, Figure 5.9).

	Arctic Tern				Common Tern			
Kruskall-Wallis	n	χ^2	d.f.	p	n	χ^2	d.f.	p
0 to 4 days	284	6.908	2	0.032	235	6.456	2	0.040
5 to 9 days	367	14.194	2	0.001	236	16.437	2	<0.001
10 to 14 days	338	27.117	2	<0.001	238	24.243	2	<0.001
15 to 19 days	296	24.483	2	<0.001	304	40.648	2	<0.001
Mann-Whitney U	n	Z		p	n	Z		p
20 to 45 days	288	4.082		<0.001	306	3.432		0.001
25 days and older	293	2.184		0.029	275	3.378		0.001

Table 5.9 Kruskall-Wallis (between broods of 1-, 2- and 3-chicks) and Mann-Whitney U (between broods of 1- and 2-chicks) analyses of the effect of brood size on Arctic and Common Tern energy delivery ($kJ.nest^{-1}.h^{-1}$) for different age groups of eldest chick

	Arctic Tern				Common Tern			
Kruskall-Wallis	n	χ^2	d.f.	p	n	χ^2	d.f.	p
Overall	1876	2.079	2	0.354	1606	14.165	2	<0.001
0 to 4 days	284	6.897	2	0.032	235	2.950	2	0.229
5 to 9 days	367	1.292	2	0.524	236	1.701	2	0.540
10 to 14 days	338	2.459	2	0.292	238	8.696	2	0.013
15 to 19 days	296	0.312	2	0.856	304	9.292	2	0.010
Mann-Whitney U	n	Z		P	N	Z		P
20 to 24 days	224	0.654		0.513	306	0.498		0.618
25 days and older	293	0.935		0.350	275	1.494		0.135

Table 5.10 Kruskall-Wallis (between broods of 1-, 2- and 3-chicks) and Mann-Whitney U (between broods of 1- and 2-chicks) analyses of the effect of Arctic and Common Tern brood size on energy delivery rate per chick ($feed.chick^{-1}.h^{-1}$) for different age groups of elder chick

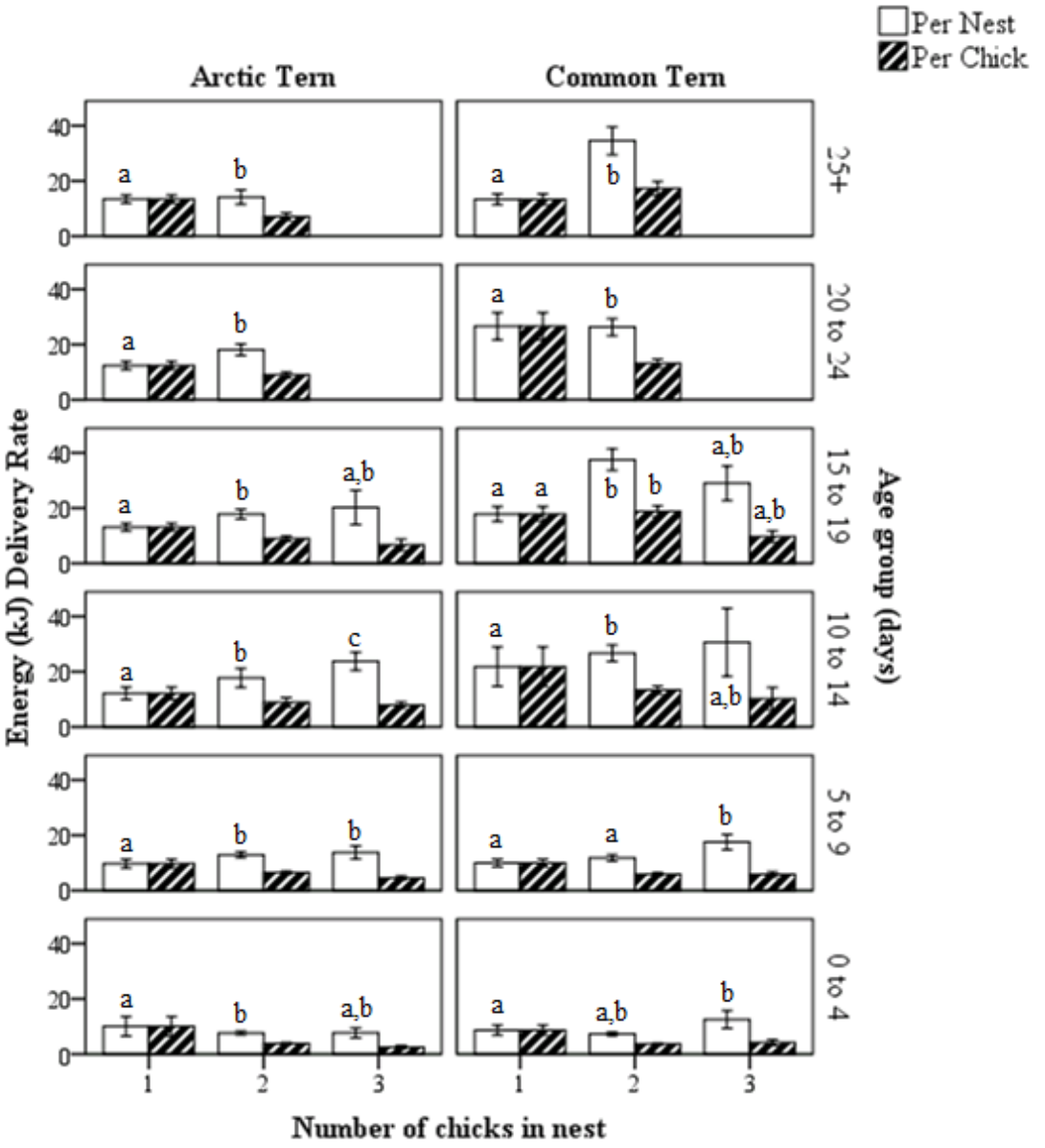


Figure 5.9 Rate of estimated energy delivery ($kJ.h^{-1}$) ±SE per nest and per chick depending on the brood size and age group for Arctic and Common Terns Columns with the same letter are not significantly different from each other ($p<0.05$).

Brood size had no effect on Arctic Tern estimated energy per feed. Common Tern energy per feed was significantly different depending on brood size for nests containing eldest chicks aged between 10 to 14 days and between 15 to 19 days (Table 5.11, Figure 5.10).

	Arctic Tern				Common Tern			
Kruskall-Wallis	n	χ^2	d.f.	p	n	χ^2	d.f.	p
0 to 4 days	242	0.465	2	0.792	215	0.869	2	0.647
5 to 9 days	328	1.944	2	0.378	218	1.158	2	0.561
10 to 14 days	298	1.203	2	0.548	204	10.305	2	0.006
15 to 19 days	245	0.631	2	0.799	241	11.518	2	0.003
Mann-Whitney U	n	Z		p	n	Z		p
24 to 25 days	231	0.725		0.468	240	0.832		0.406
25 days and older	224	0.654		0.513	203	1.189		0.234

Table 5.11 Kruskall-Wallis (between broods of 1-, 2- and 3-chicks) and Mann-Whitney U (between broods of 1- and 2-chicks) analyses of the effect of Arctic and Common Tern brood size on estimated energy per feed (kJ.feed^{-1}) for different age groups of eldest chick

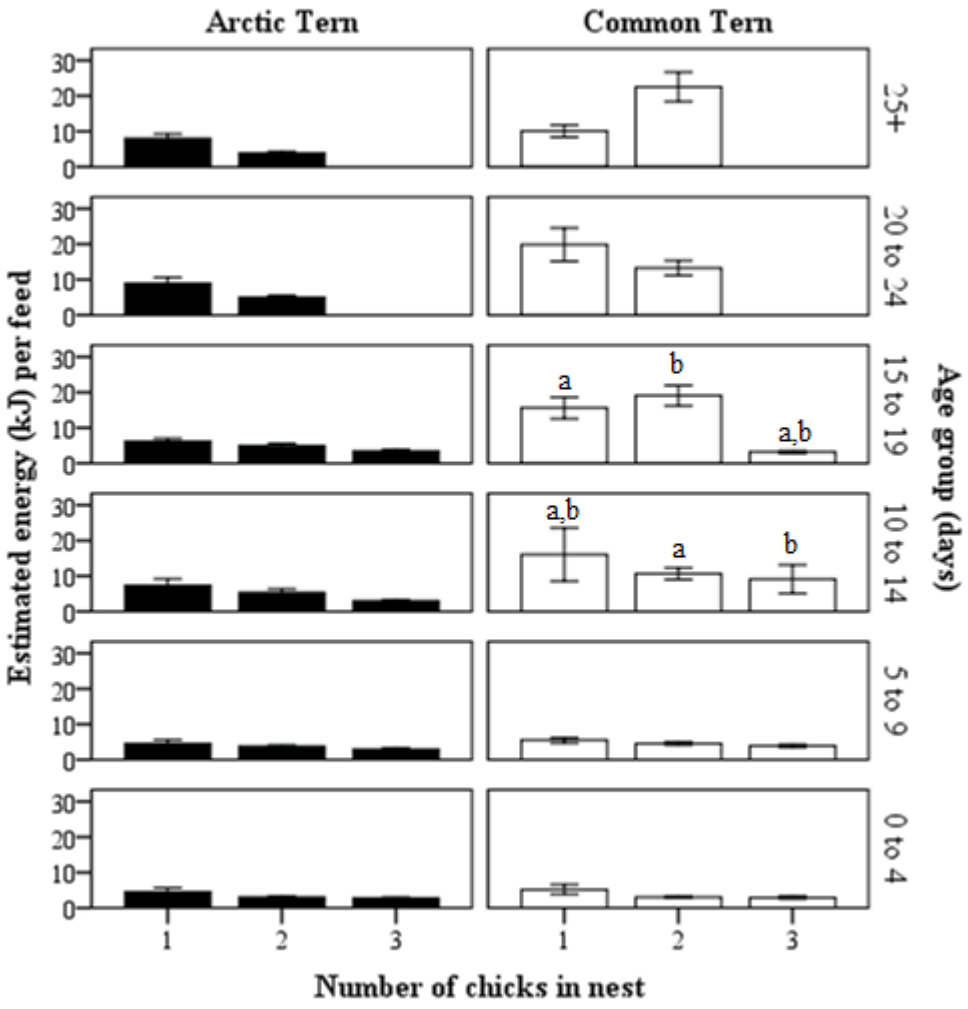


Figure 5.10 Estimated energy (kJ) per feed ± SE depending on the number of chicks in the nest and age group for Arctic and Common Terns. Letters denote columns differing significantly from one another ($p<0.05$).

5.4.6 Year and provisioning behaviour

Kruskall-Wallis analysis showed a significant difference in feed rate per chick, energy delivery rate per chick and energy per feed between years for both Arctic and Common Terns (Table 5.12, Figure 5.11, Figure 5.12, Figure 5.13).

	Arctic Tern				Common Tern			
	n	χ^2	d.f.	p	n	χ^2	d.f.	p
Feed.chick^{-1}.h^{-1}	1880	196.933	4	<0.001	1610	310.189	4	<0.001
kJ.chick^{-1}.h^{-1}	1886	185.879	4	<0.001	1599	110.369	4	<0.001
kJ.feed^{-1}	1571	149.155	4	<0.001	1335	158.883	4	<0.001

Table 5.12 Kruskall Wallis analysis of the effect of year (2006 through 2010) on Arctic and Common Tern provisioning (feed.chick^{-1}.h^{-1}). energy delivery (kJ.chick^{-1}.h^{-1}) and energy per feed (kj.feed^{-1})

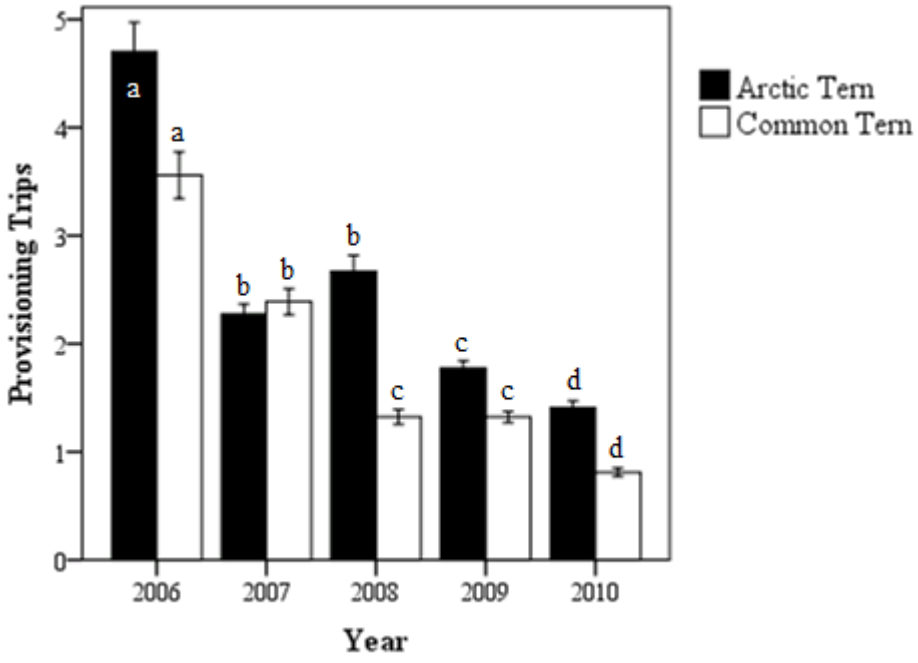


Figure 5.11 Mean rate of provisioning (feeds.chick^{-1}.h^{-1}) ± SE between years for Arctic and Common Terns. Columns with the same letter are not significantly different from each other ($p<0.05$).

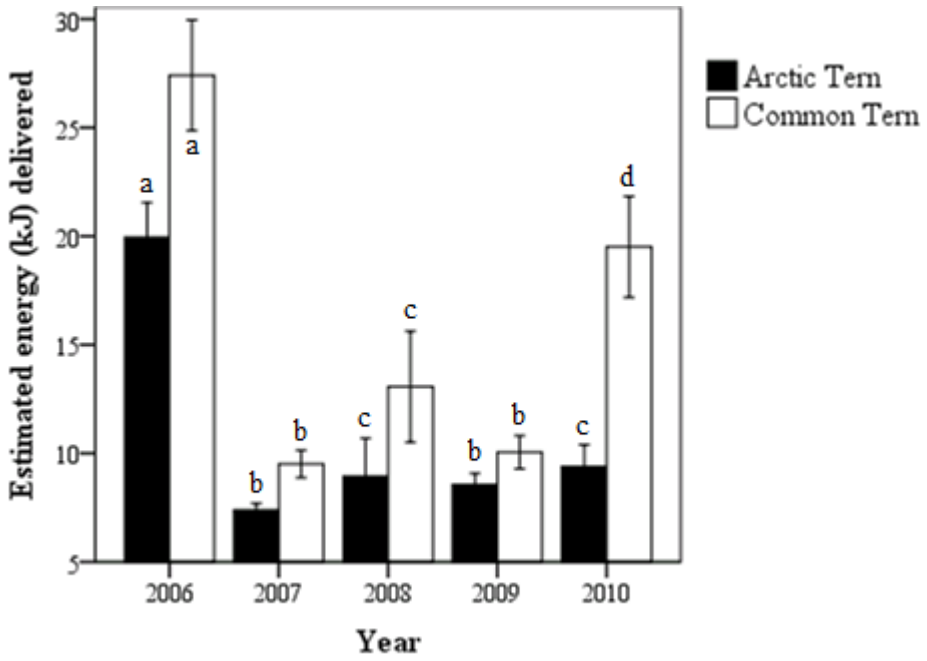


Figure 5.12 Mean rate of estimated energy delivery (kJ.chick^{-1}.h^{-1}) ± SE between years for Arctic and Common Terns. Columns with the same letter are not significantly different from each other ($p<0.05$).

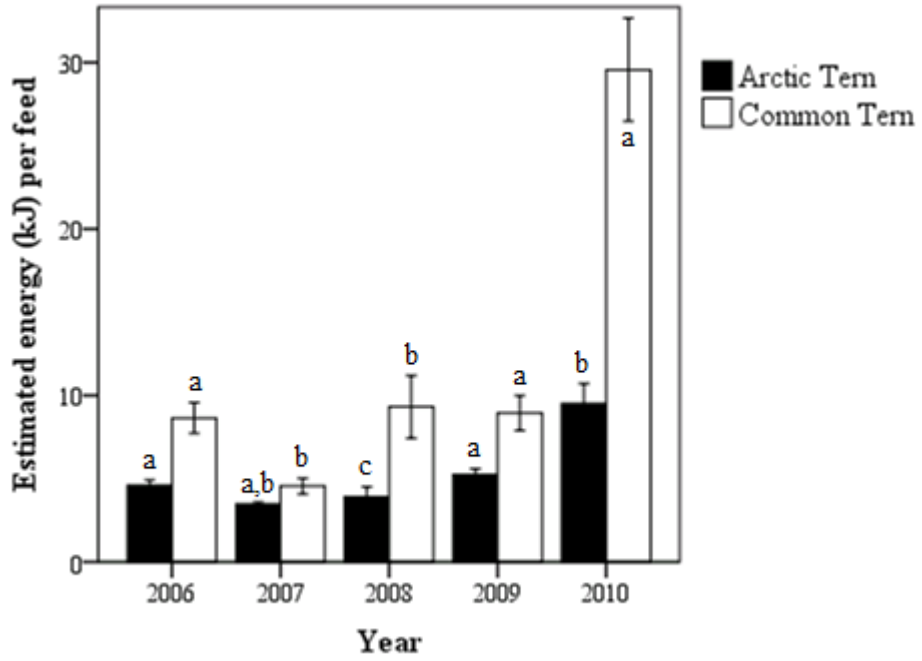


Figure 5.13 Mean estimated energy per feed (kj.feed^{-1}) ± SE between years for Arctic and Common Terns. Columns with the same letter are not significantly different from each other ($p<0.05$).

5.4.7 Year and diet

Kruskall-Wallis analysis of the effect of year on proportion of different prey species brought back to the nest by Arctic and Common Terns showed a significant effect of year for all prey species (Table 5.13, Figure 5.14).

Pair-wise analysis showed proportions of Sandeel brought to the nest to be significantly different between all years for Arctic Terns ($Z>4.298$, $p<0.001$) except between 2006 and 2007 ($Z=0.799$) and 2008 ($Z=1.381$), and between 2007 and 2008 ($Z=2.579$, $p=0.099$). For Common Terns, proportions were different between all years ($Z>3.070$, $p<0.003$) except between 2006 and 2007 ($Z=2.143$) and 2008 ($Z=2.517$), and between 2008 and 2009 ($Z=1.328$).

Proportions of Clupeid brought to the nest were significantly different between all years for Arctic Terns ($Z>4.298$, $p<0.001$) except between 2006 and 2007 ($Z=0.844$) and 2008 ($Z=0.751$), and between 2007 and 2008 ($Z=1.903$), and between 2009 and 2010 ($Z=0.166$). For Common Terns, proportions were different between all years ($Z>3.070$, $p<0.03$) except between 2006 and 2007 ($Z=2.143$) and 2008 ($Z=2.517$), and between 2008 and 2009 ($Z=1.328$).

Proportions of small fish brought to the nest were the same between all years for Arctic Tern ($Z<2.297$, $p>0.1$) except between 2007 and 2009 ($Z=3.858$**), and between 2010 and 2006 ($Z=7.630$**), 2007 ($Z=10.621$**), 2008 ($Z=8.320$**) and 2009 ($Z=6.684$**). For Common Terns, proportions were different between all years ($Z>2.849$, $p<0.05$) except between 2006 and 2007 ($Z=0.739$) and 2009 ($Z=1.140$), and between 2008 and 2009 ($Z=2.055$) and 2010 ($Z=0.761$).

Proportions of Shrimp brought to the nest by Arctic Terns were the same in all years ($Z<1.977$, $p>0.4$) except between 2010 and 2007 ($Z=3.713$**) and 2008 ($Z=2.881$*).

Proportions of Pipefish brought to the nest by Common Terns were the same in all years ($Z<2.564$, $p>0.1$) except between 2006 and 2009 ($Z=3.074$*) and 2010 ($Z=3.084$*), and between 2007 and 2009 ($Z=3.891$**) and 2010 ($Z=3.915$**).

Proportions of 'Other' fish brought to the nest by Arctic Terns were the same between all years ($Z<2.689$, $p>0.05$) except between 2007 and 2010 ($Z=3.828$**). For Common

Terns, proportions were the same between all years ($Z<2.344$, $p>0.1$) except between 2007 and 2009 ($Z=2.913$*) and 2010 ($Z=2.903$*).

	Arctic Tern				Common Tern			
	n	χ^2	d.f.	P	N	χ^2	d.f.	p
Sandeel	1565	216.902	4	<0.001	1338	147.454	4	<0.001
Clupeid	1565	80.985	4	<0.001	1338	123.575	4	<0.001
Small Fish	1565	135.772	4	<0.001	1338	49.101	4	<0.001
Shrimp	1565	15.885	4	0.003				
Pipefish					1338	27.383	4	<0.001
Other	1565	16.309	4	0.003	1338	16.214	4	0.024

Table 5.13 Kruskall-Wallis analysis of differences in proportion of different prey species brought to the nest by Arctic and Common Terns between years

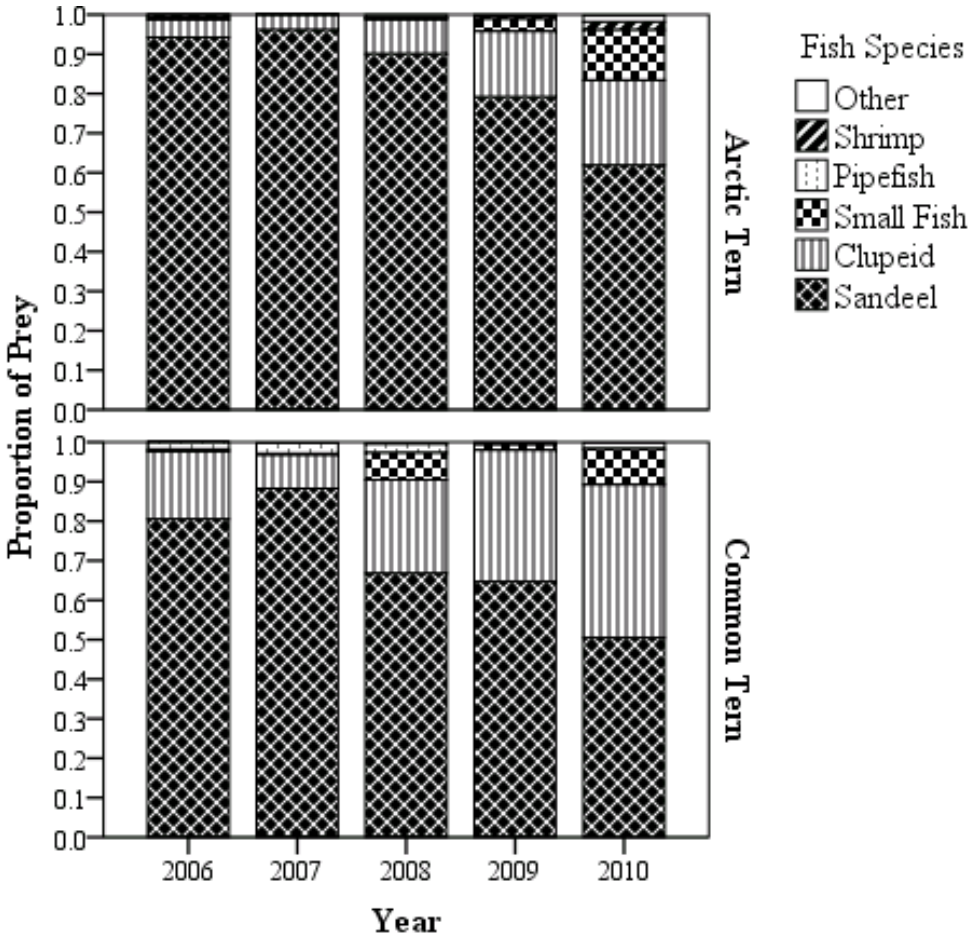


Figure 5.14 Proportions of different prey species brought to the nest by Arctic and Common Terns by year, showing a significant yearly difference in proportions of all prey species for both Arctic and Common Terns.

Year had a significant effect on the proportion of different sized Sandeel brought to the nest by Arctic Terns (Pearson's Chi-squared, n=5384, χ^2=1,943.774, df=8, p<0.001) and Common Terns (n=3614, χ^2=524.983, df=4, p<0.001). Year also had a significant effect on the proportion of different sized Clupeid brought to the nest by Arctic Terns (n=5384, χ^2=74.090, df=8, p<0.001) and Common Terns (n=708, χ^2=170.309, df=8, p<0.001) (Figure 5.15).

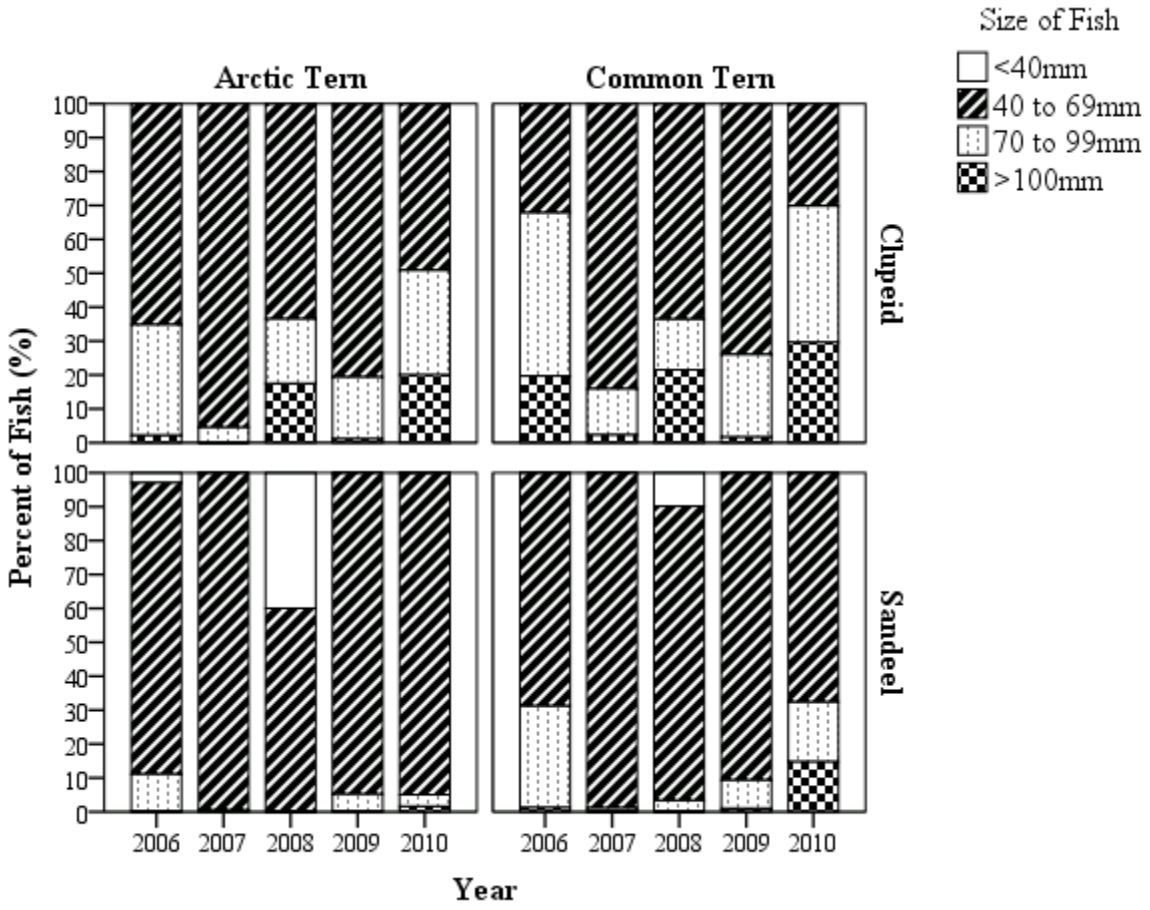


Figure 5.15 Percentage of Sandeel and Clupeid of different sizes brought to the nest by Arctic and Common Terns between years, showing a significant difference in size between years for both Sandeel and Clupeid.

Percentage of total fish of each size caught fed to chicks depending on year is shown in Table 5.14 with subscript letters denoting significant differences between values (Z test of column proportions, p<0.05).

			2006	2007	2008	2009	2010
Arctic Tern	Sandeel	<40mm	7.4_{a}	0.2_{b}	92.4_{c}	0.2_{b}	0.2_{b}
		40 to 69mm	19.8_{a}	37.3_{b}	12.6_{c}	17.6_{a}	12.6_{b}
		70 to 99mm	63.0_{a}	2.0_{b}	0.5_{b}	23.3_{c}	11.6_{d}
	Clupeid	40 to 69mm	9.5_{a}	$13.2_{a,b}$	$12.6_{a,b}$	46.1_{c}	18.6_{b}
		70 to 99mm	15.2_{a}	2.0_{b}	12.1_{a}	33.3_{c}	37.4_{c}
		>100mm	2.6_{a}	2.6_{a}	28.9_{b}	5.3_{a}	63.2_{c}
Common tern	Sandeel	40 to 69mm	$14.7_{a,c}$	52.7_{b}	10.5_{c}	$14.7_{a,c}$	7.4_{c}
		70 to 99mm	60.2_{a}	5.3_{b}	3.8_{b}	12.7_{c}	18.0_{c}
		>100mm	12.3_{a}	1.5_{b}	1.5_{b}	$7.7_{a,b}$	76.9_{c}
	Clupeid	40 to 69mm	8.9_{a}	18.3_{a}	16.8_{a}	44.2_{b}	11.9_{a}
		70 to 99mm	26.3_{a}	5.9_{b}	7.8_{b}	28.8_{a}	31.2_{a}
		>100mm	22.4_{a}	2.0_{b}	23.5_{a}	4.1_{b}	48.0_{c}

Table 5.14 Percentage of total fish of each size caught fed to chicks between years

5.5 Discussion

Here, as in other studies, both species preyed almost exclusively on surface-living fish with a high reliance on Sandeel and Clupeid (Pearson 1968; Monaghan et al. 1989; Uttley et al. 1989; Robinson & Hamer 2000), which constituted 95% of the diet of both species. Sandeel were the most common prey species of both species but were a more significant prey item for Arctic Terns than for Common Terns (83% and 71% of diet respectively), while Common Terns preyed relatively more heavily on Clupeid (24% of diet compared to 12% for Arctic Terns).

Other than in 2007, when provisioning rate was comparable between species, Arctic Terns provisioned their chicks at a consistently higher rate than Common Terns while bringing in less energy per hour and per feed. This difference in foraging rates has been observed at other locations (Pearson 1968; Lemmetyinen 1976; Chapdelaine et al. 1995; Frick & Becker 1995) and on Coquet Island (Uttley et al. 1989). However, Robinson et al. (2001) found that Common Terns on Coquet Island foraged at a faster rate than the Arctic Terns (although energy delivery was still higher than that of Arctic Terns). Some of the difference in energy delivery can be explain by differences in prey choice. Arctic Terns brought in more Sandeel which contain proportionally less energy than do Clupeid (Hislop et al. 1991), and their preference for smaller prey items with lower calorific value has a compounding effect (Hislop et al. 1991).

While both Arctic and Common Terns have access to the same prey and foraging grounds, high foraging rate for low yield implies that foraging conditions around Coquet Island were not ideal for Arctic Terns. The limited foraging ranges of both Arctic and Common Terns and their high reliance on a single prey species increase their vulnerability to fluctuations in Sandeel availability (Monaghan 1996; Croxall et al. 1999; Furness & Tasker 2000) however Arctic Tern appear to be more vulnerable than Common Tern suggesting they are less able to exploit local prey and foraging habitat than are the Common Tern. Their increased investment in foraging effort indicates difficulties in adequately provisioning chicks, and their lower productivity would support this suggestion.

Age of chick had little effect on provisioning rate but had a large effect on energy delivery rate. Energy delivery to the nest increased with increasing age, plateauing for Arctic Terns after the age of 10 days and peaking for Common Terns between the ages of 15 and 19 days. This pattern resembles the daily energy needs of the chicks, which reach a maximum around the ages of 10 to 15 days (Klassen 1989; Massias & Becker 1990; Klassen 1994). Increased energy delivery at the same foraging rate was explained by an increase in energy yield per feed.

Increasing energy delivery to the nest while maintaining provisioning rate has been shown to be achieved by selection of larger prey (Emms & Verbeck 1991; Stienen et al. 2001) or selection of different prey species (Casaux et al. 2008). Here, Common and Arctic Terns appear to be using both methods. Both species selected larger prey items for older chicks, and the proportion of the more energy-rich Clupeid in the diet increased with age of chick (especially for Common Terns, with Clupeid peaking at 33% of diet compared to 18% for Arctic Terns). Trip duration was not recorded in this study, but a study of parental attendance (Chapter 7) showed that parents of older chicks spent less time at the nest, suggesting more time was spent locating the higher-value prey.

Here again, however, Arctic Terns appeared unable to increase their foraging effort as efficiently as Common Terns. While Arctic Terns did initially increase the energy supply to the nest, there appeared to be a fairly low maximum energy yield per feed, suggesting less flexibility in prey selection. Arctic Tern parental attendance at the nest site was lower than for Common Terns and appeared to decline more rapidly with age

of chick (Chapter 7), indicating a higher foraging effort. As with the general feeding observations, this appears to indicate that foraging conditions around Coquet Island are not ideal for Arctic Terns, and that they are unable to exploit the same prey resources as efficiently as Common Terns.

Increased provisioning with increased brood size is well documented (Johnson & Best 1982; Barrett et al. 1987; Emms & Verbeck 1991; Goodbred & Holmes 1996; Robinson & Hamer 2000; Anderson et al. 2005) and Arctic and Common Terns are no exception. Provisioning rate to the brood as a whole was always greater for 2 chick broods than 1 chick broods. Provisioning to 3 chick broods was generally at a similar rate to that of 1 or 2 chick broods for Arctic Terns, while Common Terns always provisioned 3 chick broods faster than 1 chick broods and, initially, provisioned them faster than 2 chick broods. Rate of energy delivery to the broods also increased when brood size increased from 1 to 2 chicks, but 3 chick broods were provisioned at a similar energy rate to other brood sizes and no difference in energy per feed was recorded. Others have suggested that parents accommodate larger broods by increasing the size or calorific value of prey (Siikamaki et al. 1998; Wright et al 1998) but here it is suggested that larger broods result only in increased foraging rate not in differences in prey selection.

While not significant, Figure 5.9 does appear to suggest a decline with brood size in the rate of energy delivery per chick for both species. Low power might account for lack of significance due either to low numbers of 3 chick broods initially (<5% of broods for Arctic Terns) or to reduced brood size though chick mortality (<10% of Common Tern broods contained 3 chicks by the age of 10 to 14 days), especially the high early mortality of third chicks (Chapter 4), thereby reducing brood size before the energy demands of 3 chick broods outstrip those of smaller broods (Langham 1972).

It was suggested in Chapter 3 that differences in the clutch size of each species could be accounted for by differences in their provisioning behaviour, with Arctic Tern clutch size limited by their ability to provision chicks. The data in this chapter appear to support this hypothesis, with Arctic Terns showing little to no increase in foraging effort for 3 chick broods.

There was large variability in feeding conditions between years, with no two years showing comparable conditions. Both species show similar variation between years,

especially with regard to energy per hour and per feed. Provisioning behaviour often reflects local forage fish stocks (Frank 1992; Montevecchi & Myers 1995; Diamond & Devlin 2003; Wanless et al. 2005; Furness 2007), with foraging effort modified according to whether prey is scarce or not. The effects of low prey availability can be minimised by increasing the foraging effort (trip frequency or duration) (Uttley 1992; Monaghan et al. 1994; Wanless et al. 2005) or by utilising alternative prey (Monaghan et al 1989; Frick & Becker 1995).

While no data are available on local forage fish availability around Coquet Island between 2006 and 2010, the International Council for the Exploration of the Sea (ICES) stock biomass data for the Central Western North Sea (SA4) is available (ICES 2012). These data show a low presence of all age groups of Sandeel in 2008 compared to an abundance of age '0' Sandeel in 2009. While fishing effort is low in this area, these data still indicate that there are fluctuations in Sandeel population dynamics and that these fluctuations impact seabird breeding success. The low numbers of Sandeel in 2008 corresponds to the poor breeding season seen in both Arctic and Common Terns. 2009 was a successful year in terms of productivity for both species and this appears to be linked with the abundance of age class '0' Sandeel. Differences in provisioning rates and parental attendance (Chapter 7) between these two years would indicate that the birds invested different levels of effort depending on availability of Sandeel, compensating for shortages by increasing foraging effort. In addition, changes in diet were seen in both species between years. Birds are known to switch diet if preferred prey species are unavailable (Monaghan et al 1989; Frick & Becker 1995) and it appears that when there is a reduced availability of Sandeels both species will switch diet to take advantage of more accessible prey, though this did not necessarily maintain high productivity.

2010 was an interesting year in terms of productivity, with Arctic Terns experiencing the second lowest productivity seen over the five years and Common Terns the second highest. Foraging rates were low but energy per feed was high for both species. Arctic Terns spent little time at the nest site once chicks were over five days old but fairly high nest attendance by Common Tern was observed throughout the nestling period. It is apparent that foraging conditions around Coquet Island in 2010 were impacting these two species differently, with conditions being favourable for Common Terns and unfavourable for Arctic Terns. One possible explanation of the difference comes from

the ICES stock biomass data which shows an abundance of larger sized age group-1 Sandeel in SA4 in 2010 (ICES 2012), which correlates with the size of Sandeel brought to the nest and the energy per feed values seen in 2010. The data presented here show that the Arctic Tern diet generally contains smaller sized fish than that of Common Terns; if these smaller sized Sandeel were unavailable in 2010, and the larger sized fish were either inaccessible or inappropriate for Arctic Terns, then this explains the differences in productivity seen between the two species. Differences in the size of prey brought to the nest suggest that this was the case. While there was little difference in the percentage of different sized Sandeel brought to the nest by Arctic Terns in 2010 compared to other years, Common Terns appeared able exploit the availability of large Sandeels, and in 2010 15% of the Sandeel brought to the nest were over 100mm in length (corresponding to the older age groups) compared to less than 1% in other years.

As was discussed in Chapter 3, Arctic Terns either have a quantity over quality foraging strategy, or have a bias in favour of smaller prey items, or are unable to exploit the same resources as Common Terns. Why Common Terns appear to be able to better exploit foraging habitats and have a preference for larger prey items then Arctic Terns is not known. While superficially very similar birds, Arctic Terns are on average lighter, with a lower beak to skull ratio (Brown et al. 1987). They are therefore potentially limited in the depth to which they can dive and the size of prey which they can manipulate and transport. Further study into differences in the foraging habitats of the two species, and study of Sandeel distribution, would be needed to explain the differences in foraging success.

Differences in the rate of energy delivery and energy per feed between years are explained by differences in the diet of the two species. High energy years are associated with higher proportion of Clupeid in the diet and larger prey for both species. There appear to be general trends both of a decline in the levels of Sandeel and of an increase in the levels of Clupeid in the diet. There was little difference between 2006 and 2007 in the levels of Sandeel and Clupeid in the diet of each species. Thereafter, both Arctic and Common Tern diets showed a significant and steady decline in the proportion of Sandeel (96% to 62% and 88% to 50% respectively) and an increase in the proportion of Clupeid (4% to 22% and 9% to 39% respectively).

The link between food supply and breeding success is long established (Monaghan et al. 1989; Uttley et al. 1989; Massias & Becker 1990; Suddaby & Ratcliff 1997; Diamond & Devlin 2003). However, this study found no clear link between any one aspect of chick provisioning and productivity. Rather, the study shows clearly the importance of overall foraging conditions, and the fine line for chicks between good and poor conditions. Superficially similar years in terms of observed foraging behaviour can result in very different productivity, and it is only with the inclusion of other data such as nest attendance or stock biomass data that these differences can be understood.

For example, for both Arctic and Common Tern productivity was lowest in 2008. The only obvious atypical characteristic of provisioning behaviour in 2008 was prey size: both species brought to the nest a higher proportion of very small Sandeel (<40mm) and very large Clupeid (>100mm) than in other years, but energy delivery rate to the nest was comparable to other years. However, from personal observation, chicks appeared hungry, were seen mobbing any adult returning to the nest area, and exhibited frequent bouts of inter-sibling aggression. Combined with the very high chick mortality observed, this indicates that 2008 was a very poor year in terms of chick provisioning, but why?

ICES data on Sandeel stock biomass showed low levels of Sandeels and data presented in Chapter 7 show very low parental attendance at the nest site. This implies high time investment in the foraging effort due to low availability of prey and high pressure on parent birds to provision chicks. It is suggested that in 2008 both species were foraging at maximum effort (as indicated by low time spent at the nest site) but were still unable to provision chicks sufficiently to mitigate the effects of Sandeel shortage; therefore chick mortality was high and productivity low.

In conclusion, understanding the impact of foraging conditions on Arctic and Common Tern provisioning behaviour and the resulting breeding success involves more than simple foraging observations. It also requires an understanding of conditions at sea and the levels and nature of pressures the adult birds are under. Provisioning observations provide valuable data on chick provisioning and adult behaviour, but long-term, consecutive data sets, covering multiple aspects of adult behaviour, are required for a clear understanding of the impact of changing foraging conditions on breeding success.

Chapter 6. Parental Provisioning and Chick Diet in relation to State of the Tide, Diurnal Rhythms and Weather Conditions

6.1 Abstract

Arctic and Common Terns need to provide enough food to meet the daily energy requirements of their chicks. Foraging conditions, which change throughout the day and in response to unpredictable weather conditions, impact chick provisioning. Arctic Terns increased chick provisioning shortly after dawn but Common Terns showed no change during the day. Changes in diet were observed throughout the day and linked with changing activity cycles of prey species. Temperature and precipitation both impacted provisioning, but parents maintained energy delivery to chicks by altering diet and/or provisioning rate. High wind speed appeared to have a significant negative impact on chick provisioning; provisioning rate and energy delivery decreased as wind speed increased. It is suggested that high winds make it harder to capture prey, with a consequent decline in chick provisioning.

6.2 Introduction

During the breeding season, foraging behaviour is primarily driven by the need to provision chicks, with adult birds modifying their foraging effort according to chicks' needs (Langham 1972; Massias & Becker 1990; Drent et al. 1992; Gabrielsen et al. 1992; Konarzweski et al. 1993; Robinson et al. 2001; Chapter 5). However, foraging conditions often vary with diurnal and tidal cycles, and weather conditions affect prey behaviour, accessibility and ease of capture.

Seabirds have to adjust to the changing currents, foraging ground availability and distribution of prey as a result of the rhythm of the tidal cycle. Foraging rates often vary with the state of the tide (Dunn 1972; Boecker 1967 in Becker et al. 1997; Frank 1992; Noordhuis & Spaans 1992; Frick & Becker 1993; Steinen et al. 2000; Gonzalez-Solis et al. 2001; Garcia & Mariano-Jelicich 2005), and birds adjust the timing of foraging trips or choice of foraging grounds to coincide with a particular state of the tide (Becker et al. 1993; Irons 1998). Changes in diet are associated with the tidal cycle, with the proportion of different prey species in the diet varying (Frank 1992; Frick & Becker

1993; Anderson et al. 2005), possibly as a result of differences in prey behaviour or changes in foraging areas.

Diurnal rhythms in foraging have also been observed, with the foraging rate (Frank 1992; Lance & Roby 1998; Garcia & Mariano-Jelicich 2005; Stienen et al. 2000; Becker et al. 1997) and diet composition (Casaux et al. 2008; Stienen et al. 2000) varying throughout the day. Provisioning rates tend to peak in the hours shortly after dawn and occasionally before dusk and it has been proposed that this is due to the provisioning needs of chicks (Dunn 1972). The behaviour of prey species shows diurnal patterns, resulting in differences in availability or accessibility depending on time of day. For example, the two main prey fish of Arctic and Common Terns, Sandeel and Clupeidaea, show very different behaviour. Sandeel spend the night buried in sediment on the sea bed, moving up the water column with daylight (e.g. Freeman et al. 2004; Engelhard et al. 2008) while Clupeids are more active (Beyst et al. 2002) and higher in the water column at night (Blaxter & Parrish 1965 in Stienen et al. 2000; Laevastu & Hayes 1981).

As well as the predictable daily rhythms, foraging birds have to adjust to the less predictable weather conditions. The effect of weather on adult birds with chicks in the nest is twofold: a potential reduction in time available for foraging due to increased need to brood chicks (see references in Chapter 7); and a direct impact on foraging by altering prey distribution and affecting performance as predators.

Of the three weather conditions recorded in the study (temperature, wind speed and precipitation), the impact of wind speed on foraging has been the most extensively studied. Wind speed and the associated changes in water turbidity affect the energy expended on flight (Tucker 1968, Tucker1969 cited in Tucker & Schmidt-Koenig 1971) and the location (Ehrenbaum 1936 in Frank 1992; Corten & Van de Kamp 1996) and visibility of prey (Bovino & Burtt 1979). Foraging rates (Reed & Ha 1983; Taylor 1983; Frank 1992; Stienen et al. 2000; Garcia & Mariano-Jelicich 2005), foraging behaviour (Taylor 1983; Sagear & Sagear 1989), capture success (Reed & Ha 1983; Sagear & Sagear 1989; Garcia & Mariano-Jelicich 2005) and chick diet (Frank 1992; Steinen et al. 2000) have all been shown to vary with wind speed.

Less information is available on the impact of temperature and precipitation on foraging behaviour. Sea surface temperature (SST) varies with air temperature (Kaplam et al. 2003) and higher SST has been shown to reduce feeding rates over the long (Quillfeldt et al. 2007) and short term (Erwin & Congden 2007), and to reduce meal mass (Peck et al. 2004). Precipitation has been shown to reduce success rate (Bovino & Burtt 1979) but to have no effect on foraging rates (Anderson et al. 2005).

The aim of this study is to understand how provisioning behaviour and diet of Arctic and Common Terns breeding on Coquet Island vary diurnally and in response to weather conditions. Provisioning rates and diet are expected to reflect the tidal cycle and vary throughout the day, while weather conditions may have either a positive or negative impact on feeding conditions. Both species forage in similar areas around Coquet Island, although Arctic Terns forage more to the East than Common Terns, which forage mainly between the island and the mainland and to the North and South (Wilson et al. unpublished report 2012). The effects of the tide are likely to be greater nearer the coast and in the channel between the island and the mainland. It is therefore predicted that a greater tidal variability will be found in Common Tern provisioning than in that of Arctic Terns. Diurnal patterns are likely to be similar, although the greater reliance of Common Terns on Clupeids may be reflected in larger variability in diet. A comparison between these two species will increase our understanding of the foraging and provisioning constraints imposed by changing environmental conditions.

6.3 Methodology and analysis

6.3.1 Methodology

See Chapter 2, section 2.3.1, 2.3.2 and 2.4.2.

6.3.2 Analysis

Data were tested for normality using the one-sample Kolmorgorov-Smirnov test for normality and found to be non-normally distributed. Transformation of data was attempted but found to be ineffective for data normalisation therefore non-parametric statistics were used. Analyses using Generalized Linear Models (GLM) were attempted but models showed poor fit. Although GLMs would provide powerful tools for analysing the data, a more-sophisticated approach to modelling the underlying data

distributions is required but is beyond the scope of this thesis. All analysis was undertaken using IBM SPSS Statistics, version 19.

Kruskall-Wallis test was used to compare provisioning rate (feed.chick^{-1}.h^{-1}), energy delivery (kJ.chick^{-1}.h^{-1}), energy per feed (kJ.feed^{-1}) and proportions of different prey species brought back to chicks depending on state of the tide (high, ebb, low and flood) and time of day (05:00 - 0759, 08:00 - 10:59, 11:00 - 13:59, 14:00 - 16:59, 17:00 - 19:59 and 20:00 - 21:59). Pair-wise analysis (p-value adjusted for multiple comparisons) was used to compare groups. Pearson's Chi-squared test was used to compare proportions of different sized Sandeel and Clupeid brought to the nest depending on time and tide

Spearman's Rho correlation was use to examine the relationship between daily average temperatures (˚C), wind speed (km.h^{-1}) and daily precipitation (mm, when rainfall > 0) and daily provisioning rate (feed.chick^{-1}.h^{-1}), daily energy delivery (kJ.chick^{-1}.h^{-1}), daily energy per feed (kJ.feed^{-1}) and proportions of Sandeel and Clupeids brought to the nest.

6.4 Results

6.4.1 Tidal cycle and provisioning

Kruskall-Wallis analysis of provisioning behaviour (feeding rate per chick, feed.chick^{-1}.h^{-1}; estimated energy delivery rate per chick, kJ.chick^{-1}.h^{-1}; estimated energy per feed, kJ.feed^{-1}) demonstrated a significant effect of tide (high, ebb, low, flood) on the provisioning behaviour of Arctic Terns but not on that of Common Terns (Table 6.1, Figure 6.1, Figure 6.2, Figure 6.3).

	Arctic Tern				Common Tern			
	n	χ^2	d.f.	p	n	χ^2	d.f.	p
Feeds.chick^{-1}.h^{-1}	1880	37.849	3	<0.001	1610	6.616	3	0.085
kJ.chick^{-1}.h^{-1}	1876	40.165	3	<0.001	1599	2.291	3	0.514
kJ.feed^{-1}	1571	15.068	3	0.002	1335	2.399	3	0.494

Table 6.1 Kruskall-Wallis analysis of differences in feeding rate per chick (feed.chick^{-1}.h$^{-1)}$, estimated energy delivery rate per chick (kJ.chick^{-1}.h^{-1}) and estimated energy per feed (kJ.feed^{-1}) of Arctic and Common Terns depending on state of the tide

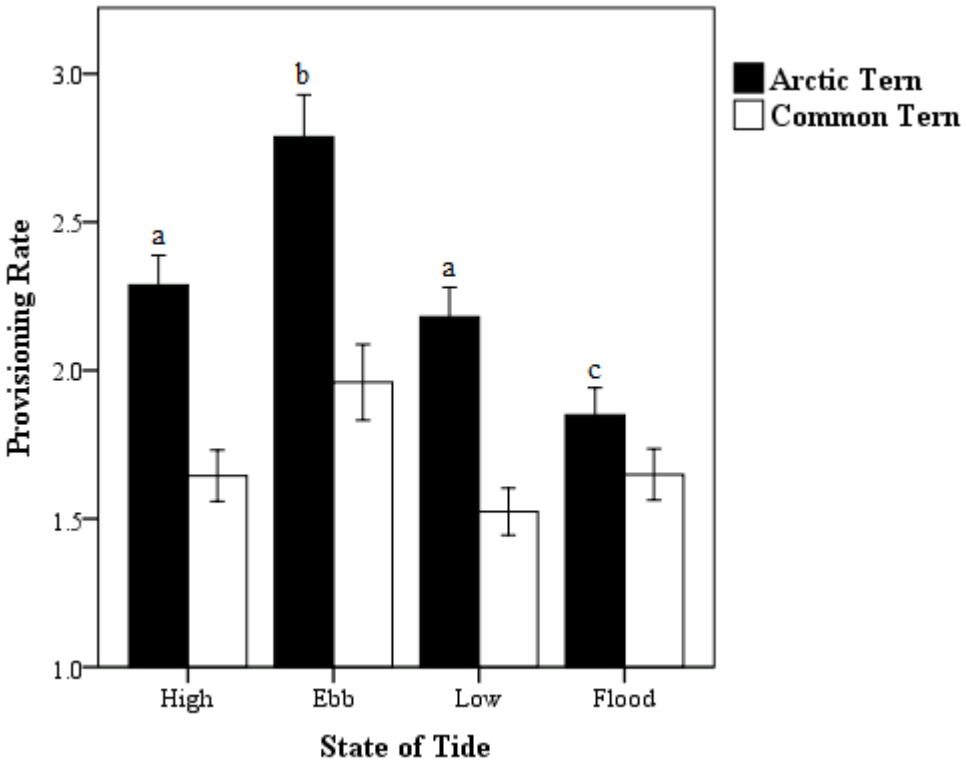


Figure 6.1 Mean Arctic and Common Tern provisioning rate per chick (feed.chick^{-1}.h^{-1}) depending on state of the tide ± SE. Columns with the same letter are not significantly different from each other ($p<0.05$).

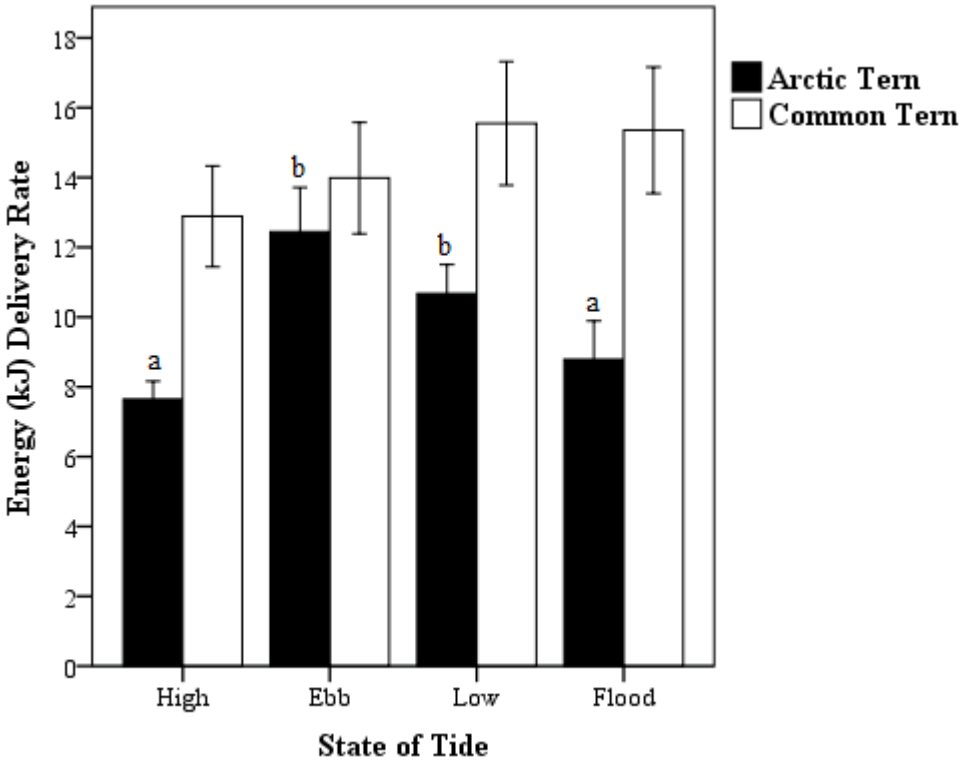


Figure 6.2 Mean Arctic and Common Tern estimated energy delivery rate per chick (kJ.chick^{-1}.h^{-1}) depending on state of the tide ± SE. Columns with the same letter are not significantly different from each other ($p<0.05$).

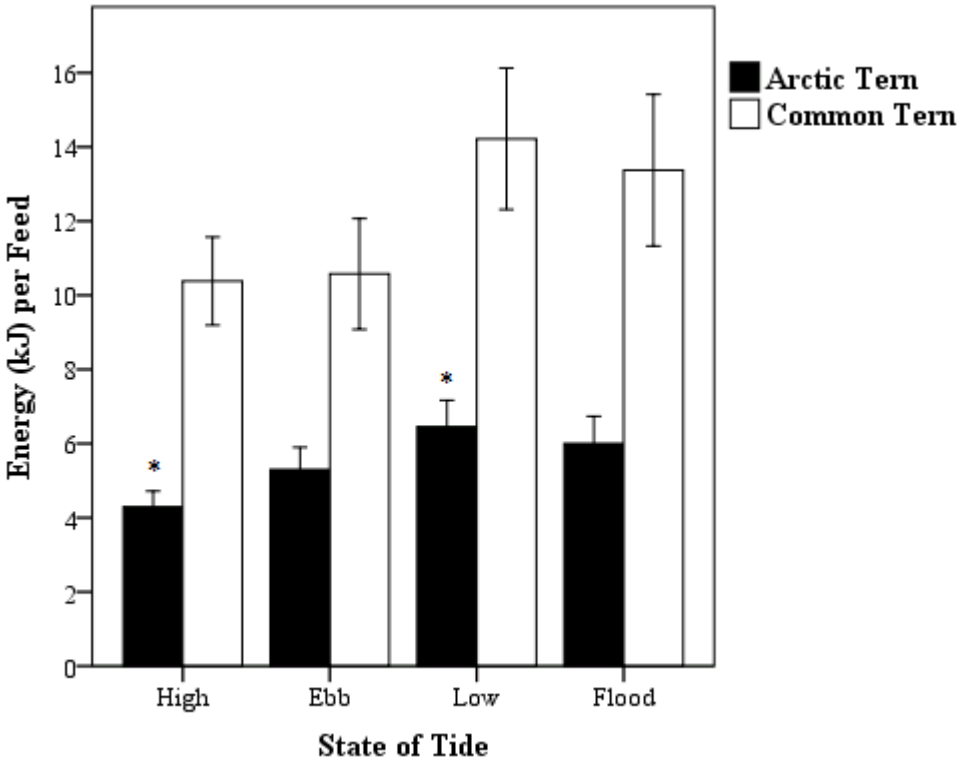


Figure 6.3 Arctic and Common Tern estimated energy per feed (kJ.feed^{-1}) depending on state of the tide ± SE. Stared columns differ significantly from one another ($p<0.05$).

6.4.2 Tidal cycle and diet

Kruskall-Wallis test demonstrated a significant effect of tide on proportions of small fish and Shrimp brought to the nest by Arctic Terns and on the proportions of Sandeel and Pipefish brought to the nest by Common Terns. Proportions of Clupeid and 'Other' fish did not vary for either species (Table 6.2).

	Arctic Tern				Common Tern			
	n	χ^2	d.f.	p	n	χ^2	d.f.	p
Sandeel	1565	0.555	3	0.907	1338	11.877	3	0.008
Clupeid	1565	4.454	3	0.216	1338	5.401	3	0.145
Small Fish	1565	9.766	3	0.021	1338	2.168	3	0.538
Shrimp	1565	8.912	3	0.030				
Pipefish					1338	27.041	3	<0.001
Other	1565	4.955	3	0.175	1338	7.017	3	0.071

Table 6.2 Kruskall-Wallis analysis of differences in proportions of different prey species brought to the nest by Arctic and Common Terns depending on state of the tide

Pair-wise analysis showed that the proportion of Sandeel brought to the nest by Common Terns was comparable between states of the tide ($Z<1.216$, $p>0.9$) apart from between low and ebbing ($Z=3.104$*) and high (2.832*) tides. Proportion of small fish brought to the nest by Arctic Terns were comparable between states of the tide ($Z<2.480$, $p>0.07$) except between low and flood tides ($Z=2.834$*). Proportion of Shrimp brought to the nest by Arctic Terns were comparable between states of the tide ($Z<1.991$, $p>0.2$) except between flood and high tides ($Z=2.846$*). Proportion of Pipefish brought to the nest by Common Terns were comparable between states of the tide ($Z<1.216$, $p>0.9$) except between low tide and flood ($Z=4.754$**), high ($Z=3.798$**) and ebb tides ($Z=3.780$**) (Figure 6.4).

The state of the tide had a significant effect of the proportions of different sized Sandeel brought to the nest by Arctic Terns (Pearson's Chi-squared, n=5366, $\chi^2=126.049$, df=6, $p<0.001$) and Common Terns (n=3576, $\chi^2=19.728$, df=6, p=0.003). Z-test of column proportions showed that for Arctic Terns the percentage by tidal state of small Sandeel (under 40mm in length) brought to the nest decreased in the order high, flood, ebb and low. For Sandeel between 40 and 69mm, percentages for ebb, low and flood were similar, with the lowest percentage at high tide. Sandeel between 70 and 99mm were more likely at low tide, with the percentages for other states of the tide similar. Common Terns were most likely to bring in Sandeel between 40 and 69mm at flood tide, with the percentages at ebb and low tide similar and the lowest percentage at high tide. Sandeel between 70 and 99mm were most likely at high tide, with the percentages for ebb and low tides similar and the lowest percentage at flood tide. For Sandeel 100mm and over, the percentages were similar (and very low) for high and low tides, and insignificant for ebb and flood tides (Figure 6.5).

Proportions of different sized Clupeid brought to the nest also varied with the state of the tide for both Arctic Terns (Pearson's Chi-squared, n=454, $\chi^2=33.782$, df=6, $p<0.001$) and Common Terns (n=708, $\chi^2=54.527$, df=6, $p<0.001$). For Arctic Terns the percentage by tidal state of Clupeid between 40 and 69mm in length brought to the nest decreased in the order high, ebb, low and flood. The percentage of Clupeid between 70 and 99mm decreased in the order flood, low, high and ebb. The percentage of Clupeid 100mm and over decreased in the order flood, ebb, low and high. Common Terns were most likely to bring in Clupeid between 40 and 69mm at ebb tide, with the percentages at high and low tides similar and the lowest percentage at flood tide. The percentage of

Clupeid between 70 and 99mm decreased in the order flood, high, low and ebb, while for Clupeid 100mm and over the order was low, ebb, flood and high (Figure 6.6).

Proportions of different sized Clupeid brought to the nest varied depending on state of the tide for both Arctic Terns (Pearson's Chi-squared, n=454, χ^2=33.782, df=6, p<0.001) and Common Terns (n=708, χ^2=54.527, df=6, p<0.001). Arctic Terns were more likely to bring in Clupeid between 40 and 69mm in length during the ebb than at high tide, and during the flood than at low tide. Clupeid between 70 and 99mm were more likely to be brought in during the ebb and high tide than the flood and low tide and Clupeid >100mm were more likely during the flood tide than at high tide. Common Terns were most likely to bring in Clupeid between 40 and 70mm during the ebb tide. Clupeid between 70 and 100mm were less likely to be brought in during the ebb and at low tide than during the flood and at high tide and Clupeid >100mm were most likely to be brought in at low tide (Figure 6.6).

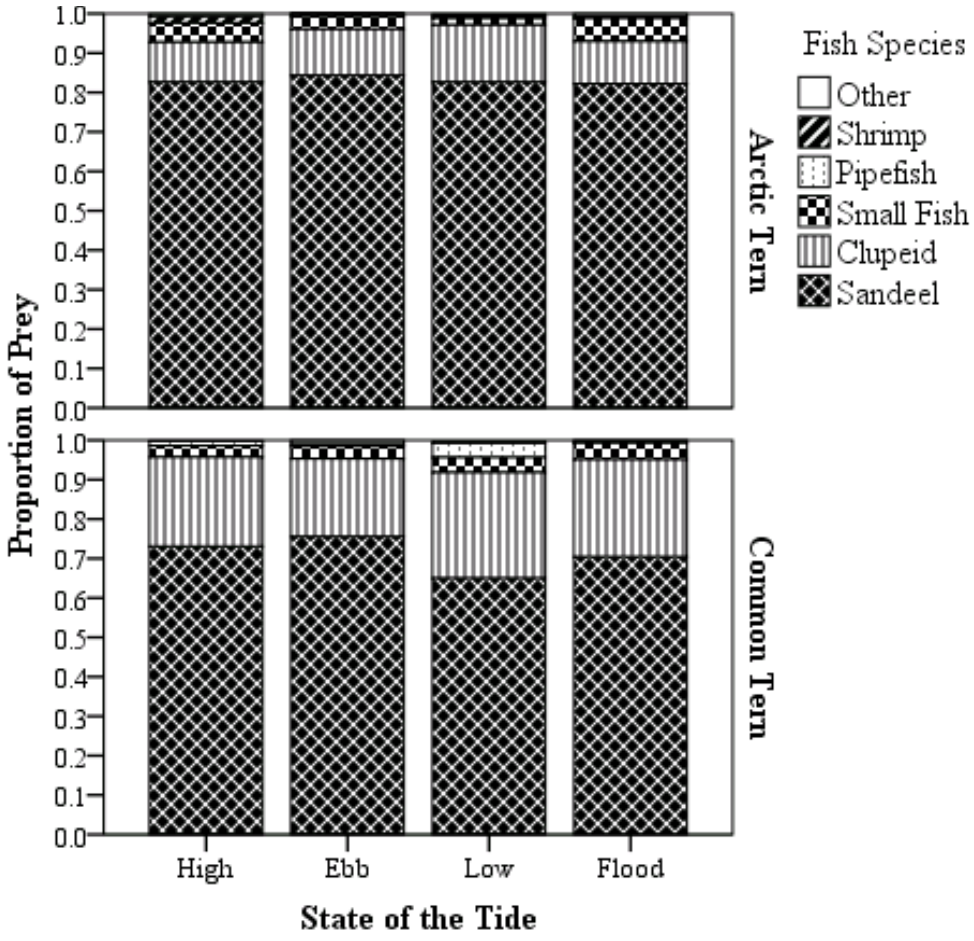


Figure 6.4 Proportion of different fish species brought to the nest by Arctic and Common Terns depending on state of the tide

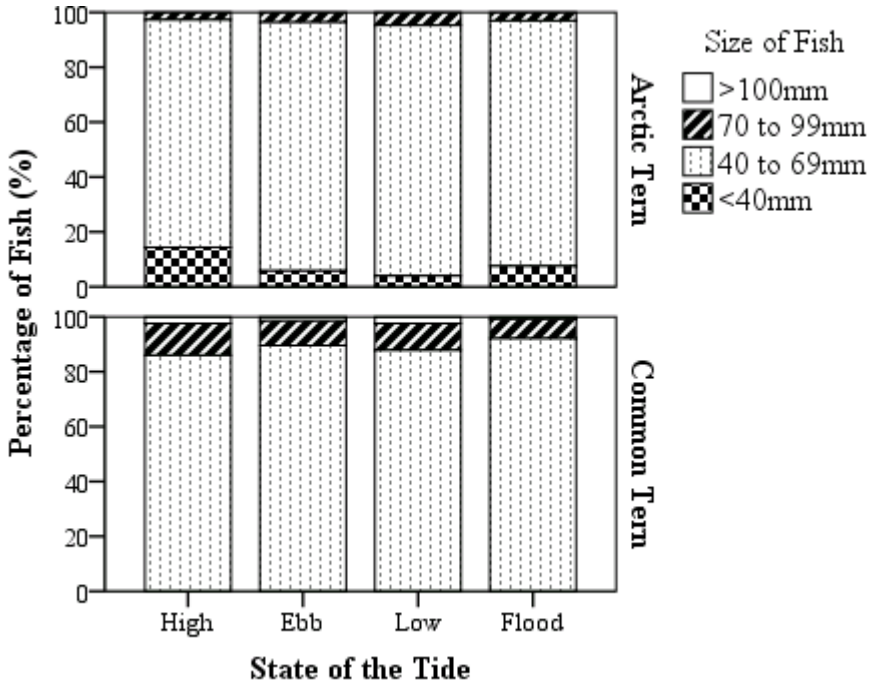


Figure 6.5 Percentage of Sandeel of different sizes brought to the nest by Arctic and Common Terns depending on state of the tide

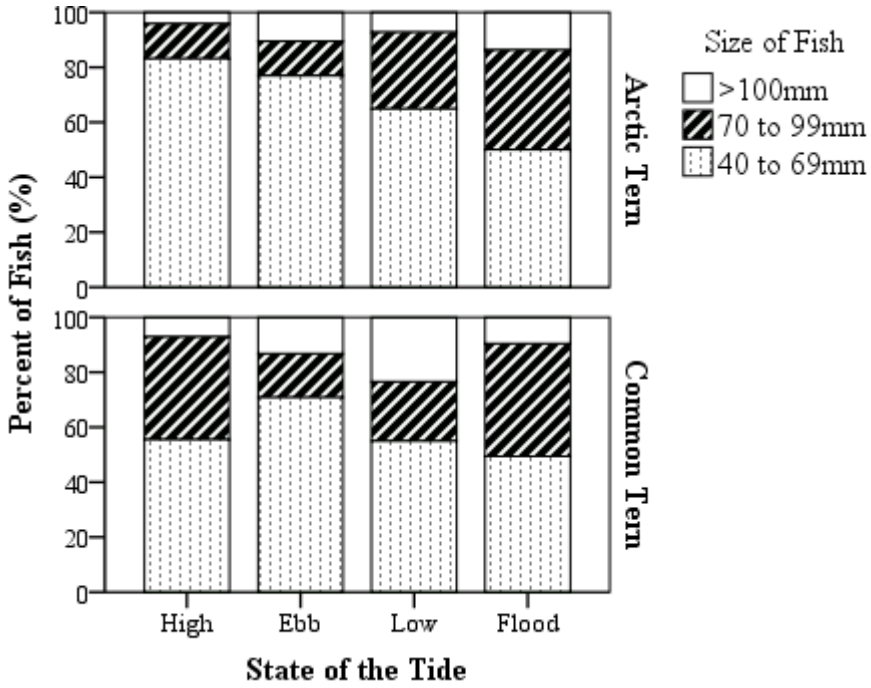


Figure 6.6 Percentage of Clupeid of different sizes brought to the nest by Arctic and Common Terns depending on state of the tide

6.4.3 Diurnal rhythm and provisioning

Kruskall-Wallis analysis of provisioning behaviour (feeding rate per chick, feed.chick^{-1}.h^{-1}; estimated energy delivery rate per chick, kJ.chick^{-1}.h^{-1}; estimated energy per feed, kJ.feed^{-1}) showed a significant effect of time (05:00 - 0759, 08:00 - 10:59, 11:00 -

13:59, 14:00 - 16:59, 17:00 - 19:59 and 20:00 - 21:59) on the provisioning behaviour of both Arctic and Common Terns (Table 6.3, Figure 6.7, Figure 6.8, Figure 6.9).

	Arctic Tern				Common Tern			
	n	χ^2	d.f.	p	n	χ^2	d.f.	p
Feeds.chick^{-1}.h^{-1}	1880	34.443	5	<0.001	1610	28.910	5	<0.001
kJ.chick^{-1}.h^{-1}	1876	57.848	5	<0.001	1599	23.425	5	<0.001
kJ.feed^{-1}	1571	23.661	5	<0.001	1335	17.915	5	0.003

Table 6.3 Kruskall-Wallis analysis of differences in feeding rate per chick (feed.chick^{-1}.h$^{-1)}$, estimated energy delivery rate per chick (kJ.chick^{-1}.h^{-1}) and estimated energy per feed (kJ.feed^{-1}) of Arctic and Common Terns depending on time of day

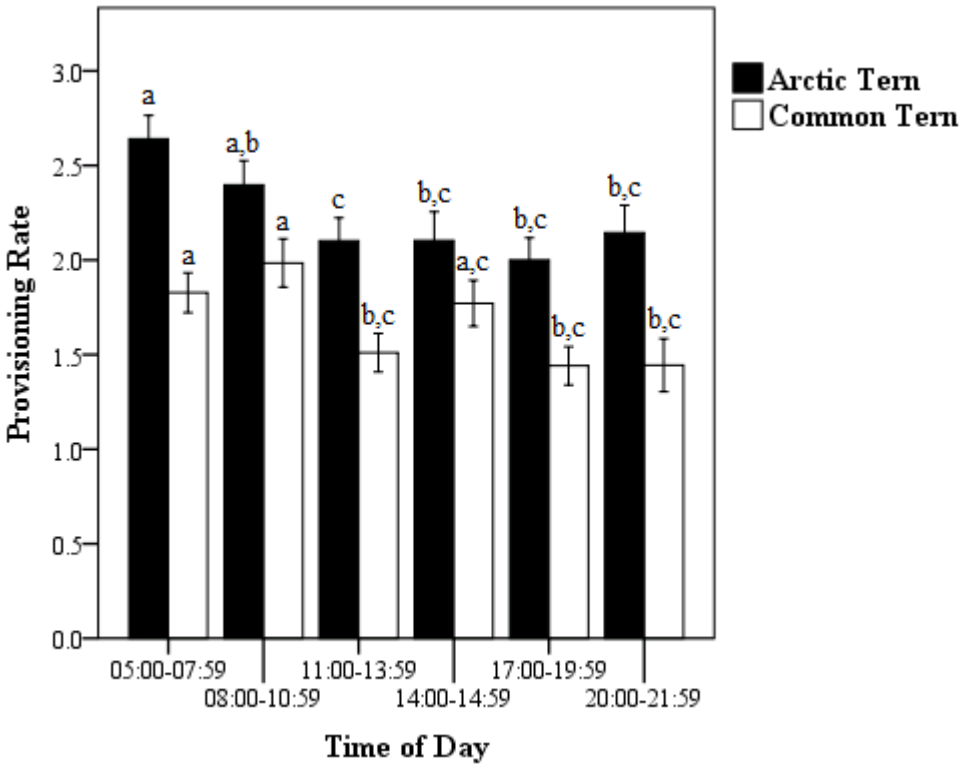


Figure 6.7 Mean Arctic and Common Tern provisioning rate per chick (feed.chick^{-1}.h^{-1}) depending on time of day ± SE. Columns with the same letter are not significantly different from each other ($p<0.05$).

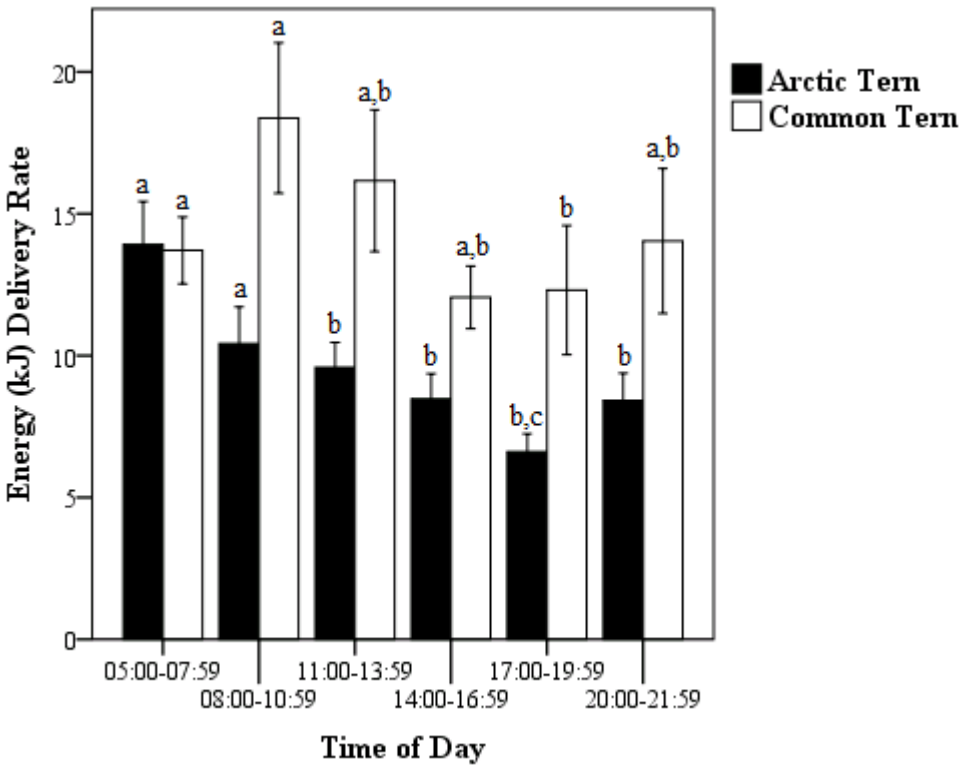


Figure 6.8 Mean Arctic and Common estimated energy delivery rate per chick (kJ.chick^{-1}.h^{-1}) depending on time of day ± SE. Columns with the same letter are not significantly different from each other ($p<0.05$).

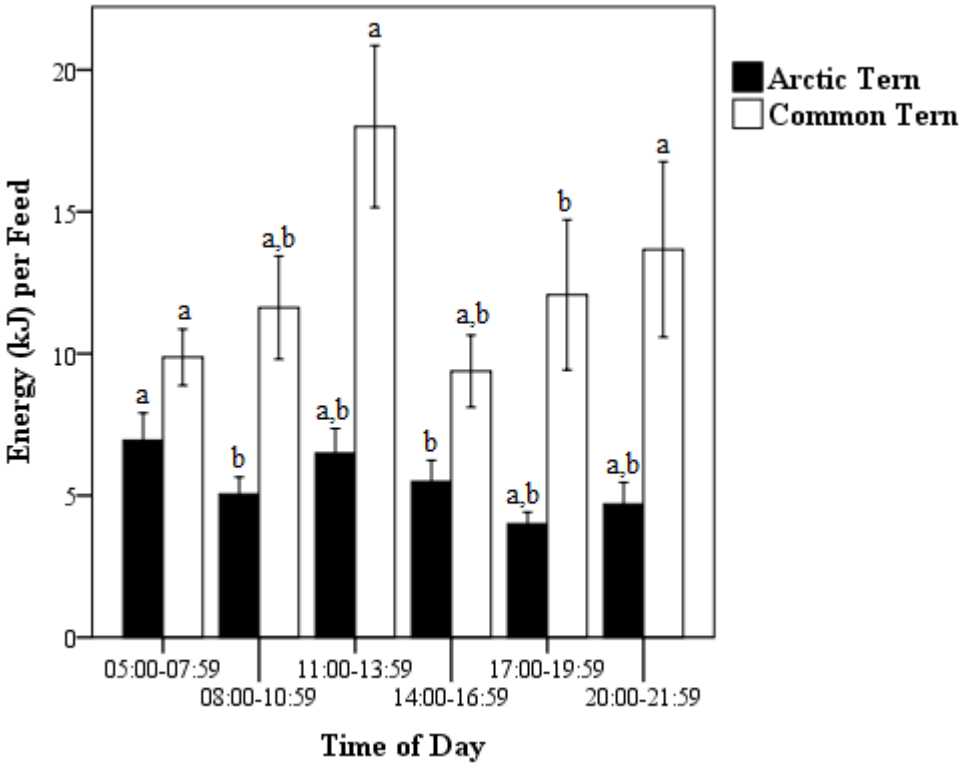


Figure 6.9 Mean Arctic and Common Tern estimated energy per feed (kJ.feed^{-1}) depending on time of day ± SE. Columns with the same letter are not significantly different from each other ($p<0.05$).

6.4.4 Diurnal rhythm and Diet

Kruskall-Wallis test showed that time of day had a significant effect of the proportions of Sandeel, small fish, Shrimp and 'Other' fish brought to the nest by Arctic Terns, and on the proportions of all species apart from 'Other' for Common Terns (Table 6.4, Figure 6.10).

	Arctic Tern				Common Tern			
	n	χ^2	d.f.	p	n	χ^2	d.f.	p
Sandeel	1565	12.849	5	0.025	1338	49.317	5	<0.001
Clupeid	1565	6.124	5	0.294	1338	41.786	5	<0.001
Small Fish	1565	23.868	5	<0.001	1338	12.378	5	0.030
Shrimp	1565	49.051	5	<0.001				
Pipefish					1338	16.828	5	0.005
Other	1565	26.029	5	<0.001	1338	3.701	5	0.593

Table 6.4 Kruskall-Wallis analysis of differences in proportion of different prey species brought to the nest by Arctic and Common Terns depending on time of day

Arctic Terns brought a similar proportion of Sandeel at all times of day ($Z<2.743$, $p>0.09$) except between 08:00 - 10:59 and 20:00 - 21:59 (Z=3.238*). Common Terns brought a similar proportion of Sandeel at all times of day (Z=2.330, $p>0.3$) except between 20:00 – 21:59 and 05:00 - 07:59 (3.449**), 08:00 - 10:59 (Z=5.884**), 11:00 - 13:59 (Z=3.946**), 14:00 - 16:59 (Z=6.203**) and 17:00 - 19:59 (Z=4.206**), and between 05:00 - 07:59 and 08:00 - 10:59 (Z=3.127*).

The proportion of Clupeid brought to the nest did not vary with time of day for Arctic Terns but did for Common Terns, with differences between 05:00 - 07:59 and 08:00 - 10:59 (Z=3.229*) and 14:00 - 16:59 (Z=3.292*), and between 20:00 - 21:59 and 08:00 - 10:59 (Z=5.176**), 14:00 - 16:59 (Z=5.217**), and 17:00 - 19:59 (Z=4.344**). There was no difference for other times ($Z<2.797$, $p>0.07$).

Arctic Terns brought in a similar proportion of small fish during the day ($Z<2.477$, $p>0.2$) except between 11:00 - 13:59 and 17:00 - 19:59 (Z=2.982*) and 20:00 - 21:59 (Z=3.483**) and between 14:00 - 16:59 and 17:00 - 19:59 (Z=3.387*) and 20:00 - 21:59 (Z=3.811**). Common Terns brought in similar proportion of small fish during the day ($Z<2.650$, $p>0.1$) except between 11:00 - 13:59 and 20:00 - 21:59 (Z=3.286*).

Arctic Terns brought in a similar proportion of Shrimp throughout the day ($Z<0.968$, $p>0.9$) except between 20:00 - 21:59 and all other times ($4.835<Z<6.072$, $p<0.01$). Common Terns brought in a similar proportion of Pipefish during the day ($Z<2.789$, $p>0.07$) except between 08:00 - 10:59 and 20:00 - 21:59 ($Z=3.274$*).

Arctic Terns brought in a similar proportion of 'Other' prey items at all times of day ($Z<2.369$, $p>0.2$) except between 20:00 - 21:59 and 05:00 - 07:59 ($Z=4.154$**), 08:00 - 10:59 ($Z=3.818$**), 14:00 - 16:59 ($Z=4.309$**) and 17:00 - 19:59 ($Z=2.959$*). The Common Tern proportion of 'Other' prey items did not vary with time of day.

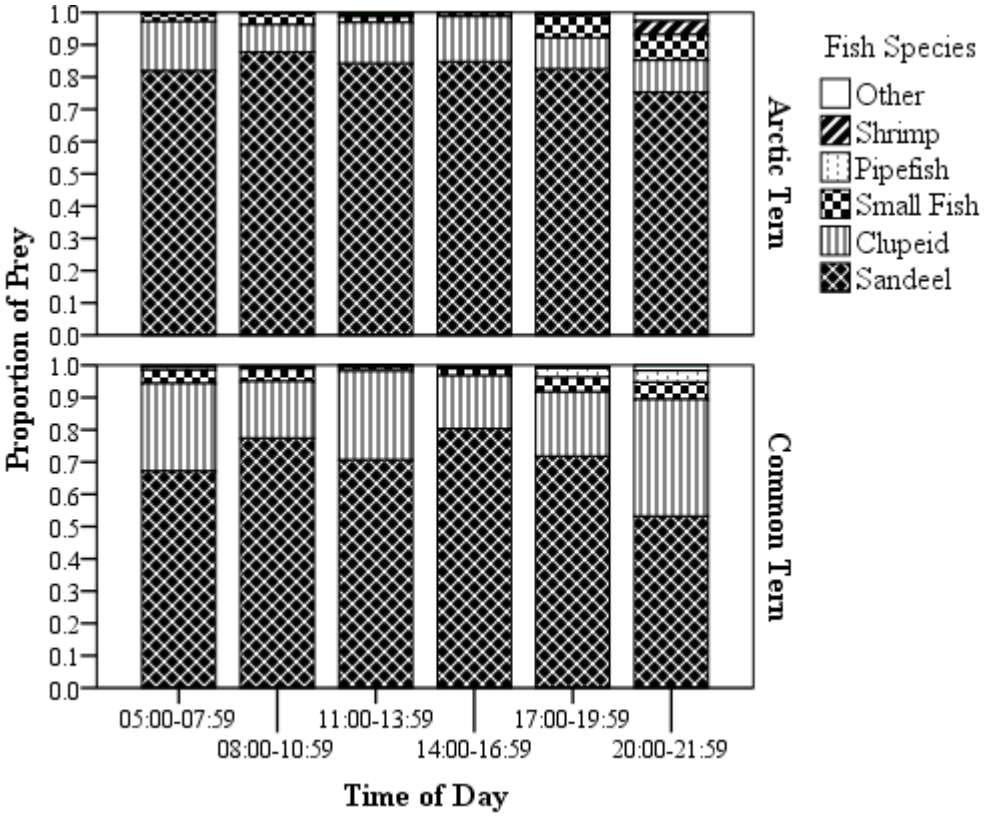


Figure 6.10 Proportion of different fish species brought back to the nest depending on time of day.

Time of day had a significant effect of the proportions of different sized Sandeel brought to the nest by Arctic Terns (Pearson's Chi-squared, n=5366, $\chi^2=238.610$, df=10, $p<0.001$) and Common Terns (n=3576, $\chi^2=53.962$, df=10, $p<0.001$). Z-test of column proportions showed Arctic Terns were most likely to bring in small Sandeel (under 40mm in length) between 14:00 - 16:59 and least likely between 05:00 - 07:59, with the

second lowest likelihood between 20:00 - 21:59. Proportions of small Sandeel were similar between 11:00 - 13:59, 17:00 - 19:59 and 20:00 - 21:59. Sandeel between 40 and 69mm were most common between 05:00 - 07:59 and 08:00 - 10:59 and least common between 14:00 - 16:59. Sandeel between 70 and 99mm most between 05:00 - 07:59 and 11:00 - 13:59 and 20:00 - 21:59, with a lower proportion brought in at other times.

Common Terns brought in the highest proportion of Sandeel between 40 and 69mm in length at 17:00 - 19:59 and 20:00 - 21:59 and the least at 08:00 - 10:59, 11:00 - 13:59 and 14:00 - 16:59. Sandeel between 70 and 99mm were more likely between 08:00 - 10:59, 11:00 - 13:59 and 14:00 - 16:59 and significantly less likely at other times. Sandeel 100mm and over were brought in most frequently between 08:00 - 10:59 and 11:00 - 13:59, percentages at other times were very low (Figure 6.11).

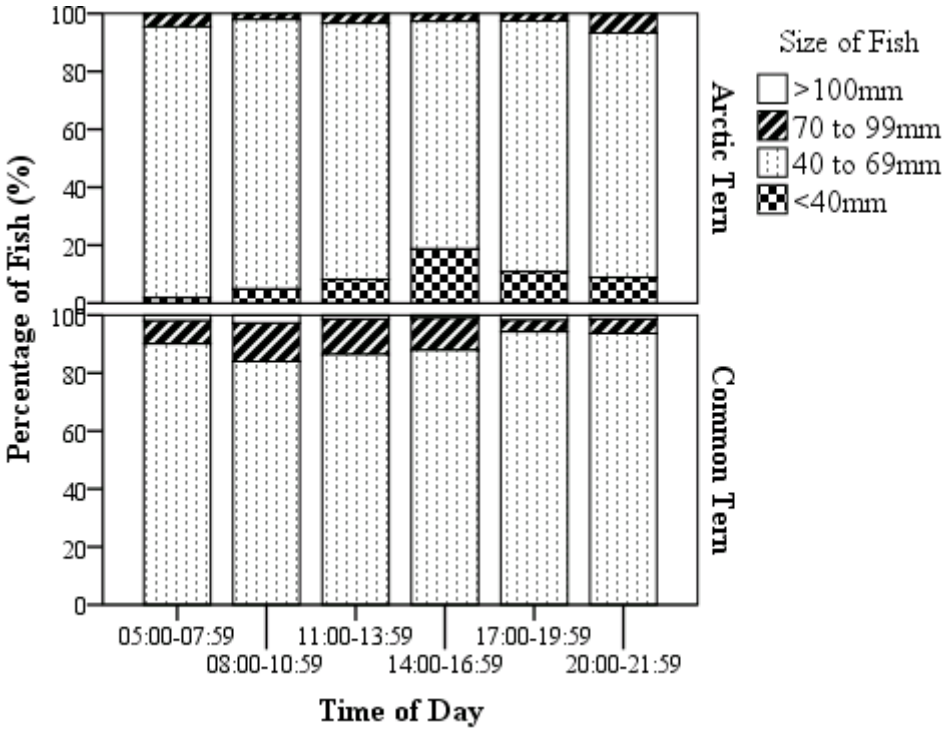


Figure 6.11 Percentage of Sandeel of different sizes brought to the nest by Arctic and Common Terns depending on time of day

Time of day had a significant effect of the proportions of different sized Clupeid brought to the nest by Arctic Terns (Pearson's Chi-squared, n=454, χ^2=26.193, df=10, p<0.001) and Common Terns (n=708, χ^2=101.712, df=10, p<0.001). Z-test of column proportions showed that Arctic Terns were most likely to bring in Clupeid between 40 and 69mm in length between 14:00 - 16:59 and 17:00 - 19:59 and least likely between 05:00 - 07:59, 11:00 - 13:59 and 20:00 - 21:59. Clupeid between 70 and 99mm were most common between 05:00 - 07:59, 11:00 - 13:59 and 20:00 - 21:59 and least

common between 08:00 - 10:59, 14:00 - 16:59 and 17:00 - 19:59. Clupeid 100mm and over were most common between 08:00 - 10:59 and 11:00 - 13:59 and least common between 05:00 - 07:59 and 14:00 - 16:59.

Common Terns were most likely to bring in Clupeid between 40 and 69mm in length between 05:00 - 07:59, 17:00 - 19:59 and 20:00 - 21:59, and significantly less likely at other times. Clupeid between 70 and 99mm were most common between 11:00 - 13:59 and 14:00 - 16:59 and significantly less common at other times. Clupeid 100mm and over were least common between 05:00 - 07:59 and most common between 08:00 - 10:59. Similar proportions were brought in between 14:00 - 16:59 and 20:00 - 21:59. These were lower than between 11:00 - 13:59 and 17:00 - 19:59 (Figure 6.12).

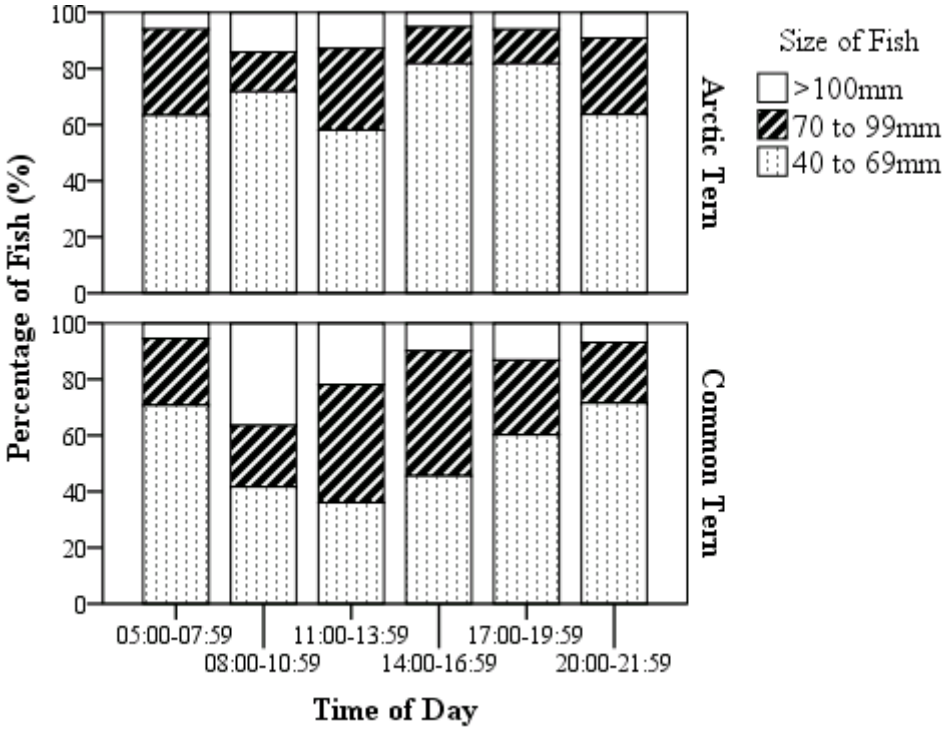


Figure 6.12 Percentage of Clupeid of different sizes brought to the nest by Arctic and Common Terns depending on time of day

6.4.5 Effect of Temperature

Mean daily temperature ranged between 9.3 and 19.5 ˚C during the study period, with observations made on days with mean temperatures ranging from 10.1 to 18.6 ˚C.

Spearman's rho analysis of the correlation between increasing mean daily temperature (˚C) and provisioning rate (feed.chick^{-1}.h^{-1}), energy delivery rate (kJ.chick^{-1}.h^{-1}), energy per feed (kJ.feed^{-1}), and proportion and size of Sandeel and Clupeid showed a

significant effect of temperature on all variables for both species, apart from feeding rate (Table 6.5). Both Arctic and Common Tern energy delivery rate (Figure 6.13) and energy per feed (Figure 6.14) increased with increasing daily temperature. With increasing temperature, proportions of Sandeel declined in the diet of both Arctic and Common Tern, while proportion of Clupeid increased (Figure 6.15) and larger prey Sandeel were brought by both Arctic and Common Terns (Figure 6.16).

	Arctic Tern			Common Tern		
	Rho	p	n	Rho	p	n
Feed.h^{-1}	-0.042	0.703	86	-0.129	0.258	79
kJ.h^{-1}	0.356	<0.001	86	0.230	0.042	79
kJ.$feed^{-1}$	0.355	<0.001	86	0.318	0.004	79
Proportion Sandeel	-0.349	<0.001	86	-0.367	<0.001	79
Proportion Clupeid	0.343	<0.001	86	0.304	0.006	79
Sandeel (mm)	0.321	0.003	86	0.251	0.025	79
Clupeid (mm)	0.080	0.536	62	0.214	0.080	68

Table 6.5 Spearman's rho analysis of the correlation between increasing daily mean temperature (˚C) and Arctic and Common Tern provisioning rate (feed.$chick^{-1}.h^{-1}$), energy delivery rate (kJ.$chick^{-1}.h^{-1}$), energy per feed (kJ.$feed^{-1}$), proportion of prey brought back to the nest being Sandeel and Clupeid, and size of both Sandeel and Clupeid (mm)

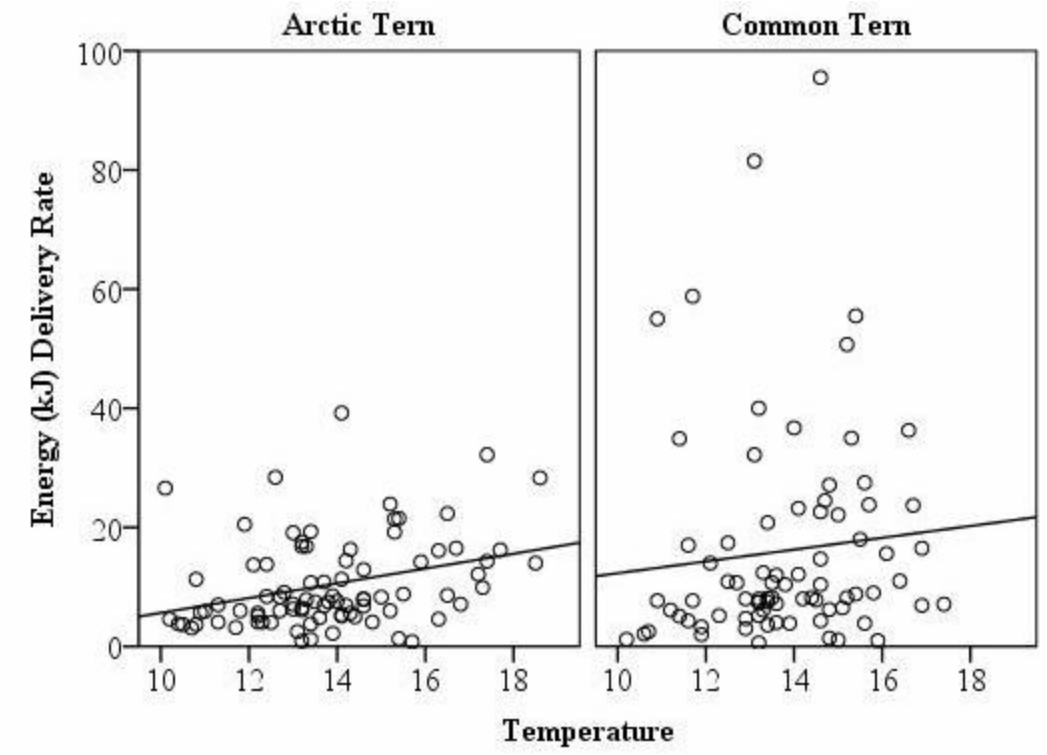


Figure 6.13 Average daily energy delivery rate (kJ.chick^{-1}.h^{-1}) depending on mean daily temperature (˚C)

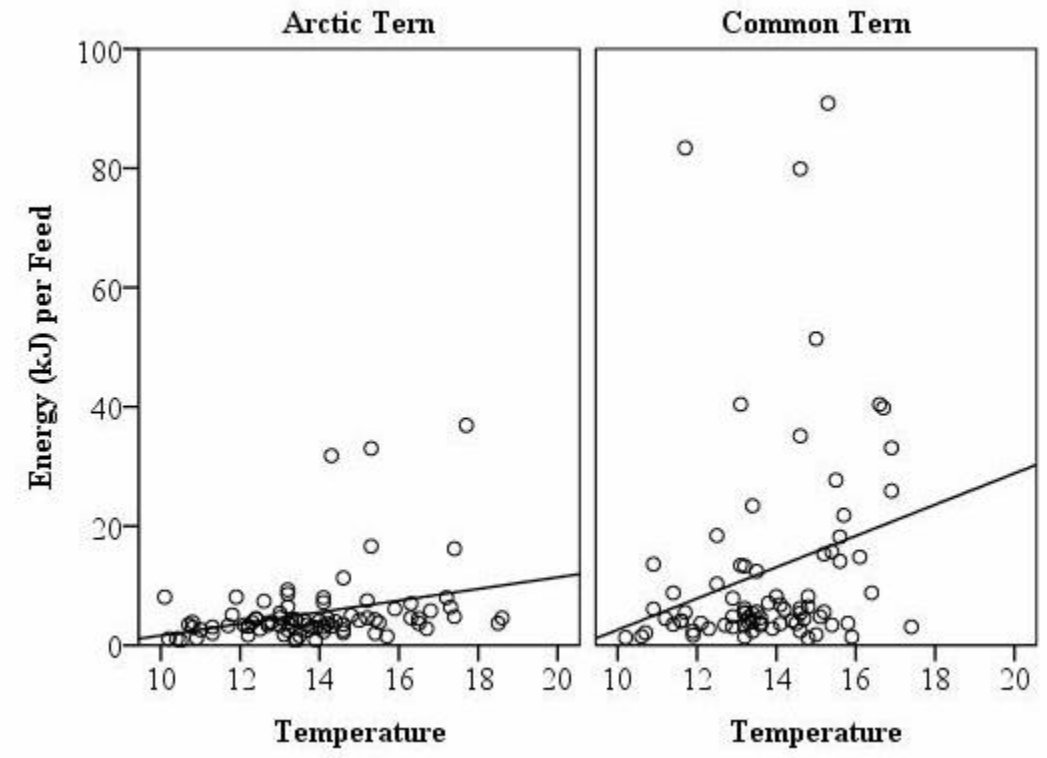


Figure 6.14 Average daily energy per feed (kJ.feed^{-1}) depending on mean daily temperature (˚C)

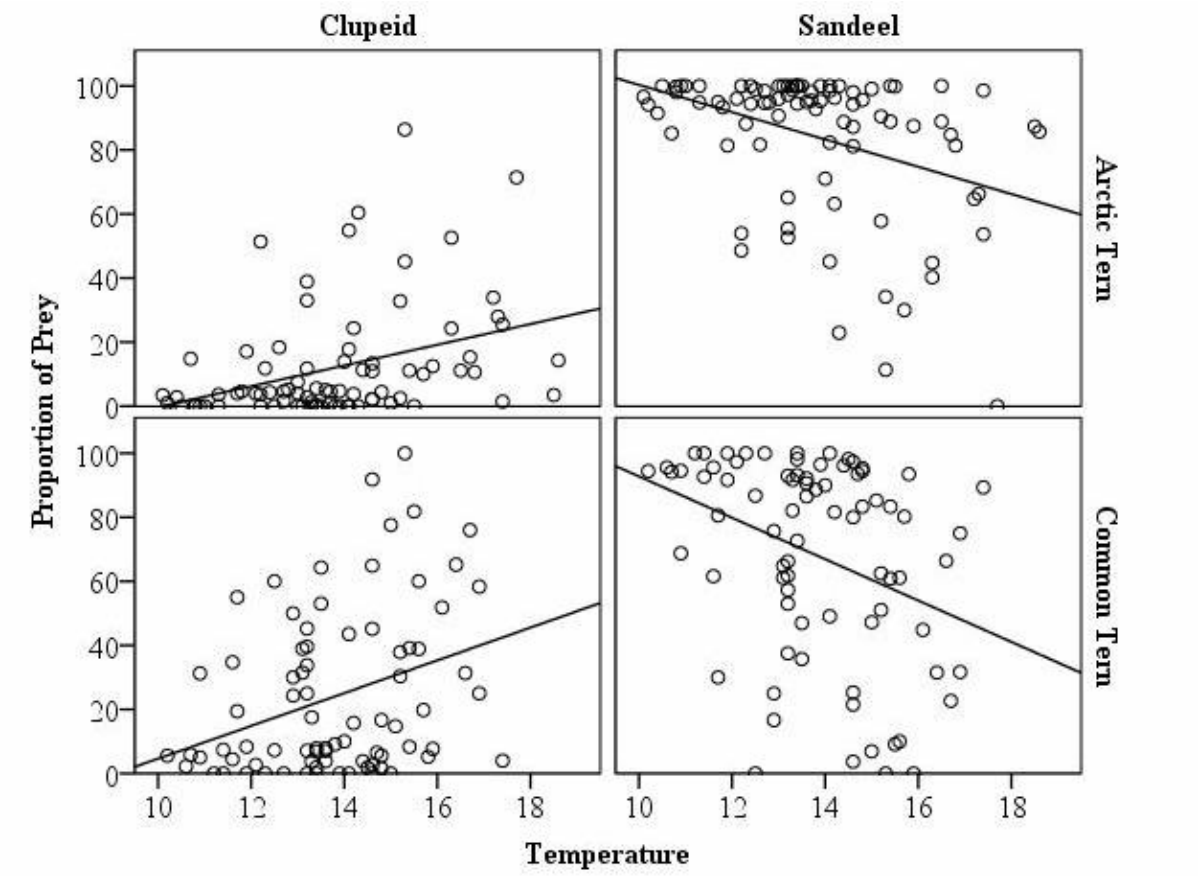


Figure 6.15 Proportion of Arctic and Common Tern diet consisting of Sandeel and Clupeid depending on mean daily temperature (˚C)

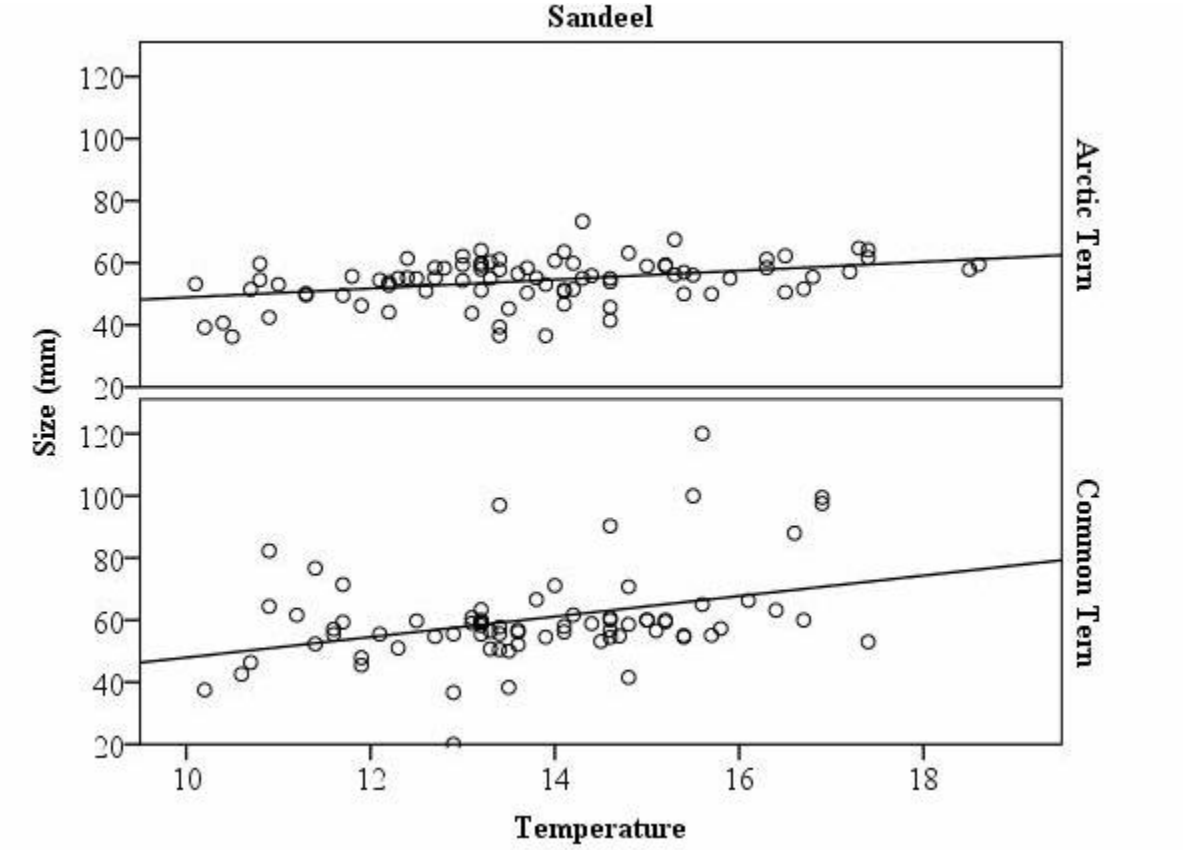


Figure 6.16 Size of Sandeel brought to the nest by Arctic and Common Terns depending on mean daily temperature (˚C)

6.4.6 Effect of wind speed

Mean daily wind speed ranged between 5.7 and 50.0 $km.h^{-1}$ during the study period, with observations made on days with mean wind speed ranging from 7.0 to 26.5 $km.h^{-1}$.

Spearman's rho analysis of the correlation between increasing mean daily wind speed ($km.h^{-1}$) and provisioning rate ($feed.chick^{-1}.h^{-1}$), energy delivery rate ($kJ.chick^{-1}.h^{-1}$), energy per feed ($kJ.feed^{-1}$), proportion and size of Sandeel and Clupeid was undertaken with no significant correlations found (Table 6.6).

	Arctic Tern			Common Tern		
	Rho	p	n	Rho	p	n
$Feed.h^{-1}$	-0.009	0.931	86	-0.009	0.935	79
$kJ.h^{-1}$	0.027	0.802	86	0.033	0.770	79
$kJ.feed^{-1}$	0.032	0.769	86	-0.028	0.805	79
Proportion Sandeel	-0.062	0.571	86	-0.017	0.882	79
Proportion Clupeid	-0.014	0.896	86	-0.057	0.616	79
Sandeel (mm)	-0.133	0.221	86	-0.129	0.258	79
Clupeid (mm)	0.199	0.121	62	0.174	0.157	68

Table 6.6 Spearman's rho analysis of the correlation between increasing mean daily wind speed ($km.h^{-1}$) and Arctic and Common Tern provisioning rate ($feed.chick^{-1}.h^{-1}$), energy delivery rate ($kJ.chick^{-1}.h^{-1}$), energy per feed ($kJ.feed^{-1}$), proportion of prey brought back to the nest being Sandeel and Clupeid, and size of both Sandeel and Clupeid (mm)

6.4.7 Effect of precipitation

Mean daily precipitation ranged between 0.0 and 48 mm during the study period with observations made on days with rainfall of between 0 and 31mm.

Spearman's rho analysis of the correlation between increasing precipitation ($mm.day^{-1}$) and provisioning rate ($feed.chick^{-1}.h^{-1}$), energy delivery rate ($kJ.chick^{-1}.h^{-1}$), energy per feed ($kJ.feed^{-1}$), proportion and size of Sandeel and Clupeid was undertaken with analysis presented below (Table 6.7). Precipitation had no effect on provisioning rate for either species. There was a positive relationship between increase precipitation and increased energy delivery rate (Figure 6.17) and energy per feed (Figure 6.18) for Common Tern but not Arctic Tern. Proportion and size of Sandeel and Clupeid showed no effect of precipitation for either species.

	Arctic Tern			Common Tern		
	Rho	p	n	Rho	p	n
Feed.h^{-1}	-0.147	0.398	35	0.193	0.266	35
kJ.h^{-1}	0.125	0.473	35	0.495	0.002	35
kJ.feed^{-1}	0.044	0.802	35	0.377	0.026	35
Proportion Sandeel	0.030	0.865	35	0.007	0.970	35
Proportion Clupeid	0.052	0.768	35	0.170	0.329	35
Sandeel (mm)	0.216	0.213	35	0.147	0.399	35
Clupeid (mm)	-0.064	0.761	25	0.237	0.225	28

Table 6.7 Spearman's rho analysis of the correlation between increasing daily precipitation (mm.day^{-1}) and Arctic and Common Tern provisioning rate (feed.chick^{-1}.h^{-1}), energy delivery rate (kJ.chick^{-1}.h^{-1}), energy per feed (kJ.feed^{-1}), proportion of prey brought back to the nest being Sandeel and Clupeid, and size of both Sandeel and Clupeid (mm)

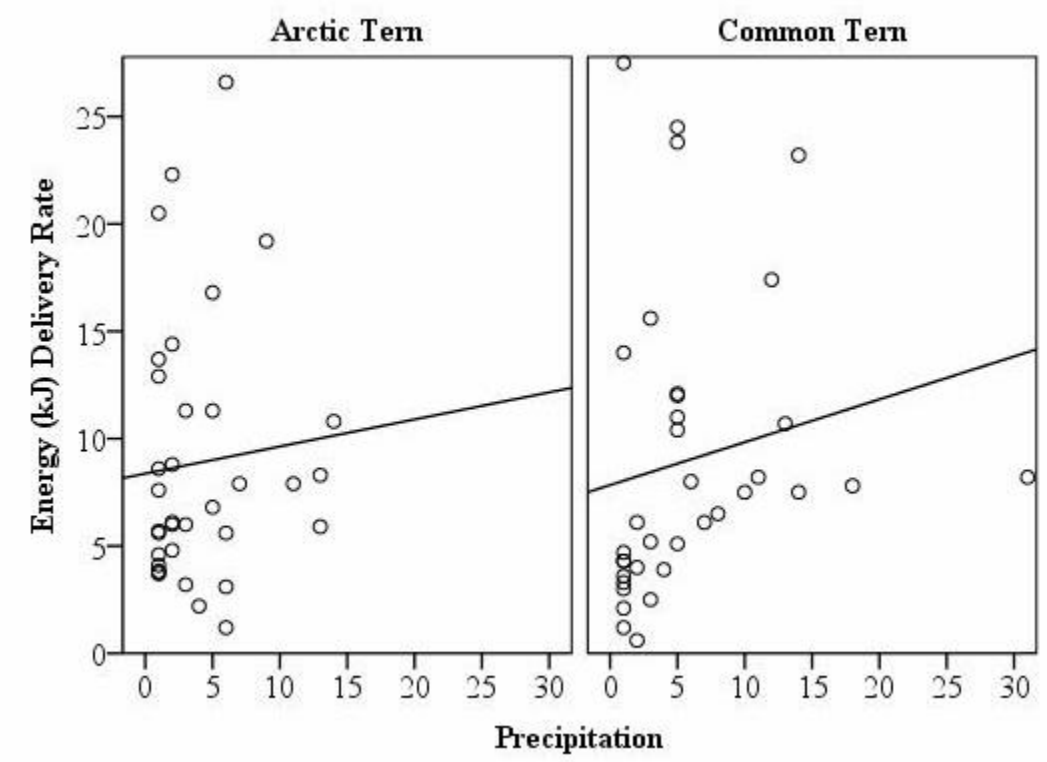


Figure 6.17 Average daily energy delivery rate (kJ.chick^{-1}.h^{-1}) depending on daily precipitation (mm)

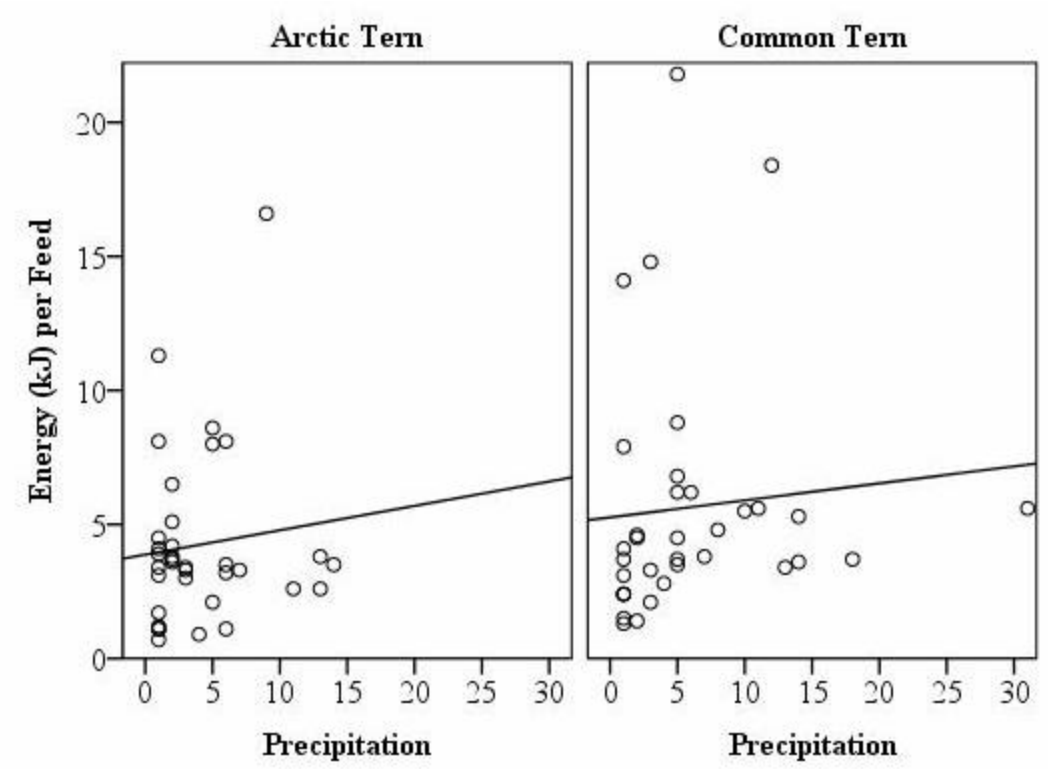


Figure 6.18 Average daily energy per feed (kJ.feed^{-1}) depending on daily precipitation (mm)

6.5 Discussion

The state of the tide affected Arctic Tern provisioning greatly but had no effect on that of Common Terns. This confounded predictions but is similar to results seen by Frick & Becker (1995). With regard to rate of provisioning and energy delivery, feeding was greatest during the ebb tide and lowest during the high and flood tides. Meal quality varied only between high and low tides, with more energy rich meals brought to chicks at low tide. This arose predominantly from differences in size of prey, especially Sandeel, with smaller Sandeel being caught at high and flood tides.

The tidal range (difference between the heights of high and low water) at Coquet Island varies on average between 4.4m at spring tides and 2.1m at neap tides. The size of the island increases significantly at neap low tide and very significantly at spring low tide (Figure 2.1), changing the immediate foraging environment. During the ebb tide, fish migrate out with the water. Moving fish are likely to be an easier target for foraging birds, as are fish that become stranded in shallow water or rock pools as the tide recedes.

The diet of Arctic Tern chicks did not vary throughout the tidal cycle for preferred prey (Sandeel and Clupeid) but Shrimp were predominantly caught at high tide and small fish at low tide. Shrimp species (Brown Shrimp, *Crangon crangon*) are known to bury themselves as the water recedes and are therefore less accessible to predators (references in Beyst et al. 2002). Small fish species were not identified, but it is possible that smaller fish are more likely to remain in rock pools as the tide falls, becoming easier prey. The diet of Common Tern chicks varied during the tidal cycle, with Sandeel being less present during low tide. Pipefish were almost exclusively caught at low tide and, although not significant, the data are suggestive of an increase in 'Other' species and Clupeids at low tide. Caspian Terns have been shown to exploit estuarine species during low tide (Anderson et al. 2005), so the decreased reliance on the marine Sandeel could be due to exploitation of the Coquet River estuary and harbour at low tide. The observed increase of Pipefish in the diet at low tide was probably due to their preferred habitat of seaweed beds becoming exposed at low water, making them more accessible to surface feeding predators (Hayward et al. 1996) and indicates that there is a separation of foraging areas between the two tern species.

An early morning peak in chick provisioning was seen in Arctic Terns but not in Common Terns. Increased provisioning of chicks by parent birds shortly after dawn has been associated with the need to feed chicks after the night, during which chicks are not fed (Frank 1992; Lance & Roby 1998; Garcia & Mariano-Jelicich 2005; Stienen et al. 2000; Becker et al. 1997).

The proportion of Sandeel in the diet of both species was lowest in the evenings and slightly lower in the early morning, while proportions of Clupeids were highest in the early mornings and evenings. These two species have opposite activity cycles: Sandeel migrate down the water column in the evening to spend the night buried in sediment on the seabed (Freeman et al 2004; Englehard et al. 2008) while Clupeid species are more active higher up the water column during the night and migrate down during daylight (Blaxter & Parrish 1965 and Laevastue & Hayes 1981 in Stienen et al. 2000). Therefore Sandeel are least accessible and Clupeids most accessible to foraging adults just after dawn and just before dusk. Shrimp (Arctic Tern) and Pipefish (Common Tern) are predominantly caught in the evening; Shrimp show increased nocturnal activity (Brown Shrimp: Pihl & Rosenberg 1984). No information was available on the circadian behaviour patterns of Snake Pipefish.

Other studies have shown decreased provisioning rates (Kaplam et al. 2003; Erwin & Congden 2007; Quillfeldt et al. 2007) and meal size (Peck et al. 2004) to be associated with increased temperature. Here, however both species were found to provide chicks with more estimated energy per hour and larger, more energy rich prey items. The diet of both species showed a higher proportion of the more energy-rich Clupeid in the diet and a corresponding decline in Sandeel when temperatures increased, and both species brought in larger sized Sandeel. It is not known how prey availability and distribution altered with temperature, but these data suggest an increased availability of Clupeid and larger fish with increased temperatures.

Wind speed had no effect on the chick provisioning behaviour of either species. This is at odds with predictions and findings in other studies. A possible explanation is that only the linear relationship between increasing wind speed and foraging was investigated while others have shown a non-linear relationship, with provisioning increasing with wind speed up to a point and then declining if wind speed continues to increase (Taylor 1983; Frank 1992; Stienen et al. 2000; Garcia & Mariano-Jelicich 2005). Data on parental attendance at the nest site depending on wind speed (Chapter 7) suggest an increased effort invested in foraging when wind speed increases, with adults reducing the time spent at the nest site. Capture success declines with increased wind speed (Reed & Ha 1983; Sagear & Sagear 1989; Garcia & Mariano-Jelicich 2005); therefore lower parental attendance may reflect the need to spend more time foraging.

Precipitation had no impact on Arctic Tern provisioning but Common Terns showed an increase in the rate of energy delivery and the energy value per feed, although this was not reflected in changes in the diet. It is probable that precipitation alters prey behaviour by affecting the salinity of the upper levels of the water column (Delacroix et al. 1996), and the greater outflow from the River Coquet may be a factor. After significant precipitation, aggregations of feeding terns were frequently seen along the boundary between turbid river water and clear sea water (personal observations).

In conclusion, Arctic Terns showed a more pronounced daily rhythm than Common Terns, with a peak in foraging in the early morning and changes in foraging with the tide. Changes in diet of both species were observed and could be explained by differences in the behaviour of prey species either during the tidal cycle or throughout

the day. Weather conditions impacted both species. Increased temperature resulted in more energy rich prey, thereby increasing the energy delivery to chicks. With precipitation, the energy delivered to Common Tern chicks increased, but no effect on Arctic Terns was observed. While wind speed had no impact on the provisioning of chicks of either species, data from parental attendance (Chapter 7) support the suggestion that at higher wind speeds birds spend longer at sea foraging.

Chapter 7. The effects of chick age and weather on parental attendance at the nest site

7.1 Abstract

At hatching, chicks have little thermoregulatory capability and high thermal conductivity. With age, the ability to thermoregulate develops and a chick's reliance on parental brooding declines. A study of Arctic and Common Tern parental attendance at the nest site showed a significant decline in parental attendance with age of chicks, reflecting their improving thermoregulation and the increased need for parents to provision chicks. Differences between species and between years corresponded with differences in reproductive success. Low parental attendance suggests increased pressure on parents to provision chicks, with adults reducing time at the nest and increasing time foraging. It is suggested that for very young chicks, parental attendance is necessary regardless of conditions. Parental attendance at the nests of mid-age chicks reflects a balance between brooding and provisioning needs. Attendance at this age showed larger variability between years and was affected by weather conditions, suggesting that parents modified their behaviour depending on chick requirements. Once chicks were over 14 days old, parental attendance was very low. At this age, parental attendance at the nest can be thought of more as time not foraging than as time actively tending chicks. Thus increased attendance at this point suggests parents adequately provisioning chicks and can afford to take time off from foraging. Differences observed in parental attendance between Arctic and Common Terns strengthens the argument presented previously that on Coquet Island, Arctic Terns are under greater pressure than Common Terns to adequately provide for their chicks.

7.2 Introduction

On hatching, chicks, including semi-precocial tern chicks, are poikilothermal, with very high thermal conductivity; as chicks grow and body mass increases, their basal metabolic rate increases, they develop the ability to thermoregulate and their thermal conductivity declines (Chappel 1979; Bech et al. 1982; Evans 1984; Klassen 1989; Montevecchi & Vaughan 1989; Visser & Ricklefs 1993; Klassen 1994; Ostnes et al. 2001; Bakken et al. 2002).

Before the development of thermoregulation, chicks are entirely dependent on their parents for maintaining a stable body temperature and therefore need to be constantly brooded (Dawson et al. 1976; Kirkham & Montevecchi 1982; Evans 1984). Brooding declines with age and usually stops completely by the time chicks are fully functionally able to regulate their body temperature (although parents may still be present at the nest site) (LeCroy & Collins 1972; Dawson et al. 1976; Kirkham & Montevecchi 1982; Evans 1984; Gabrielsen et al. 1992; Uttley 1992; Klassen 1994; Robinson et al. 2001).

Expenditure of energy on thermoregulation accounts for some 18% of total nestling energy requirements for Arctic Terns (Klassen el al. 1989). Parental brooding can defray 30% to 80% of the costs of thermoregulation, although the cost benefit declines with age (Gabrielsen et al. 1992; Klassen 1994). Parental care of chicks requires both time away from the nest foraging for their food and time at the nest brooding or defending them. These are mutually exclusive activities (at least once the energy demands of a brood outstrip what one parent can provide), and parent birds need to balance the energy needs of the chicks (provisioning) with their energy expenditure (cost of thermoregulation) and the risk of hypothermia.

The decline of parental brooding with age is well documented. Less well studied is the relationship between brooding and external factors such as weather and feeding conditions. Uttley et al. (1992) compared parental brooding by Arctic Terns between two sites of differing food supply and found reduced attendance where food was scarce. Klassen (1994) investigated differences in Arctic Tern brooding between a Northerly with a Southerly site and found slight increase in brooding with decreased ambient temperatures. Robinson et al. (2001) studied Arctic and Common Terns breeding at the same site and linked differences in time spent brooding with increased pressure on Arctic Terns to provide for their young.

Arctic and Common Terns breed on Coquet Island between May and August, and first chicks usually hatch during the first 10 days of June. As a result, both species experience the same conditions at comparable stages of chick development, enabling a comparison between the two. Parental attendance at the nest site is expected to reduce with age of chick, while weather conditions are likely to affect the amount of time parent birds spend at the nest (although the effects are likely to reduce with age of

chick). Observing parental attendance over a number of seasons (2006 through 2010) will enable species differences and the effect of age and weather conditions to be assessed from a large data set (thereby reducing the effects of yearly variation), and yearly differences will be linked with yearly foraging conditions and foraging effort. Differences in the foraging behaviour of the two species have been observed (Chapter 5, Chapter 6) and decreased parental attendance is expected to be associated with increased foraging effort.

7.3 Methodology and Analysis

7.3.1 Methodology

See Chapter 2, sections 2.3.1, 2.3.3 and 2.4.2.

7.3.2 Analysis

For analysis, nests were divided into six groups by age range of eldest chick in the brood: 0 to 4 days; 5 to 9 days; 10 to 14 days; 15 to 19 days; 20 to 24 days; and 25 days and over.

All data were tested for normality using one-sample Kolmogorov-Smirnoff test and found to be non-normal. Transformation of data was attempted but found to be ineffective for data normalisation, therefore non-parametric statistics were used. All analysis was undertaken using IBM SPSS Statistics, version 19.

Analyses of inter-species comparisons of parental attendance (minutes at the nest per hour) were made using Mann-Whitney U test. Intra-species differences in parental attendance depending on age group of chick or between years were analysed using Kruskall-Wallis test, with pair-wise analyses (adjusted p-value for comparison across multiple groups) of comparisons between groups.

Parental attendance at the nest was correlated with daily average temperature (˚C) and wind speed ($km.h^{-1}$) using Spearman's rho non-parametric correlation. Parental attendance depending on occurrence of rain was analysed using Mann-Whitney U test to compare attendance during an hour when rain fell with attendance when it did not. Analysis was broken down by age of eldest chick in the nest as the impact of weather conditions on chicks changes throughout their development.

7.4 Results

Arctic Terns spent an average of 14.6±23.0 $min.h^{-1}$ at the nest throughout the breeding season and Common Terns spent an average of 22.5±26.0 $min.h^{-1}$. Parental attendance (PA) varied from 0 $min.h^{-1}$ to 60 $min.h^{-1}$ for both species, but Mann-Whitney U analysis showed a significant difference in distribution of PA between Arctic and Common Terns, both overall and between age groups of eldest chick in the nest (Table 7.1, Figure 7.1), and mean PA was always lower for Arctic Terns than for Common Terns.

	n	Z	p
Overall	3,469	9.604	<0.001
0 to 4 days	516	5.316	<0.001
5 to 9 days	605	8.330	<0.001
10 to 14 days	575	4.619	<0.001
15 to 19 days	605	7.051	<0.001
20 to 24 days	596	6.912	<0.001
25+ days	572	3.367	0.001

Table 7.1 Mann-Whitney U analysis comparing parental attendance at the nest site ($min.h^{-1}$) between Arctic and Common Terns overall and depending on age of eldest chick in the nest

7.4.1 Age of chick

Age of chick significantly affected PA for Arctic Terns (Kruskall-Wallis, n=1869, χ^2=738.610, df=5, p<0.001) and Common Terns (n=1603, χ^2=690.147, df=5, p<0.001) but pair-wise analysis implied that the relationship was not linear, with large differences between younger age groups and less difference between older age groups (Figure 7.1).

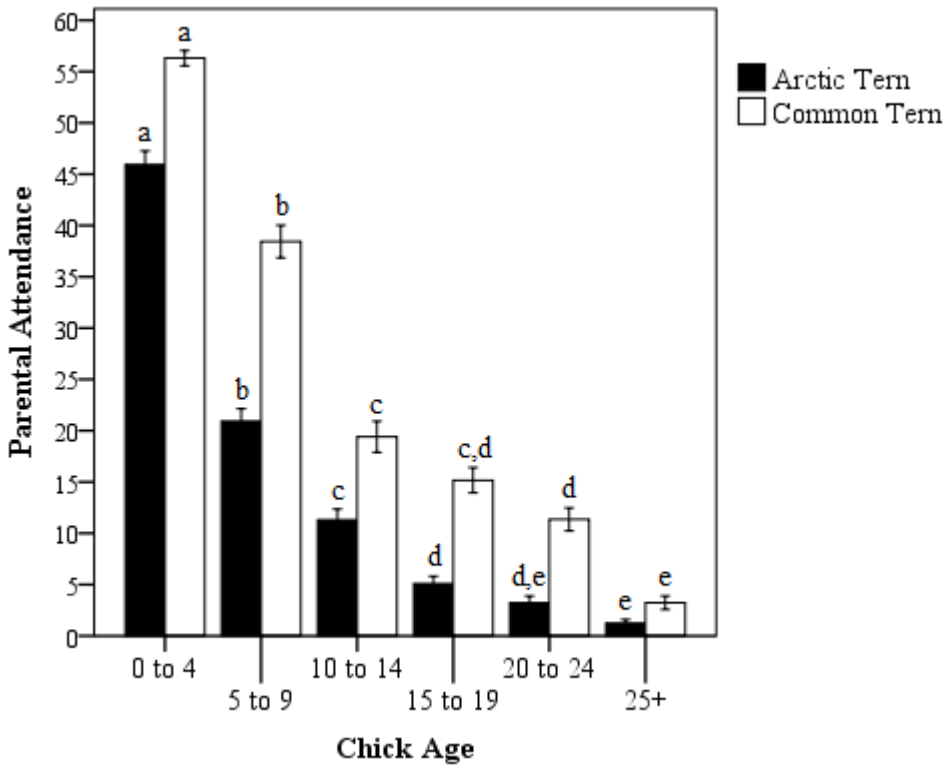


Figure 7.1 Mean parental attendance (min.h^{-1}) ± SE depending on the age of the eldest chick in the nest. Columns with the same letter are not significantly different from each other ($p<0.05$).

7.4.2 Inter-annual variation

PA was significantly different between years regardless of age of chick for both Arctic Terns (Kruskall-Wallis, n=1869, χ^2=86.742, d.f.=4, $p<0.001$) and Common Terns (n=1603, χ^2=14.505, d.f.=4, p=0.006) (Figure 7.2).

PA depending on age also showed a significant effect of year for both species, with Arctic Tern PA differing between years for all age groups and Common Tern PA differing between years for age groups 0 to 4 days, 15 to 19 days, and 25+ days (Table 7.2, Figure 7.3).

PA between years at nests with eldest chick aged between 0 and 4 days was significantly different for Arctic Terns between 2008 and 2007 (Z=3.183**) and 2009 (Z=3.352**). PA also showed a significant effect of year for Common Terns but pair-wise analysis did not reveal any differences between years.

Arctic Tern PA at nests with chicks aged between 5 and 9 days was significantly different between 2010 and 2007 (Z=5.963**), 2008 (Z=3.744**) and 2009 (Z=5.268**).

Arctic Terns PA at nests with chicks aged between 10 and 14 days was significantly different between all years ($p<0.002$) except between 2006 and 2007 (Z=2.673) and 2009 (Z=2.119), between 2007 and 2009 (Z=1.125), and between 2008 and 2010 (Z=0.639).

Arctic Tern PA at nests with chicks aged between 15 and 19 days was significantly different between 2006 and 2010 (Z=3.074**) and between 2008 and 2006 (Z=4.644**), 2007 (Z=3.547**) and 2009 (Z=3.686**). Common Tern PA was significantly different between 2008 and 2010 (Z=4.083**).

Arctic Tern PA at nests with chicks aged between 20 and 24 days was significantly different between 2006 and 2008 (Z=2.932*) and 2010 (Z=3.348**), and between 2009 and 2008 (Z=2.860*) and 2010 (Z=3.368**).

Arctic Tern PA at nests with chicks aged 25 days and over was significantly different between 2009 and 2007 (Z=3.838**) and 2010 (Z=3.493**). While there was a significant effect of year for Common Terns, pair-wise analysis did not reveal a significant difference between years.

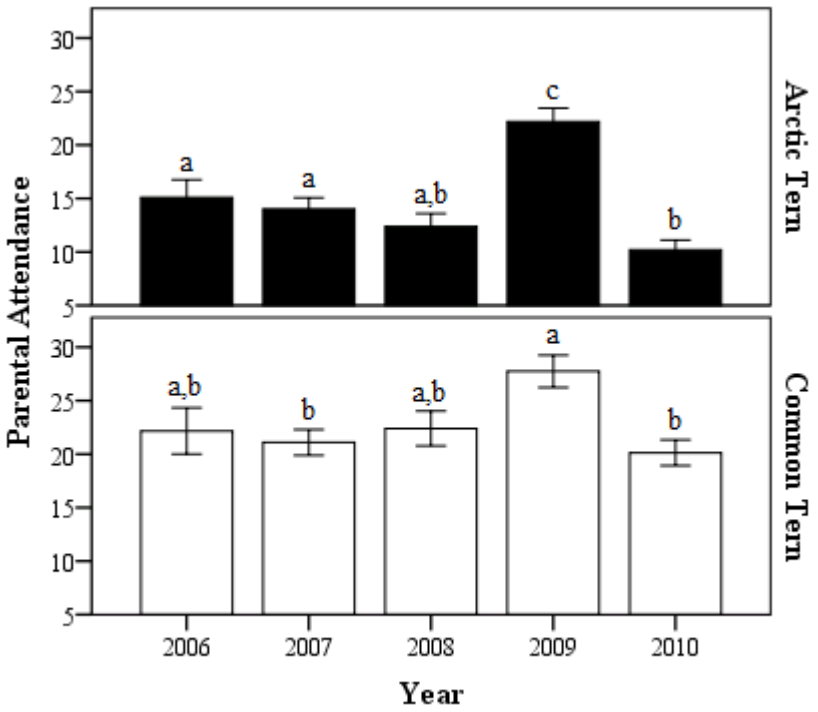


Figure 7.2 Mean parental attendance (min.h^{-1}) ± SE of Arctic and Common Terns depending on year. Columns with the same letter are not significantly different from each other ($p<0.05$).

	Arctic Tern				Common Tern			
	n	χ^2	d.f	p	n	χ^2	d.f	p
0 to 4 days	283	15.146	4	0.004	236	9.488	4	0.050
5 to 9 days	368	41.652	4	<0.001	237	8.958	4	0.062
10 to 14 days	340	72.856	4	<0.001	235	9.248	4	0.055
15 to 19 days	297	27.892	4	<0.001	308	17.931	4	0.001
20 to 24 days	288	21.191	4	<0.001	308	6.662	4	0.155
25+ days	293	16.109	4	0.003	279	10.489	4	0.033

Table 7.2 Kruskall-Wallis analysis of effect of year on parental attendance at the nest site (min.h^{-1}) for Arctic and Common Terns depending on age of eldest chick in the nest

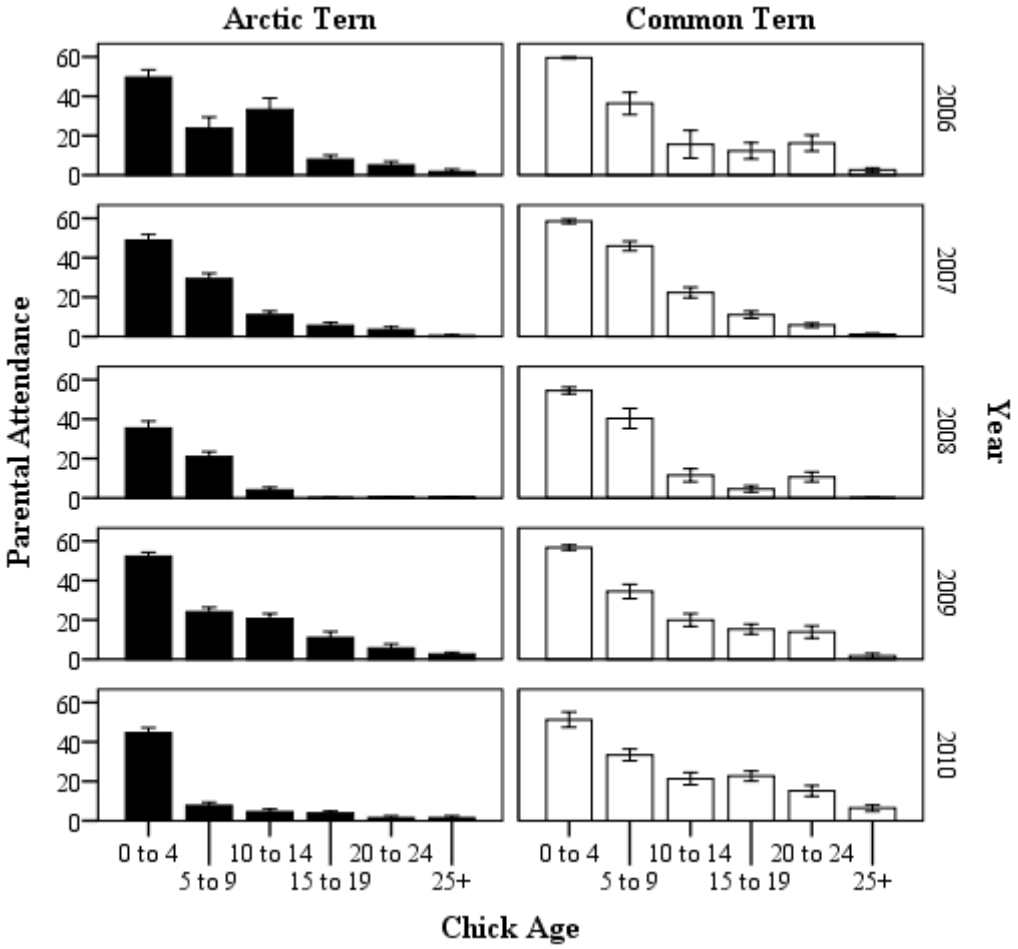


Figure 7.3 Mean parental attendance (min.h^{-1}) ± SE of Arctic and Common Terns depending on year and age of eldest chick in the nest

7.4.3 Weather

Spearman's rho correlation of PA with mean daily temperature (˚C) showed a weak but significant negative correlation for Arctic Terns with chicks aged between 5 and 9 days and Common Terns with chicks aged between 10 and 14 days, and a positive correlation for Arctic Terns with chicks aged between 10 and 14 days (Table 7.3, Figure 7.4, Figure 7.5, Figure 7.6).

	Arctic Tern			Common Tern		
	n	Spearman's rho	p	N	Spearman's rho	p
0 to 4 days	283	-0.006	0.925	236	0.076	0.053
5 to 9 days	368	-0.123	0.018	237	0.110	0.094
10 to 14 days	340	0.137	0.012	235	-0.174	0.007
15 to 19 days	297	0.027	0.640	308	-0.025	0.667
20 to 24 days	288	0.031	0.600	308	0.001	0.986
25+ days	293	0.011	0.853	279	0.028	0.644

Table 7.3 Spearman's rho correlation of Arctic and Common Tern parental attendance at the nest (min.h^{-1}) depending on daily average temperatures (˚C) for nests containing chicks of different age groups

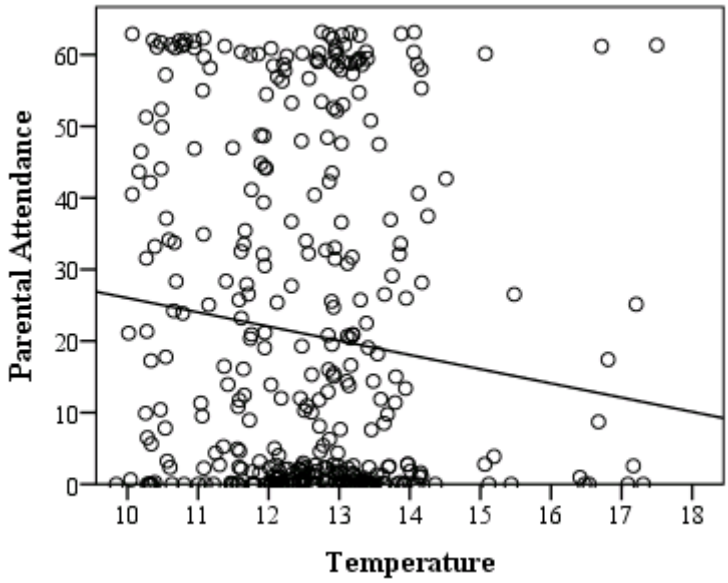


Figure 7.4 Distribution of parental attendance (min.h^{-1}) depending on average daily temperature (˚C) for Arctic Terns at nests whose eldest chick was aged between 5 and 9 days, jittered points

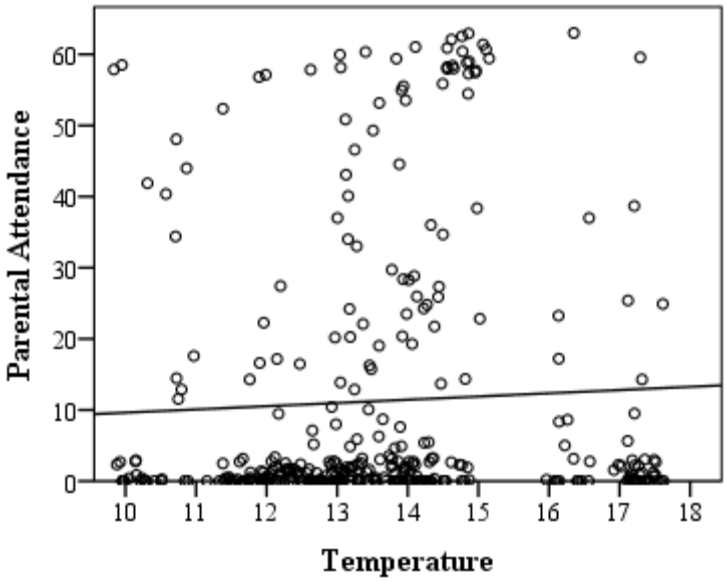


Figure 7.5 Distribution of parental attendance (min.h^{-1}) depending on average daily temperature (˚C) for Arctic Terns at nests whose eldest chick was aged between 10 and 14 days, jittered points

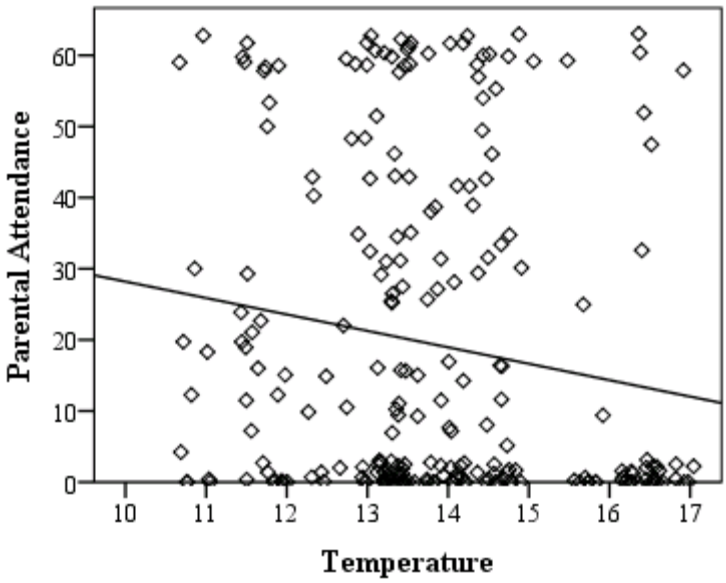


Figure 7.6 Distribution of parental attendance (min.h^{-1}) depending on average daily temperature (˚C) for Common Terns at nests whose eldest chick was aged between 10 and 14 days, jittered points

Spearman's rho correlation of PA with mean daily wind speed (km.h^{-1}) showed a significant negative correlation for Arctic Terns and Common Terns with eldest chick aged between 10 and 14 days and for Arctic Terns with chicks aged between 15 and 19 days (Table 7.4, Figure 7.7, Figure 7.8, Figure 7.9).

	Arctic Tern			Common Tern		
	n	Spearman's rho	p	N	Spearman's rho	P
0 to 4 days	283	-0.039	0.514	236	-0.126	0.053
5 to 9 days	368	-0.062	0.233	237	0.099	0.129
10 to 14 days	340	-0.354	<0.001	235	-0.172	0.008
15 to 19 days	297	-0.246	<0.001	308	-0.077	0.178
20 to 24 days	288	-0.047	0.424	308	-0.045	0.429
25+ days	293	0.019	0.749	279	-0.038	0.529

Table 7.4 Spearman's rho correlation of Arctic and Common Tern parental attendance (min.h^{-1}) depending on mean daily wind speed (km.h^{-1}) for nests containing chicks of different age groups

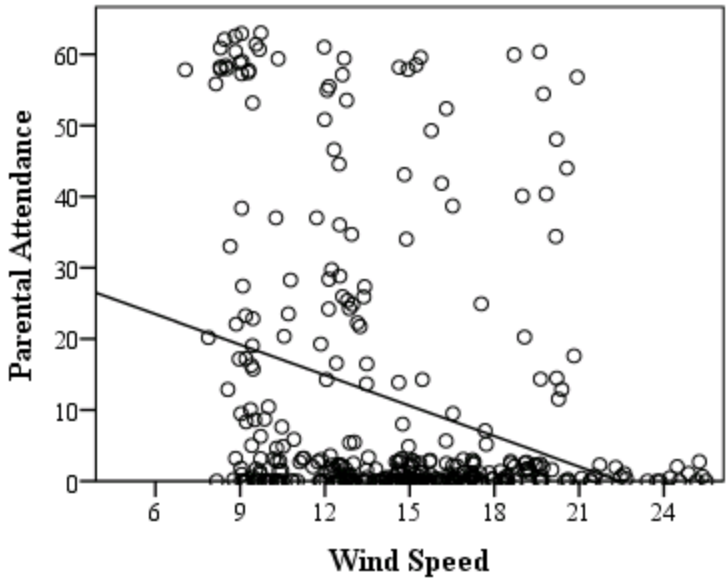


Figure 7.7 Distribution of parental attendance (min.h^{-1}) depending on mean daily wind speed (km.h^{-1}) for Arctic Terns at nests whose eldest chick was aged between 10 and 14 days, jittered points

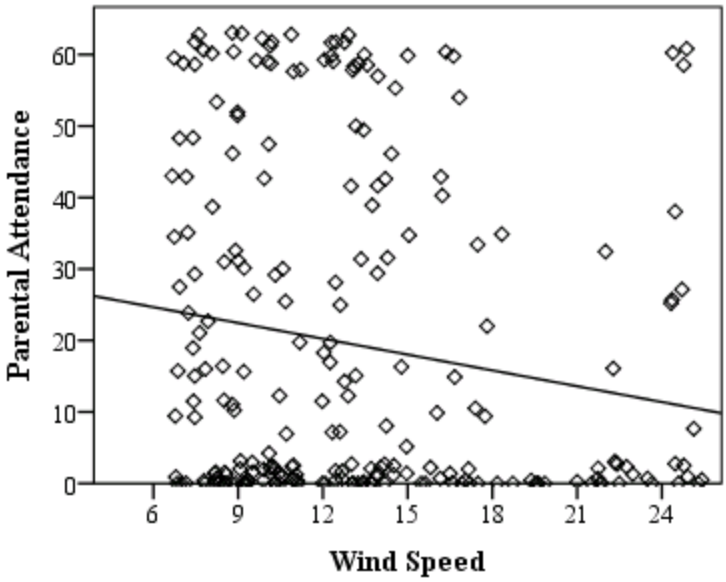


Figure 7.8 Distribution of parental attendance (min.h^{-1}) depending on mean daily wind speed (km.h^{-1}) for Common Terns at nests whose eldest chick was aged between 10 and 14 days, jittered points

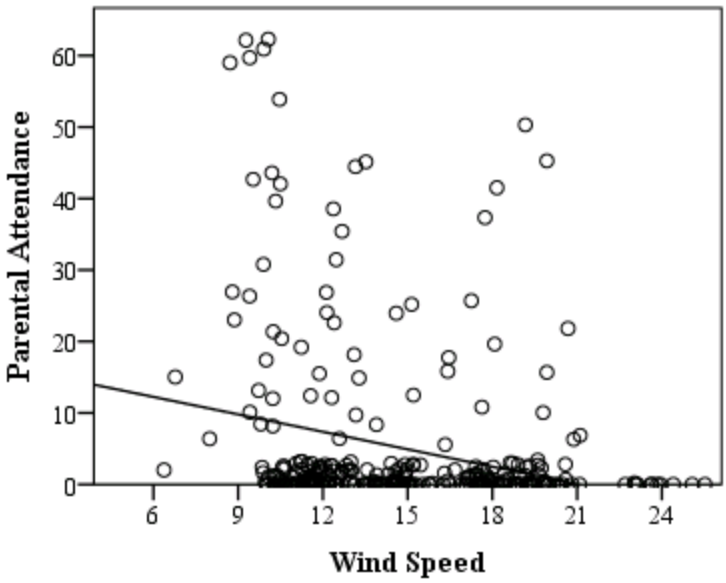


Figure 7.9 Distribution of parental attendance (min.h^{-1}) depending on mean daily wind speed (km.h^{-1}) for Arctic Terns at nests whose eldest chick was aged between 15 and 19 days, jittered points

Mann-Whitney U analysis showed that Arctic Tern PA was higher during rain when nests contained eldest chicks aged between 5 and 9 and 10 and 14 days. Common Tern PA was higher during rain when nest contained eldest chicks ages between 5 and 9 and 10 and 14 days (Table 7.5, Figure 7.10).

	Arctic Tern			Common Tern		
	n	Z	p	n	Z	p
0 to 4 days	283	-0.053	0.958	236	2.149	0.032
5 to 9 days	368	2.999	0.003	237	-0.264	0.792
10 to 14 days	340	2.194	0.028	235	-0.482	0.630
15 to 19 days	297	0.334	0.739	308	-2.546	0.011
20 to 24 days	288	0.720	0.471	308	-2.537	0.011
25+ days	293	-1.229	0.219	279	-2.026	0.043

Table 7.5 Mann-Whitney U analysis comparing Arctic and Common Tern mean parental attendance (min.h^{-1}) depending on whether or not there was rain during the hour for nests containing chicks of different age groups

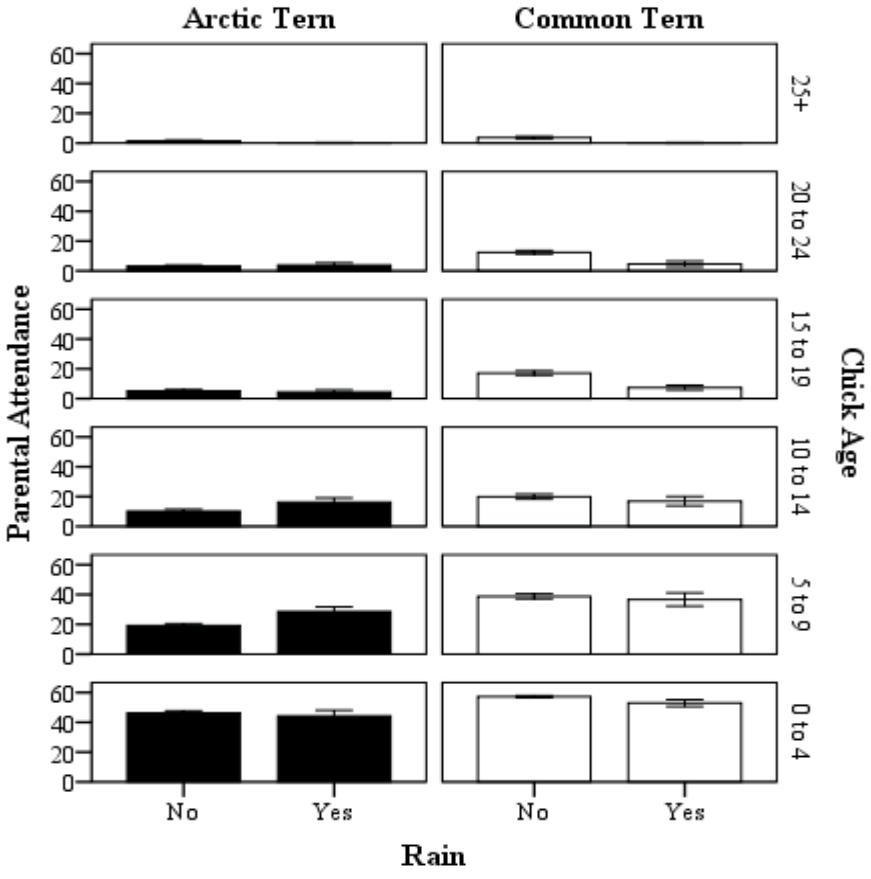


Figure 7.10 Mean parental attendance (min.h^{-1}) ± SE depending on whether or not rain fell during the hour for different age groups of eldest chick

7.5 Discussion

Parental attendance declined with age for both Arctic and Common Terns, with an adult present from 70% and 94% of the time respectively when chicks were newly hatched, and from to 2% and 5% once chicks were near fledging. The decline of brooding with age of chick is well documented and has long been associated with the increase in thermoregulatory capability of chicks, with brooding often ceasing completely once chicks are capable of regulating their body temperature (Dawson et al. 1976; Kirkham & Montevecchi 1982; Evans 1984; Gabrielsen et al. 1992; Uttley 1992; Klassen 1994; Robinson et al. 2001).

At a young age chicks are entirely dependent on parents for thermoregulation (Dawson et al. 1976; Kirkham & Montevecchi 1982; Evans 1984) and parental attendance can be considered a necessity. Once chicks begin to develop the ability to thermoregulate, parental attendance becomes less important and adults can spend more time away from the nest, brooding only when necessary. It is likely that at this age parental behaviour is dictated by chick calls. Chicks give different and mutually exclusive calls depending on whether they want to be fed or brooded (Evans 1994). During this period the energy needs of chicks are increasing (Klassen 1989; Massias & Becker 1990; Klassen 1994) and adult foraging effort increases to meet demands (Chapter 5), resulting in a decline in parental attendance.

By the age of around 10 days tern chicks are likely to be able to fully thermoregulate and the cost of thermoregulation has fallen almost to adult levels (Klassen 1989). At this point there is little energy benefit to brooding, at least during daylight hours (Gabrielsen et al. 1992; Klassen 1994), and a chick's energy needs have reached their peak (Klassen 1989; Massias & Becker 1990; Klassen 1994). Parental activity at the nest was not recorded in this study. However, it has previously been shown that parents of chicks capable of thermoregulation tend to spend time at the nest engaging in other activities rather rather than brooding (Gabrielsen et al.1992; Robinson et al. 2001). This is confirmed by personal observations, and suggests that parental attendance at this age is indicative of foraging conditions, with adults spending time at the nest site when they can afford to take time away from foraging.

This theory is supported by differences in parental attendance between years, suggesting external pressures are dictating time spent at the nest, at least once the need to brood is no longer paramount. In both species, high parental attendance was seen in 2009 and low parental attendance in 2010 (and in 2008 for Arctic Terns). While provisioning rates and productivity were different between these years (Chapter 4, Chapter 5), the relationship was not always clearly defined. However, differences in parental attendance are suggestive of increased pressure on adults to provision chicks adequately (Hamer et al. 1991; ibid. 1993; Uttley 1992; Kitaysky et al. 2000; Rindorf et al. 2000; Robinson et al. 2001; Wanless et al. 2005), and could explain differences seen in productivity between years of apparently similar provisioning rates.

2008 and 2010 were disastrous years for Arctic Terns, with 79% of chicks dying in 2008 and 59% dying in 2010. In these years, parental attendance was low overall, but also lower for nests containing younger chicks (Figures 7.2, Figure 7.3). At this age chicks are at least partially reliant on adults for warmth (and nests may contain younger chicks still vulnerable to changing temperatures). Low parental attendance indicates that parent birds were forgoing brooding in favour of foraging, suggesting increased difficulties in adequately provisioning chicks. Conversely, 2009 was an especially good year with high productivity and low chick mortality for both Arctic and Common Terns (chick mortality was 15% and 22% respectively). Provisioning rate was fairly low (similar to rates seen in 2010) but parental attendance was high, suggesting that easily accessibly prey and sufficiently well-fed chicks allowed parents to take time off at the nest site between foraging flights.

It is suggested that parental attendance at nests with older chicks may be thought of as time off from foraging rather than as time actively looking after chicks at the nest. If this is the case, then parental attendance at this age is a good indicator of how the season is progressing with regard to provisioning conditions. High attendance suggests good supply of prey and well fed chicks, while low attendance suggests that parents have to spend all available time foraging as food is scarce or of poor quality. It is likely that chick behaviour influences parental behaviour, with chicks calling to be brooded or fed depending on which is the greater need (Evans1994).

Arctic Tern parental attendance was found to be lower than that of Common Terns regardless of age. This supports the findings of a study conducted by Robinson et al.

(2001) on Coquet Island in 1997. Arctic Tern chicks expend more energy on thermoregulation than do Common Terns and parental brooding saves a higher percentage of energy (Klassen 1994). If chick brooding needs were the sole determinant of parental attendance, one would therefore expect higher not lower parental attendance. However, several factors indicate that Arctic Terns are breeding under far from ideal conditions on Coquet: they have lower productivity (Chapter 3); higher and more variable chick mortality (Chapter 4); and are provisioning at a higher rate but bringing in lower energy yield (Chapter 5) than are Common Terns. It is therefore suggested that the lower parental attendance of Arctic Terns is due to less 'time off' for parent birds as a result of greater pressure to provision their chicks adequately.

This low brooding of vulnerable chicks by parent Arctic Terns could be a factor in lower productivity. When adults forgo brooding in favour of foraging, they may be leaving chicks unattended and un-brooded at an age when they are reliant on parents for warmth and protection. If Arctic Tern chicks are therefore expending more energy on thermoregulation but receiving insufficient food to compensate, then increases in chick mortality are to be expected. This is likely to be most marked when foraging conditions are poor for an extended period of time.

Weather conditions affect thermoregulation, with declining ambient temperature resulting in decreased body temperature (even for older chicks, although the difference is less) (Dawson et al. 1976; Ricklefs & White 1981; Bech et al. 1982; Kirkham & Montevecchi 1982). Increasing wind speed results in a large increase in thermal conductivity and a decline in body temperature (Chappell 1979; Bakken et al. 2002), and thermal conductivity of wet feathers and down is higher than dry (Nye 1964; Webb & King 1984; McCafferty et al. 1997).

The effect of weather on parental attendance appears to be limited by age of chicks. At a young age chicks need to be brooded almost constantly whatever the weather. Once chicks are over 2 weeks old the benefits of brooding are limited whatever the weather conditions. However, for nests containing eldest chicks aged between 5 and 14 days, weather does appear to affect attendance at the nest. During this time chicks are developing their thermoregulatory capabilities and their thermal conductivity is declining; thermoregulation is still costly and brooding reduces these costs. In addition,

nests may contain younger chicks with less well developed thermoregulatory capabilities who are more dependent on parental brooding.

It was expected that brooding would have increased with lower ambient temperatures due to their impact on chicks (see references above). Surprisingly, temperature appeared to have little effect on parental brooding, with both positive and negative correlations. It is suggested that the limited differences recorded in ambient temperatures (8˚C temperature range) mean that even at 5 days of age chicks are capable of maintaining body temperature at an energy cost that does not necessitate parental attendance.

Increased wind speed is associated with increased thermal conductivity (Chapple 1979; Bakken et al. 2002). However, wind speed has a generally negative effect on parental attendance. This appears contrary to the expected consequence of the increased costs and conductivity associated with increased wind speed. It suggested that foraging conditions are the controlling factor on parental attendance with increased wind speed. If adults were abandoning provisioning in favour of brooding, an increase rather than a decrease in attendance would be expected. As this is not the case it is suggested that adult birds spend longer foraging when wind speeds increase because of the greater difficulty in either locating or catching prey and in order to try and maintain chick provisioning. Attendance at the nest falls as a consequence. This is likely to have a negative impact on chick fitness and survival, as chicks expend greater energy maintaining body temperature under windy conditions while receiving less food.

One would expect increased parental attendance in wet conditions, both as protection from rain and to brood chilled chicks. Arctic Tern attendance did not change significantly with rainfall for parents of young and older chicks, but - as expected - increased with rainfall when chicks were in the mid-age range. The results for Common Terns initially appear counterintuitive, with decreased attendance with rainfall (Figure 7.10). Precipitation has little effect on Arctic Tern provisioning behaviour but it increases Common Tern foraging rate and lowers nest attendance. Nests with mid-aged chicks show no difference in attendance between wet and dry conditions, implying that Common Terns forgo foraging in favour of brooding when chicks are at this vulnerable age.

In conclusion, parental attendance is initially determined by the thermal needs of chicks, with attendance declining as chicks become more capable of regulating and maintaining their own body temperature. For young chicks, parental attendance was almost constant, as they are completely reliant on parents for warmth. Once chicks develop some thermoregulatory capabilities parents can spend longer away from the nest, and the proportion of time spent brooding became more affected by weather conditions. Older nestlings no longer need to be brooded so parental attendance at the nest is likely to reflect parents taking time off from foraging. Differences in parental attendance between years and species suggest variability in the pressures associated with provisioning chicks. Low parental attendance suggests that adults are under pressure to provision chicks and are spending longer out foraging so have less time to spend at the nest. Parental attendance shows no clear pattern with increased temperature, but parents increase brooding of vulnerable chicks when conditions are wet. Parental attendance falls when wind speed increases; this is thought to be because the increased foraging effort needed to provision chicks has priority over their brooding needs.

Chapter 8. The effects of weather and feeding conditions on chick mortality

8.1 Abstract

Environmental factors during the nestling period are likely to play a major role in chick survival. Binomial logistic regression was used to find the best models to explain Arctic and Common Tern chick mortality during the early (ages 0 to 10 days), middle (ages 11 to 20 days) and late (21 to 30 days) nestling stages with regard to the weather conditions (temperature, rainfall and wind speed) and feeding conditions (provisioning rate, energy delivery rate and energy per feed) experienced. Early-stage mortality was higher when conditions were windy and the feeding rate poor. Feeding conditions had a greater impact on younger siblings than a-chicks. It is suggested that this was the effect of brood hierarchy, with a-chicks controlling primary access to food. Analysis of mid-stage mortality was limited by sample size to b-chicks only. Feeding and weather conditions were still found to be important, with high wind speeds and low feeding rates resulting in higher mortality. Arctic Tern chick mortality was influenced by conditions experienced during early development, indicating their continuing impact on fitness and ability to survive. Analysis of late-stage mortality was limited by sample size to Arctic Tern a-chicks only. Weather conditions no longer influenced chick mortality, but the importance of good feeding throughout the nestling period was clear. It is suggested that moderate temperatures and wind speeds and an absence of storms coupled with sustained good provisioning are the optimal conditions for chick survival.

8.2 Introduction

The road from hatching to fledging is a perilous one. For a chick to survive this journey it must be protected from predation, injury, starvation and hypothermia. Congenital defects or injury can cause death whatever the feeding and weather conditions, and survival of healthy chicks is influenced by such 'fixed' factors as parental quality (Bolton 1991; Nisbet et al. 1998), egg/hatchling size (Bolton 1991; Hipfner & Gaston 1999; Pelayo & Clark 2003) and hatching order (Chapter 4). However, the conditions experienced by the chick ultimately determine whether it dies or survives to fledging.

Mortality within the season is usually linked with feeding or weather conditions, or a combination of the two.

A common cause of tern chick mortality is starvation due to low food supply, with high mortality rates seen when chicks are under average body mass (e.g. Langham 1972; Becker & Specht 1991; Quillfeldt 2001; Buber et al. 2004). The link between foraging conditions and provisioning is well established: if conditions are poor at sea then provisioning of chicks is similarly poor (Frank 1992; Montevecchi & Myers 1995; Diamond & Devlin 2003; Wanless et al. 2005; Furness 2007). Poor provisioning of chicks either through low rate of provisioning (Barrett et al. 1987; Croxall et al. 1999; Buber et al. 2004), lack of preferred prey species (Murphy et al. 1984; Monaghan et al. 1989; Hamer et al. 1991; Suddaby & Ratcliffe 1997; Kato et al. 2001; Furness 2007) or low quality of prey (Golet et al. 2000; Wanless et al. 2005; Osterblom et al. 2006; Romano et al. 2006) has been linked with higher chick mortality. In the short term, reduced food supply results in low weight gain while continuing severe reductions have been shown to delay physiological development (Moe et al. 2004) and reduce metabolic activity and effect thermoregulation (Klassen & beck 1992; Moe et al. 2004).

Cold air temperature, high wind speeds and rainfall increase the thermoregulatory costs of maintaining a stable body temperature (e.g. Chapple 1979; Klassen et al. 1989; McCafferty et al. 1997; Bakken et al. 2002). In addition, during periods of poor weather the foraging by parent birds may also be hampered, either through impaired foraging ability or reduced accessibility of prey (e.g. Frank 1992; Corten & Van de Kamp 1996; Stienen et al. 2000; Taylor et al. 1983; Garcia & Mariano-Jelicich 2005). Combined, these factors mean that chicks are often receiving less food while having to expend more energy on thermoregulation, and low growth rates and high rates of mortality have been linked with periods of poor weather (Dunn 1975; Becker & Specht 1991; Ritz et al. 2005).

The risk of death is present throughout the nestling period. However, the degree of risk changes as a chick develops. Here we investigate how weather conditions (temperature, rainfall and wind speed) and provisioning conditions (provisioning rate and energy value) on Coquet Island between 2007 and 2010 affected chick mortality throughout nestling development. It is expected that the vulnerability of chicks will depend on the conditions encountered and on their age (affecting thermoregulatory ability and feather

covering) and hatching order (the effects of the brood hierarchy, Chapter 4). Therefore, the effects of conditions on chick mortality will be analysed over three stages: early-, mid- and late-stages of development. This will show when chicks are most vulnerable and how the impact varies with chick development. It is expected that first hatched chicks (a-chicks) will be less vulnerable to feeding constraints than younger siblings as they have primary access to food (Braun & Hunt 1983; Hunt & Evans 1997; Smith et al. 2005). The impact of weather conditions is expected to decline with chick age, as chicks increase in size and become capable of thermoregulation. There is expected to be both a short and long term impact of the conditions examined, as they affect a chick's ability to cope with future challenges.

8.3 Methodology and Analysis

8.3.1 Methodology

See Chapter 2, sections 2.2.3, 2.4.2 and 2.5.2.

8.3.2 Analysis

Analysis of data for Arctic and Common Terns was undertaken separately and split by hatching order. The nestling period was divided into 3 stages: early-stage development was classed as days 0 through10 after hatching, mid-stage as between 11 and 20 days after hatching and late-stage as between 21 and 30 days after hatching.

Differences in mortality rates of a-chick, b-chick and c-chick (Common Terns only) between age groups were analysed using Pearson's Chi squared test with z-test of column proportions with Bonferroni adjusted p-value used for differences between groups using IBM SPSS Statistics, version 19.

Binomial logistic regression was used to find the best model parameters for predicting a chick's likelihood of surviving. Mortality of chicks (dependant variable, 0=died, 1= survived) during each stage was predicted using daily temperature (˚C), precipitation (mm), and wind speed ($km.h^{-1}$), hourly chick provisioning rate ($feed.chick^{-1}.h^{-1}$), energy delivery rate ($kJ.h^{-1}$) and energy per feed ($kJ.feed^{-1}$), averaged over that period. Early mortality was predicted using conditions during the first 10 days after hatching (early). Mid-stage mortality was predicted using both early conditions and conditions between days 11 and 20 after hatching (mid). Late-stage mortality was predicted using early, mid

and late (conditions between days 21 and 30 after hatching) conditions. Due to small sample size and number of parameters in the models Akaikes' Information Criterion (AIC) was corrected for small sample size and models were ranked according to Corrected AIC (AICc). All models with $\Delta AICc < 2$ are presented with number of model parameters including intercept (para), difference in AICc from the top ranked model ($\Delta AICc$), relative log likelihood (rel.LL), Aikaike weights (wi) and deviance expalained by the model compared to the null model (Dev). The two highest ranking models according to AICc are shown in full. Analysis was undertaken using R, version 2.14.1.

Low mortality of Common Tern a-chicks throughout the nestling period meant mortality analysis was not undertaken. For the same reason, analysis was not undertaken of Arctic Tern a-chick mortality during the mid-stage or of Arctic and Common Tern b-chick mortality during the late-stage. Common Tern c-chick mortality was limited to the early-stage because of low sample size for subsequent stages. Only chicks that survived their first two days were included in the analysis, as it was felt that external conditions were unlikely be to a significant cause of earlier mortality. Age at death was not recorded in 2006 therefore all data presented here was collected between 2007 and 2010.

8.4 Results

8.4.1 Mortality between groups

Pearson's Chi squared analysis showed a significant difference in the proportion of chicks dying between nestling stages for Arctic Tern a- and b-chicks and Common Tern b- and c-chicks but not a-chicks (Table 8.1).

		n	χ^2	d.f.	p
Arctic Tern	a-chick	287	6.621	2	0.036
	b-chick	188	9.635	2	0.008
Common Tern	a-chick	322	0.037	2	0.982
	b-chick	243	23.95	2	<0.001
	c-chick	81	6.388	2	0.041

Table 8.1 Pearson's Chi-squared analysis of differences in the proportions of Arctic and Common Tern chicks dying between early- (ages 0 to 10days), mid- (ages 11 to 20 days) and late- (ages 20 to 30 days) nestling stages depending on hatching order

Z test of column proportions showed Arctic Tern a-chick mortality was more likely during early- than mid-stage development. B-chick mortality was comparably high between early- and mid-stage, but was significantly lower in late-stage development. Common Tern a-chick mortality did not vary with nestling stage while b-chick mortality was highest during the mid-stage and lowest during the late-stage. C-chick mortality was comparably high between early- and mid-stages but declined significantly during late-stage development (although population size was low) (Table 8.2).

			Early	Mid	Late
Arctic Tern	a-chick	%	17.3	5.5	11.6
		n	110	91	86
	b-chick	%	38.3	37.9	11.1
		n	94	58	36
Common Tern	a-chick	%	7.8	7.5	7.1
		n	116	107	71
	b-chick	%	24.3	42.9	4.2
		n	111	84	48
	c-chick	%	68.4	66.7	16.7
		n	57	18	6

Table 8.2 Percentage of Arctic and Common Tern chick population which died during early-, mid- and late-stages of nestling development. Split by hatching order

8.4.2 Early-stage mortality

Binomial logistic regression analysis was undertaken of Arctic Tern a- and b-chick and Common Tern b- and c-chick mortality depending on conditions during the first 10 days of a chick's life. Chick mortality was the dependant variable (1=survived, 0=died), with temperature (temp), wind speed (wind), rainfall (rain), provisioning rate (feed), energy delivery rate (kJ) and energy per feed ($kJ.feed^{-1}$) as model predictors. All combinations of model predictors were run (63 models) and ranked according to AICc. Models with $\Delta AIC < 2$ are presented in Table 8.3.

	Model	Para	AICc	ΔAICc	rel.LL	wi	Dev
Arctic Tern a-chick	**Wind+feed**	**3**	**61.365**	**0**	**1**	**0.135**	**0.144**
	Temp+wind+feed	**4**	**62.824**	**1.459**	**0.482**	**0.065**	**0.155**
	Rain+wind+feed	4	63.19	1.832	0.400	0.054	0.149
	Temp+wind+feed +kJ.feed^{-1}	5	63.267	1.902	0.386	0.052	0.183
	Wind+feed +kJ.feed^{-1}	4	63.301	1.937	0.380	0.051	0.148
Arctic Tern b-chick	**Temp+wind+feed +kJ.feed^{-1}**	**5**	**92.966**	**0**	**1**	**0.142**	**0.165**
	Temp+wind+feed +kJ	**5**	**93.000**	**0.034**	**0.983**	**0.139**	**0.165**
	Wind+feed	3	93.487	0.521	0.771	0.109	0.114
	Temp+wind+feed +kJ+kJ.feed^{-1}	6	94.781	1.815	0.404	0.057	0.171
Common Tern b-chick	**Wind+feed +kJ.feed^{-1}**	**4**	**98.517**	**0**	**1**	**0.159**	**0.160**
	Wind+feed+kJ +kJ.feed^{-1}	**5**	**99.240**	**0.723**	**0.697**	**0.111**	**0.174**
	Rain+wind+feed +kJ.feed^{-1}	5	100.059	1.542	0.463	0.073	0.167
	Temp+wind+feed +kJ.feed^{-1}	5	100.432	1.915	0.384	0.061	0.163
Common Tern c-chick	**Wind+kJ +kJ.feed^{-1}**	**4**	**39.355**	**0**	**1**	**0.176**	**0.475**
	Temp+kJ.feed^{-1}	**3**	**40.534**	**1.179**	**0.554**	**0.097**	**0.413**
	Wind+feed+kJ +kJ.feed^{-1}	5	41.171	1.817	0.403	0.071	0.487

Table 8.3 Binomial logistic regression models for Arctic and Common Tern chicks depending on hatching order. Survival between the ages of 2 and 10 days (0=died, 1=survived) as dependant variable. Presenting top models as selected by delta-AIC <2 ranked in order of AICc. Models in bold are the two highest ranking models according to AICc.

The highest ranking Arctic Tern a-chick model according to AICc had the model parameters wind speed and feed with a significant negative relationship between wind speed and chick survival and a non-significant (p=0.057) positive relationship between feed and chick survival. The second highest ranking model contained the parameters temperature, wind speed and feed, with only wind speed having a significant negative effect on chick survival (Table 8.4, Figure 8.1).

	Z	p	Coefficients ± SE
AICc: 61.365			
Intercept	2.587	0.010	10.453 ± 4.041
Wind	**-2.612**	**0.009**	**-0.772 ± 0.296**
Feed	1.902	0.057	1.341 ± 0.705
AICc: 62.834			
Intercept	2.099	0.036	15.600 ± 7.432
Temp	-0.880	0.379	-0.446 ± 0.507
Wind	**-2.466**	**0.014**	**-0.707 ± 0.287**
Feed	1.452	0.147	1.085 ± 0.748

Table 8.4 Full binomial regression of the two highest ranked Arctic Tern a-chick early-stage models (according to AICc)

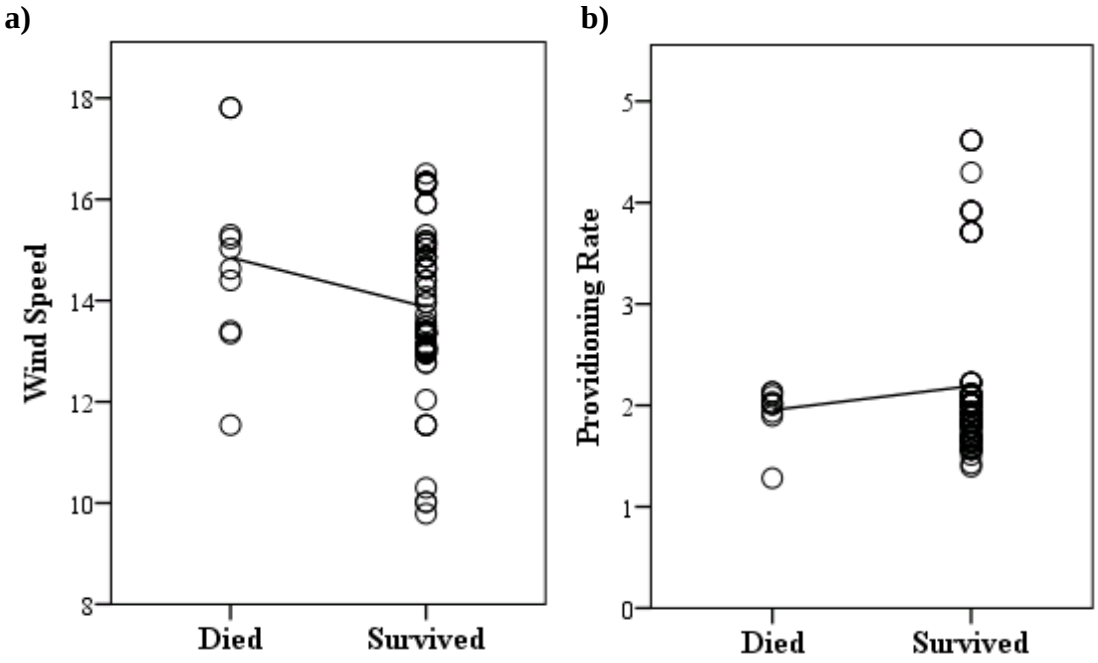


Figure 8.1 Survival of 110 Arctic Tern a-chicks between 2 and 10 days after hatching in relation to **a)** wind speed (km.h^{-1}) and **b)** provisioning rate (feed.chick^{-1}.h^{-1})

The highest ranking Arctic Tern b-chick model according to AICc had the model parameters temperature, wind speed, feed and kJ.feed^{-1}, with a significant negative relationship between wind speed and chick survival and an almost significant negative relationship between temperature and chick survival. Provisioning rate had a significant positive relationship with chick survival and kJ.feed^{-1} an almost significant relationship (p=0.060). The second highest ranking model had wind speed and temperature as a significant negative parameters, feed as a significant positive parameter and energy delivery rate as and almost significant positive parameter (p=0.052), (Table 8.5, Figure 8.2).

	Z	p	Estimate of coefficients ± SE
AICc: 92.966			
Intercept	1.889	0.060	17.049 ± 9.028
Temp	-1.254	0.061	-1.254 ± 0.670
Wind	**-2.428**	**0.015**	**-0.712 ± 0.293**
Feed	**2.692**	**0.007**	**2.992 ± 1.112**
kJ.feed^{-1}	1.882	0.060	0.969 ± 0.515
AICc: 93.000			
Intercept	2.086	0.037	17.856 ± 8.557
Temp	**-1.976**	**0.048**	**-1.166 ± 0.590**
Wind	**-2.578**	**0.010**	**-0.734 ± 0.285**
Feed	**2.673**	**0.008**	**1.909 ± 0.714**
kJ	1.946	0.052	0.595**± 0.052**

Table 8.5 Full binomial regression of the two highest ranking Arctic Tern b-chick early-stage models (according to AICc)

The highest ranking Common Tern b-chick model according to AICc had the model parameters wind speed, feeding rate and energy per feed, with a significant negative relationship between wind speed, provisioning and energy per feed and chick survival. The second highest ranking model had the model parameters wind speed, provisioning rate, energy delivery rate and energy per feed. All parameters had significant negative relationship with chick mortality, except for energy delivery rate, which was non-significant (Table 8.6, Figure 8.3).

	Z	p	Estimate of coefficients ± SE
AICc: 98.517			
Intercept	3.812	<0.001	9.554 ± 2.506
Wind	**-2.064**	**0.039**	**-0.304 ± 0.147**
Feed	**-2.308**	**0.021**	**-1.997 ± 0.865**
kJ.Feed^{-1}	**-2.412**	**0.016**	**-0.095 ± 0.039**
AICc: 99.240			
Intercept	3.486	<0.001	11.556 ± 3.430
Wind	**-2.301**	**0.021**	**-0.451 ± 0.196**
Feed	**-2.428**	**0.015**	**-2.467 ± 1.016**
kJ	1.223	0.221	0.104 ± 0.085
kJ.Feed^{-1}	**-2.247**	**0.025**	**-0.171 ± 0.076**

Table 8.6 Full binomial regression of the two highest ranking Common Tern b-chick early-stage models (according to AICc)

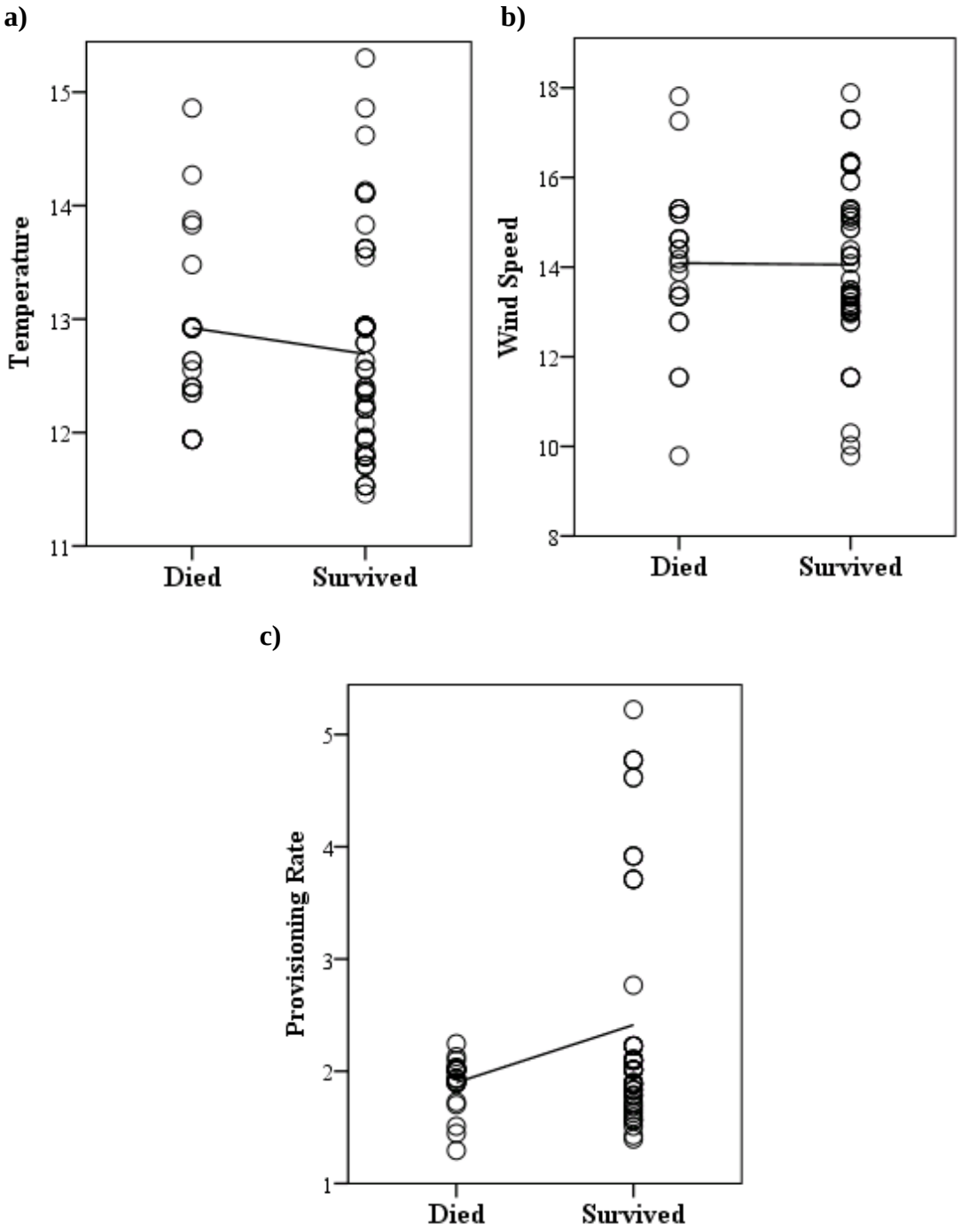


Figure 8.2 Survival of 94 Arctic Tern b-chicks between 2 and 10 days after hatching in relation to **a)** temperature (ºC) **b)** wind speed ($km.h^{-1}$) and **c)** provisioning rate ($feed.chick^{-1}.h^{-1}$)

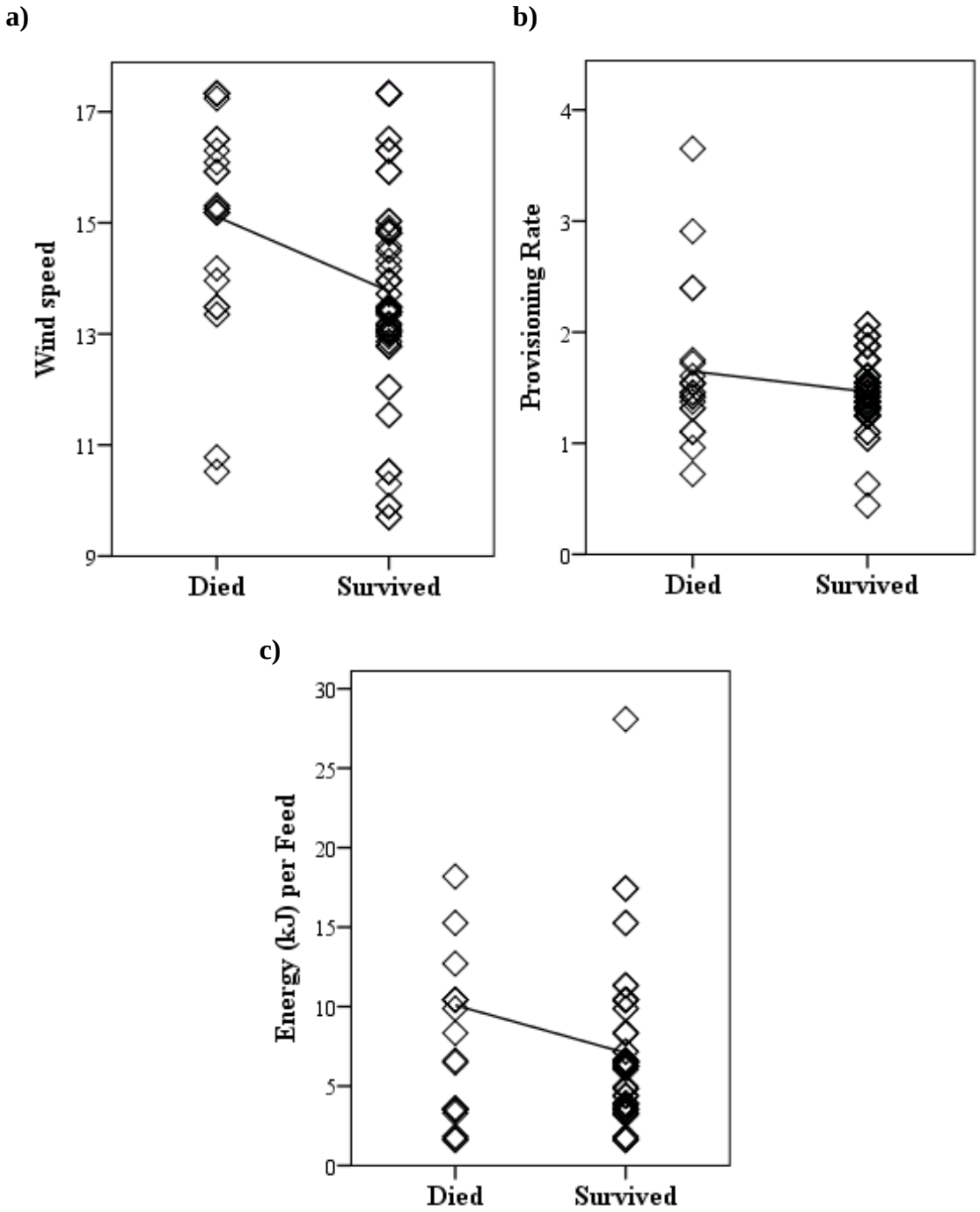


Figure 8.3 Survival of 111 Common Tern b-chicks between 2 and 10 days after hatching in relation to **a)** wind speed ($km.h^{-1}$), **b)** provisioning rate ($feed.chick^{-1}.h^{-1}$) and **c)** energy per feed ($kJ.feed^{-1}$)

The highest ranking Common Tern c-chick model had the parameters wind speed, energy delivery rate and energy per feed, with a significant negative relationship between wind speed and energy per feed and chick survival, and a significant positive relationship between energy delivery rate and chick survival. The second highest ranking model had the parameters temperature and energy per feed with significant positive relationship between temperature and chick survival and a significant negative relationship between energy per feed and chick survival (Table 8.7, Figure 8.4).

	Z	p	Estimate of coefficients ± SE
AICc: 39.355			
Intercept	2.995	0.003	22.834 ± 7.727
Wind	**-2.817**	**0.005**	**-1.835 ± 0.652**
kJ	**2.063**	**0.039**	**0.733 ± 0.355**
kJ.feed^{-1}	**-2.684**	**0.007**	**-0.877 ± 0.327**
AICc: 40.534			
Intercept	-2.596	0.009	-20.891 ± 8.047
Temp	**2.711**	**0.007**	**1.838 ± 0.678**
kJ.Feed^{-1}	**-3.087**	**0.002**	**-0.481 ± 0.156**

Table 8.7 Full binomial regression of the two highest ranking Common Tern c-chick early-stage models (according to AICc)

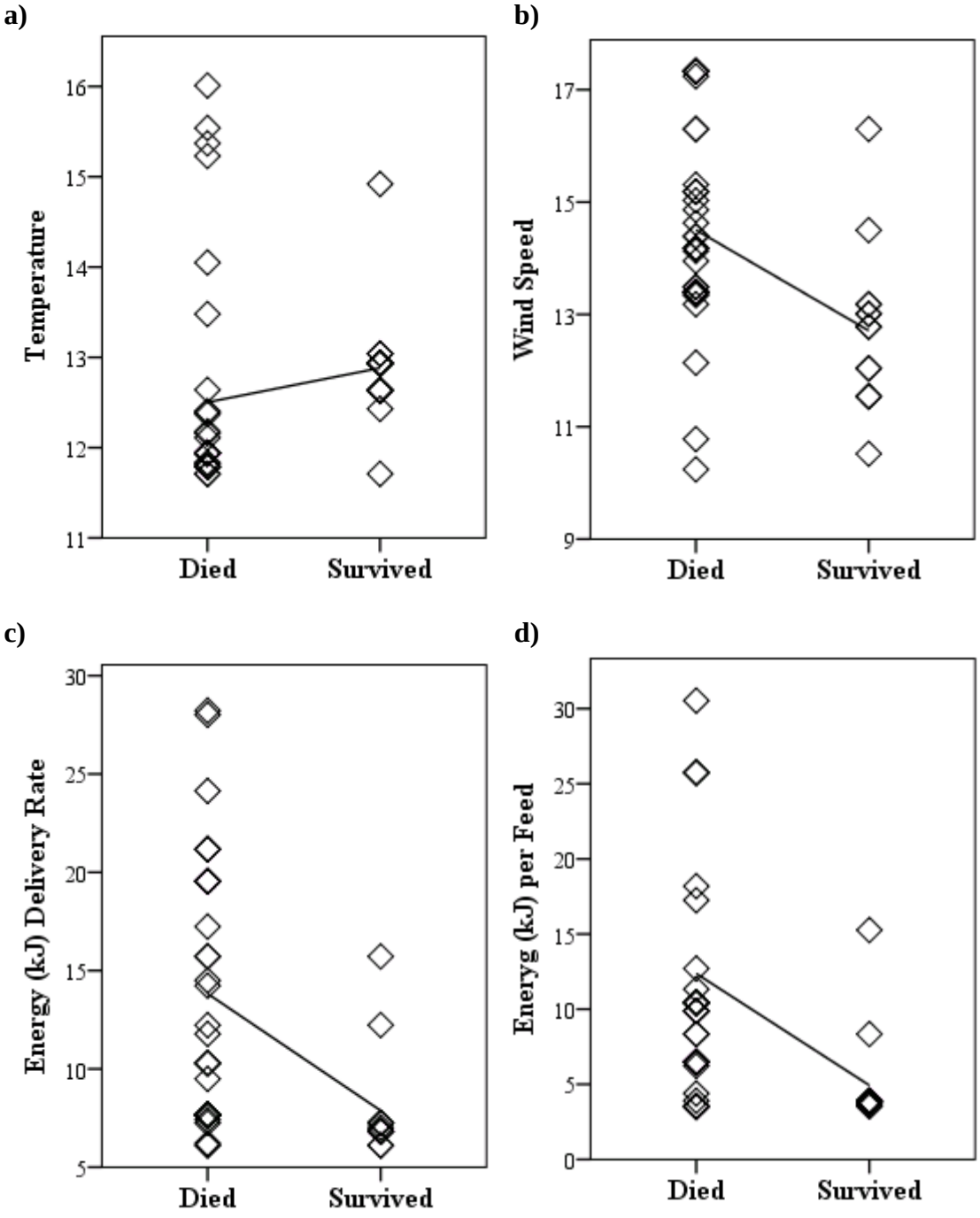


Figure 8.4 Survival of 57 Common Tern c-chicks between 2 and 10 days after hatching in relation to **a)** temperature (ºC) **b)** wind speed ($km.h^{-1}$), **c)** energy delivery rate ($kJ.chick^{-1}.h^{-1}$) and **d)** energy per feed ($kJ.feed^{-1}$)

8.4.3 Mid-stage mortality

Binomial logistic regression analysis was undertaken of Arctic and Common Tern b-chick mortality depending on conditions during the second stage of nestling development (ages 11 to 20 days) and during first stage. Chick mortality was the dependant variable (1=survived, 0=died) with temperature, wind speed, rainfall, feed, kJ and $kJ.feed^{-1}$ during both early- and mid-stages as model predictors. Early-stage models

(e) were run initially. The significant variables in the highest ranking models with ΔAIC <2 (temp(e) and kJ.feed^{-1}(e) for Arctic Terns; temp(e), feed(e) and kJ.feed^{-1}(e) for Common Terns) were then used in all combinations with mid-stage variables (m), resulting in 315 and 378 models for Arctic and Common Terns respectively. Models were ranked according to AICc with models with ΔAIC <2 presented in Table 8.8.

	Model	Para	AICc	ΔAIC	rel.LL	wi	Dev
Arctic Tern b-chick	**Temp(e)+wind(m)**	**3**	**33.241**	**0**	**1**	**0.059**	**0.643**
	Temp(e)+kJ.feed^{-1}(e)	**3**	**33.877**	**0.636**	**0.728**	**0.043**	**0.634**
	kJ.feed^{-1}(e)+feed(m)	3	34.725	1.484	0.476	0.028	0.623
	Temp(e)+kJ.feed^{-1}(e) +wind(m)	4	34.790	1.549	0.461	0.027	0.653
	Temp(e)+temp(m) +wind(m)	4	35.096	1.855	0.396	0.023	0.649
	Rain(m)+wind(m)	4	35.135	1.894	0.388	0.023	0.643
	Temp(e)+kJ.feed^{-1}(e) +feed(m)	4	35.223	1.982	0.371	0.022	0.647
Common Tern b-chick	**Temp(m)+wind(m)**	**3**	**94.684**	**0**	**1**	**0.143**	**0.206**
	Feed(e)+wind(m)	**3**	**95.299**	**0.616**	**0.735**	**0.105**	**0.200**
	Wind(m)+feed(m)	3	95.670	0.986	0.611	0.087	0.197
	Rain(m)+wind(m) +feed(m)	4	95.696	1.013	0.603	0.086	0.216
	Wind(m)+feed(m) +kJ.feed^{-1}(m)	4	95.983	1.299	0.522	0.075	0.214
	Temp(e)+wind(m) +feed(m)	4	96.103	1.420	0.492	0.070	0.213
	Temp(m)+wind(m) +kJ.feed^{-1}(m)	4	96.151	1.468	0.480	0.068	0.212
	Temp(m)+wind(m) +kJ(m)	4	96.185	1.501	0.472	0.067	0.212
	Wind(m)+feed(m) +kJ(m)	4	96.270	1.586	0.452	0.065	0.211
	Wind(m)	2	96.371	1.687	0.430	0.061	0.171
	Feed(e)+temp(m) +wind(m)	4	96.394	1.711	0.425	0.061	0.210
	Feed(e)+wind(m) +kJ.feed^{-1}(m)	4	96.426	1.742	0.419	0.060	0.210

Table 8.8 Binomial logistic regression models for Arctic and Common Tern b-chicks. Survival of nestling between the ages of 11 and 20 days (0=died, 1=survived) as dependant variable. Presenting top models as selected by delta-AIC ≤2 ranked in order of AIC. Models in bold are the two highest ranking models according to AIC.

The highest ranking model for Arctic Tern b-chick mortality during the mid-stage of nestling development had the model parameters early-stage temperature and mid-stage

wind speed. Temperature during the early stage had a significant positive relationship with chick survival while wind speed during the mid-stage had a significant negative relationship with chick survival. The second highest ranking model contained the parameters early-stage temperature and energy per feed. Temperature had a significant positive effect on chick survival and energy per feed had an almost significant positive effect on chick survival (p=0.055) (Table 8.9, Figure 8.5).

	Z	p	Coefficients ± SE
AICc: 33.241			
Intercept	-2.192	0.284	-31.517 ± 14.376
Temp(e)	**3.030**	**0.002**	**3.709 ± 1.224**
Wind(m)	**-2.037**	**0.042**	**-0.927 ± 0.455**
AICc: 33.877			
Intercept	-3.277	0.001	-44.989 ± 13.721
Temp(e)	**2.909**	**0.004**	**3.263 ± 1.122**
$kJ.Feed^{-1}$(e)	1.921	0.055	1.697 ± 0.884

Table 8.9 Full binomial regression of the two highest ranked Arctic Tern b-chick mid-stage mortality models (according to AICc)

The highest ranking model for explaining Common Tern b-chick mortality during the mid-stage of nestling development had the parameters mid-stage temperature and wind speed. Temperature had a significant positive relationship and wind speed a significant negative relationship with chick survival. The second highest ranking model had the parameters early-stage provisioning rate and mid-stage wind speed. Wind speed had a significant negative effect on survival and provisioning rate was non-significant (Table 8.10, Figure 8.6).

	Z	p	Coefficients ± SE
AICc: 98.517			
Intercept	-0.009	0.993	-0.040 ±4.494
Temp(m)	1.929	0.054	0.489 ± 0.254
Wind(m)	**-2.832**	**0.005**	**-0.414 ± 0.146**
AICc: 99.240			
Intercept	10.344	<0.001	10.344 ± 2.706
Feed(e)	1.419	0.728	3.855 ± 2.717
Wind(m)	**-3.523**	**<0.001**	**-0.500 ± 0.142**

Table 8.10 Full binomial regression of the two highest ranking Common Tern b-chick mid-stage mortality models (according to AICc)

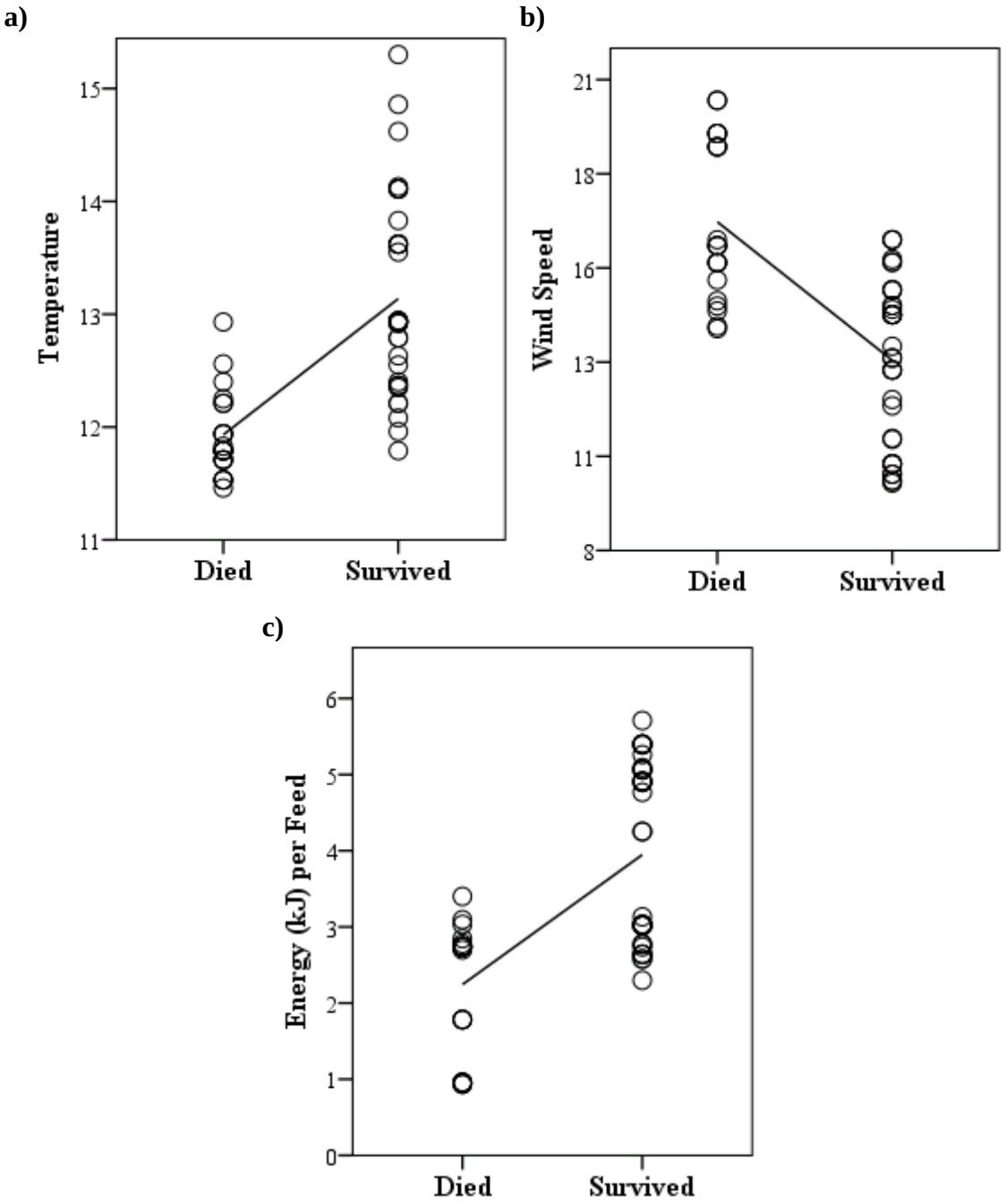


Figure 8.5 Survival of 58 Arctic Tern b-chicks between 11 and 20 days after hatching in relation to **a)** early-stage temperature (°C), **b)** mid-stage wind speed ($km.h^{-1}$), and **c)** early-stage energy per feed ($kJ.feed^{-1}$)

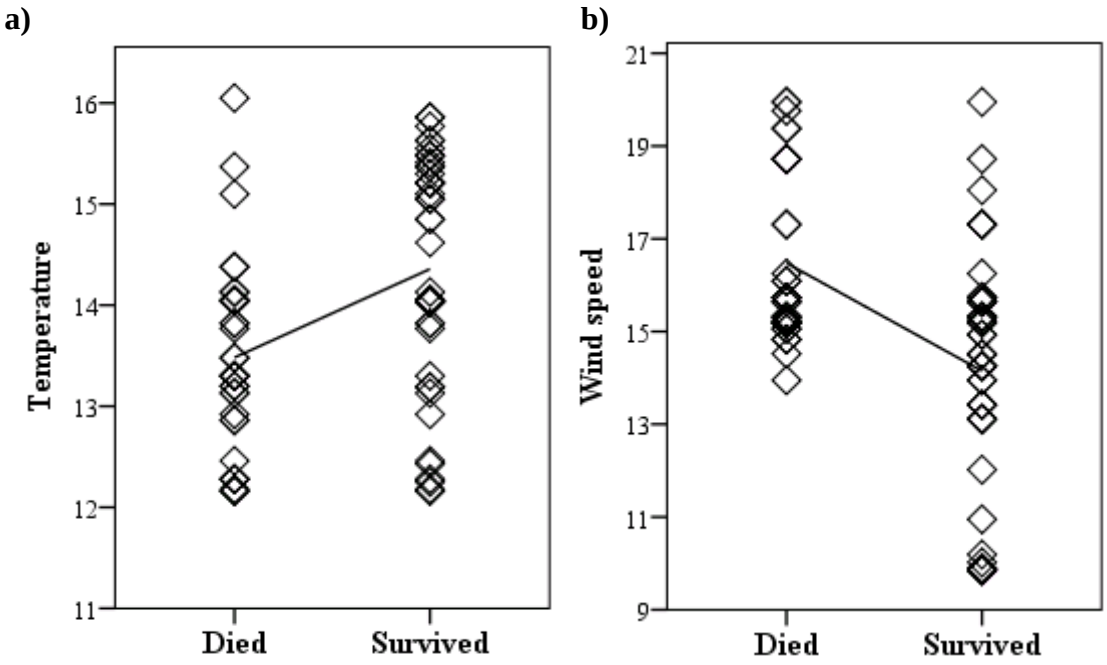


Figure 8.6 Survival of 84 Common Tern b-chicks between 11 and 20 days after hatching in relation to **a)** mid-stage temperature (°C) and **b)** mid-stage wind speed ($km.h^{-1}$)

8.4.4 Late-stage mortality

For Arctic Terns only a-chick sample size and mortality rate was sufficient for analysis using binary logistic regression for survival during late-stage nestling development (days 21 through 30). Chick mortality was the dependant variable (1=survived, 0=died) and temperature, wind speed, rainfall, feed, kJ and $kJ.feed^{-1}$, during early-stage (e), mid-stage (m) and late-stage (l) development, as model predictors. Early-only and mid-only models were run initially and the significant variables in the highest ranking models with $\Delta AIC < 2$ were then used in all combinations with late-stage variables, resulting in 603 models (early-stage variable: wind(e), feed(e); mid-stage variable: kJ(m)). The models were ranked according to AICc with models with $\Delta AIC < 2$ presented in Table 8.11.

Model	Para	AICc	ΔAIC	rel.LL	weights	Dev.
kJ(m)+kJ.feed^{-1}(l)	**3**	**55.737**	**0**	**1**	**0.212**	**0.177**
kJ(l)	**2**	**56.614**	**0.878**	**0.645**	**0.136**	**0.126**
kJ(m)+feed(l)	3	56.650	0.914	0.633	0.134	0.161
Feed(e)+kJ(m)+kJ.feed^{-1}(l)	4	56.686	0.949	0.622	0.132	0.198
kJ(m)+kJ(l)	3	56.979	1.242	0.537	0.114	0.156
kJ(m)+temp(l)+kJ.feed^{-1}(l)	4	57.333	1.596	0.450	0.095	0.187
Feed(e)+kJ(m)+kJ(l)	4	57.334	1.597	0.450	0.095	0.187
kJ(m)+wind(l)+kJ.feed^{-1}(l)	4	57.631	1.895	0.388	0.082	0.182

Table 8.11 Binomial logistic regression models for Arctic Tern a-chicks. Survival of nestling between the ages of 21 and 30 days (0=died, 1=survived). Presenting highest ranking models as selected by delta-AIC ≤2 ranked in order of AIC. Models in bold are the two highest ranking models according to AIC.

The highest ranking model for Arctic Tern a-chick mortality during the final stage of nestling development had the model parameters mid-stage energy delivery rate and late-stage energy per feed. There was a significant negative relationship between survival and mid-stage energy delivery rate and an almost significant positive relationship with late-stage energy per feed (p=0.076). The second highest ranking model had the parameter late-stage energy delivery rate, which had a significant positive relationship with chick survival (Table 8.12, Figure 8.7).

	z	p-value	Coefficients ± SE
AICc: 55.737			
Intercept	2.383	0.017	5.705 ± 2.394
kJ(m)	**-2.210**	**0.027**	**-0.502 ± 0.227**
kJ.feed^{-1}(l)	1.772	0.076	0.243 ± 0.137
AICc: 56.614			
Intercept	1.241	0.215	-1.800 ± 1.450
kJ (l)	**2.446**	**0.015**	**0.460 ± 0.188**

Table 8.12 Full binomial regression of the two highest ranking Arctic Tern a-chick late-stage mortality models (according to AICc)

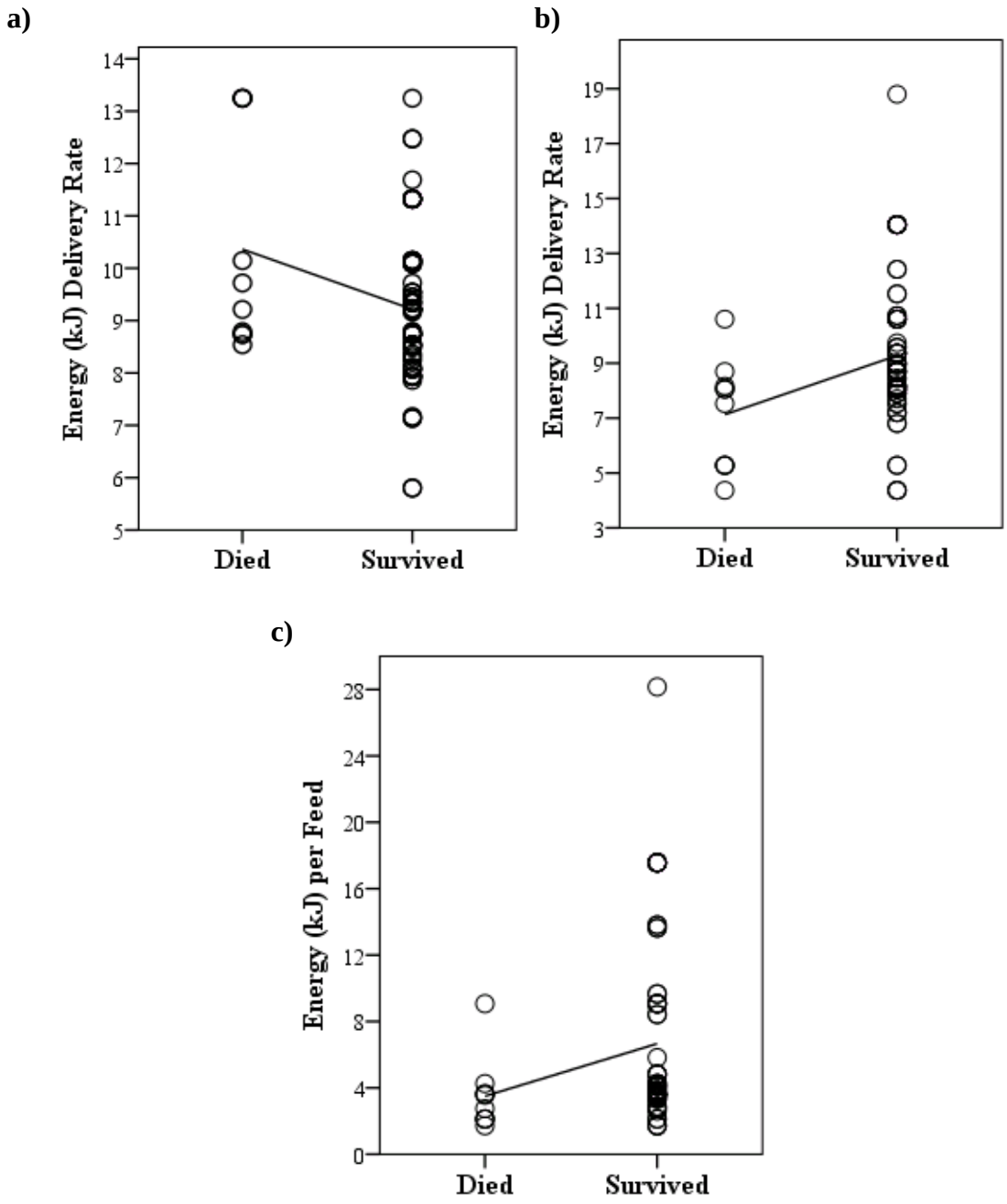


Figure 8.7 Survival of 86 Arctic Tern a-chicks during days 21 to 30 after hatching in relation to **a)** mid-stage energy delivery rate (kJ.chick^{-1}.h^{-1}), **b)** late-stage energy delivery rate and **c)** late-stage energy per feed (kJ.feed^{-1})

8.5 Discussion

Mortality rates were generally higher in the early- and mid-stages of chick development. As expected, a-chick mortality was fairly low throughout development with little variation depending on age, although mortality in chicks aged 11 to 20 days was lower than in the other two age groups. Arctic Tern b-chick mortality was relatively high until

chicks reached the age of 20 days while Common Tern b-chick mortality was highest in chicks aged between 11 and 20 days, with almost all b-chicks surviving to fledging after 20 days of age. Common Tern c-chick mortality was of a similar pattern to Arctic Tern b-chicks but mortality was higher overall, with very few chicks surviving to 20 days.

The low and fairly similar rate of mortality for a-chicks throughout development is not unexpected: these eldest chicks enjoy primary access to food and all the benefits associated with a brood hierarchy (Chapter 4). As one would expect, while the risk of mortality is still present, it declines with age and development.

More significant is the difference between the pattern of mortality in Arctic Tern b-chicks and Common Tern b-chicks and the similarity with c-chicks. Both Arctic b- and Common Tern c-chicks show comparably high mortality between ages 0 to 10 days and 11 to 20 days, unlike Common Tern b-chicks who show a peak in mortality between the ages of 11 and 20 days and almost no mortality once chicks are over 20 days old. It is proposed that this is due to the effects of the brood hierarchy and differences in the breeding ecology of the two species. As was discussed in Chapter 4, the Arctic Tern breeding strategy is to lay two eggs and generally fledge only one chick unless conditions are optimal. In a similar way, when Common Terns lay three eggs they fledge two chicks unless conditions are optimal. In both species, the last chicks may be sacrificed to their older siblings if parents are under pressure to provision larger broods; therefore last chicks are always at risk. Low mortality once they are over the age of 20 days is likely to be either due to older sibling mortality or indicative of a good season and healthy chicks.

The pattern of mortality seen in Common Tern b-chicks is different to that in the other siblings, with the peak in mortality seen in chicks aged between 11 and 20 days. As above, it is proposed that this is due to brood reduction and the ability of Common Tern parents to provision multiple chicks. It is suggested that under normal conditions Common Terns are able to provision both a- and b-chicks adequately when they are young. However, as siblings grow and the energy demand of the brood increases, Common Terns start to come under pressure to provision both siblings. If foraging is poor then this is likely to cause an increase in b-chick mortality.

During the first 10 days after hatching, all chick mortality irrespective of hatching order was affected by a combination of feeding and weather conditions. Wind speed and temperature were present in all of the highest ranking models for chick mortality regardless of hatching order or species. High wind speeds were associated with increased mortality, while temperature, though never a significant variable, showed a negative relationship with chick survival. All models contained at least one feeding parameter, generally with increased provisioning rate per chick, energy per hour or energy per feed resulting in decreased mortality.

The highest ranking Common Tern b-chick models contained a provisioning rate with a negative coefficient. This appears counterintuitive; however, examination of data showed that the 4 chicks that died when feeding conditions were apparently good were all found dead on 30 June 2007 aged between 8 and 10 days. Weather conditions on 29 and 30 of June were stormy, with relatively cold temperatures, high rainfall and gales. It is suggested that these chicks succumbed to the storm despite the good feeding. There was also a negative relationship between Common Tern c-chick (and b-chick, though this was non-significant) survival and energy per feed. Higher energy content suggests larger prey, which younger siblings would have more difficulty handling and from whom it is more likely to be stolen. Larger prey are associated with a lower provisioning rate (Spearman's Rho, Common Tern, n=1570, Rho=-0.088, p=0.001), therefore elder chicks are likely to be hungry by the time food arrives, and to compete aggressively for it with their younger siblings. These factors may explain this relationship.

Food supply appears to be of more significance for younger siblings. One effect of brood hierarchy is a disproportionate allocation of food between siblings; generally, elder siblings have primary access to food and younger chicks receive food only after their elders are satiated or if they are able to out compete them (Braunt & Hunt 1983; Hunt & Evans 1997; Smith et al. 2005). When feeding conditions deteriorate, elder siblings are able to maintain their food intake, at least initially, by taking a larger share of the food brought to the nest. This mitigates the effect on them of reduced supply, but increases its impact on younger chicks, who now receive a smaller share of a reduced supply. For this reason, younger siblings are more reliant on a good rate of provisioning than their elders, and they show high sensitivity to reduced food supply.

While these models clearly show the impact of conditions experienced on chick survival, the deviance explained by the model parameters compared to the null models is low, implying that other factors are present. Attacks on young chicks from neighbouring adult birds were a fairly common occurrence during the study period, with some being sustained and aggressive, especially those on chicks that lacked the mobility to try and escape (personal observation). These attacks, though rarely fatal at the time, may have caused injuries that subsequently proved fatal. Congenital defects and poor parenting are also likely to become more evident with time and could account for some of the mortality observed. The impact of discrete events such as storms can kill chicks regardless of previously prevailing conditions (as was the case for four Common Tern chicks – see above).

Such factors were not taken into account in the models and this is likely to contribute to their low performance. The models are valid for their parameters, but there is clearly a need to consider additional factors. It is also worth noting that only linear relationships were considered in these models while some factors may have a non-linear effect on chick mortality.

Mortality of b-chicks during the middle stage was linked with conditions experienced during that and the early stage (less so for Common Tern than for Arctic Tern chicks). Although not significant in the models, increased energy per feed (Arctic Terns) and increased provisioning rate (Common Terns) during the first 10 days after hatching were associated with increased survival of chicks during the second 10 days. While conditions experienced at the time are of primary importance to chick survival, it is apparent that chicks that have enjoyed good conditions during early development will have a better chance of survival if conditions then deteriorate.

As with early-stage mortality, mid-stage mortality was significantly associated with increased wind speed at the time. Wind speed appears to be particularly important for predicting chick mortality. Higher wind speed has been associated with low growth rate and low mass of chicks (Dunn 1975; Becker & Specht 1991), although whether this is a result of the direct cost of decreased insulation and increased thermoregulation at higher wind speed (Bakken et al. 2002) or of the impact on adult foraging behaviour (Reed & Ha 1983; Taylor 1983; Frank 1992; Veen 1997; Stienen et al. 2000; Garcia & Mariano-Jelicich 2005) is hard to determine. Ritz et al (2005) found that supplementary feeding

of chicks reduced the impact of poor weather, suggesting that restricted food supply is at least partly responsible for low growth. It has been shown here (Chapter 6, Chapter 7) that wind speed did not affect provisioning behaviour of Arctic or Common Terns but that parental attendance at the nest declined. This reduction of potential brooding time would add to the demands of increased wind speed on the chicks' thermoregulation, and therefore heighten the risk of hypothermia. In addition, if chicks were expending more energy on maintaining body temperature but were not receiving more food, an energy deficit would occur. If it this continued over a long period of time it could negatively impact chick growth and weight and increase the risk of mortality. It is therefore suggested that the direct negative impact of higher wind speeds on chick thermoregulation is exacerbated by its impact on parents and the consequent reduced brooding and increased energy expenditure of chicks, and that this combination explains the high association between chick mortality and wind speed.

High ambient temperature appeared to have a negative impact on early-stage chick survival (non-significant but present in top models for both species). This appears counter intuitive as warm temperatures are associated with lower costs of thermoregulation and less risk of hypothermia. However, hyperthermia is also a risk when temperatures are high, especially for unattended non-mobile and featherless or thinly fledged younger chicks unable to take cover in shade (Dawson et al. 1979). Rising temperature is associated with an increase in size of Sandeel and proportion of Clupeid in the diet. These larger and more bulky fish may not be suitable prey for small chicks under 10 days old and could lead to increased losses of prey items due to chicks being unable to handle prey competently or simply being unable to swallow and digest the prey efficiently.

Once chicks were over 10 days of age, the relationship between temperature and survival changed and warmer temperatures had a significant positive effect. Hyperthermia is no longer a great risk as chicks are able to control body temperature (Klassen et al. 1989), and chicks are fully mobile so able to seek shelter in the shade if necessary. Increased ambient temperature is therefore beneficial because of decreased costs of thermoregulation. Larger prey items are no longer a problem for the chicks once they are over 10 days old, and they can benefit from the increased energy content of these fish and so derive an additional benefit from the warm temperatures.

Deviance explained by the top ranking models was high for Arctic Terns (around 64%). It is suggested that Arctic Tern b-chick mortality between 11 and 20 days after hatching is primarily linked with chick fitness and wind condition, with relatively low mortality caused by other factors. The Common Tern model was less robust, explaining only 22% of the deviance. A large number of the Common Tern b-chicks that died between 11 and 20 days after hatching were found dead on 30 June 2007 (12 chicks). As with the younger chicks that died that day, it is felt that these chicks succumbed to the storm and that other factors were not significant in their deaths. Their inclusion reduces the robustness of the model and could account for the low levels of deviance explained.

Common Terns appear to be raising chicks under more favourable conditions than Arctic Terns (Chapter 4, Chapter 5, Chapter 7), and the effect of adverse conditions on their b-chicks may be mitigated by the capacity of parent birds to increase either brooding or foraging effort depending on chick requirements. The low robustness of the model in their regard may therefore be the net result of multiple factors affecting mortality, including others not considered here.

The storm in late June 2007 had a high impact on Common Terns, with 31 chicks dying at the time or in the aftermath, compared to 5 Arctic Tern chicks. Why was the impact so different? The shelter from vegetation was similar in both nesting areas, and the chicks of both species were of similar age ranges. There was, however, a significant difference in the effect of wind direction. The full force of the storm came from the South-East. The Arctic Tern enclosures were sheltered from this quarter by the eastern wall and the lighthouse building. The location of the Common Tern enclosures afforded no such protection for their chicks. It is therefore likely that their greater direct exposure explains why many more Common than Arctic Tern chicks died as a consequence of this storm. This illustrates the need to take into account multiple factors when considering causes of chick mortality.

Late-stage mortality was only analysed for Arctic Tern a-chicks as almost all Common Tern a-chick survived to fledging. The analysis showed that by this stage weather was no longer an important factor, but that feeding conditions remained significant. Feeding conditions throughout development play an important role in chick fitness, and fitness ultimately dictates whether a chick will successfully fledge or not. Here again, the best model only explained 20% of the deviance seen in chick mortality. At this age the birds

are starting to fly, although they still spend most of their time in the nest. Early flight increases the risk of injury, with inexpert flyers damaging themselves against solid objects or when landing (personal observation). At this stage, chicks which sustained injuries when younger or have congenital defects may die or be abandoned by parents.

Weather appears to be an important determinant of success only for younger chicks. The impact of temperature and wind speed changes as a chick develops. By the age of 10 days Tern chicks are capable of full thermoregulation (Klassen 1989), but they are still small, with limited feather covering. Mass has an important effect on thermoregulatory ability, with a positive correlation between increased body mass and index of homeothermy and basal metabolic rate (BMR), and a negative correlation with thermal conductivity and BMR (Klassen & Bech 1992; Visser & Ricklefs 1993; Bakken et al. 2002; Moe et al 2005). The model of Visser and Riclefs (1993) postulated that at a lower temperature a smaller chick would have to increase its BMR significantly more than would a larger chick of a comparable age. From this it can be inferred that during periods of poor weather smaller, younger chicks are more at risk of chilling as they need to expend more energy to keep warm, and so are more likely to show suppressed growth rates and higher mortality. Once chicks are near fledging age, they are fully feathered and capable of thermoregulation at costs similar to those of adults (Klassen et al. 1989). Weather conditions would therefore have low impact on chicks of this age. This explains the impact of adverse weather conditions on younger chicks, an impact that is magnified if feeding conditions are also poor.

Feeding conditions were important throughout development of chicks and had long term impacts on chick survival. The single main cause of mortality among chicks is starvation (Langham 1972; Quillfeldt 2001; Buber et al. 2004). Mortality rates are significantly related to the number of chicks with less than normal body mass (Becker & Specht 1991; Stienen & Brenninkmeijer 2002). Variable chick mortality rates and chick mass have been linked to changes in food abundance and provisioning (Buber et al. 2004; Suddaby & Ratcliffe 1997; Croxall et al. 1999; Suryan et al. 1999). Increased provisioning frequency and energy delivery rate always resulted in increased survival rate (when not considering the chicks killed in the June 2007 storm). However, the energy content of prey is associated with both increased and reduced survival rates. Suryan et al. (1999) found that rate of consumption was more important than quality of individual meals for chicks and that frequent small meals were more beneficial than a

similar energy supply from infrequent large meals. Large prey may be more easily lost or stolen (either by siblings or through kleptoparasitism) or be harder to digest resulting in ‘wasted’ energy, especially when chicks are young. Small prey may not be delivered at a sufficiently high rate to compensate for low energy. It is therefore suggested that when prey size is limited to the two extremes of its range, chick survival declines.

In conclusion, both feeding and weather conditions influence chick survival. Of the weather conditions, wind speed has the highest impact, with high winds during the early- and mid-stages of development being associated with high mortality. Higher temperatures appear to have an adverse impact on chicks during the first stage of development but thereafter increase their chances of survival. High rates of provisioning and energy delivery were important for chick survival throughout development and especially so for younger siblings. Highest mortality was seen in the early- and mid-stages of development. Younger chicks are more vulnerable to adverse weather conditions because of their smaller size, less developed thermoregulatory abilities and the increased cost of thermoregulation.

Younger siblings were more affected by reduced food supply than older siblings because brood hierarchy gave older siblings priority access to food. Unlike feeding conditions, weather ceases to influence chick mortality as chicks near fledging age, though severe storms will always be life-threatening. Ideal chick rearing conditions appear to be characterized by moderate temperatures, no more than moderate wind speeds, and frequent provisioning with moderate sized prey. While it is clear that other factors also influence chick mortality, the conditions experienced throughout the nestling period significantly impact chick survival and future fitness.

Chapter 9. Arctic and Common Tern Breeding Ecology: Causes for Concern?

9.1 Breeding ecology

Arctic Terns laid smaller, less plastic clutches than Common Terns and exhibited a clear modal clutch size of 2, while Common Terns laid similar numbers of 2 and 3 egg clutches. Clutch size is limited by ability to produce eggs (Winkler & Walters 1983) and ability to raise chicks (Lack 1954; Charnov & Krebbs 1974). Maximum clutch size of both species was 3 eggs (with the occasional exception of Common Tern clutches with 4 eggs), indicating that maximum egg production was usually limited to 3 eggs. The plasticity of Common Tern clutch size implies that maternal condition affects whether 2 or 3 eggs are laid. On the other hand, the normal limit of Arctic Tern clutch size to 2 eggs suggests that either incubation costs of the forthcoming chick or provisioning is a constraining factor. As their hatching success did not indicate problems with incubation, it is suggested that Arctic Tern clutch size is limited by ability to raise chicks, with foraging behaviour (see below) restricting the number of chicks that can be provisioned successfully.

Arctic Tern productivity was consistently lower than Common Tern productivity during the study period. Lower productivity in Arctic Terns compared to Common Terns is seen throughout the British Isles (Mavor et al. 2007 but see all reports). While a lower productivity may be expected from a species that lays fewer eggs, what is concerning are the more frequent years of very poor productivity, such as those where fewer 0.5 chicks fledge per pair, and the high number of areas nationally recording complete reproductive failure. This indicates that Arctic Terns are struggling in comparison with Common Terns, possibly due to their foraging behaviour (see 9.2).

Both species hatched chicks asynchronously, resulting in the establishment of a brood hierarchy and differential mortality down the brood. Younger sibling mortality showed high yearly variation, but also declined if an older sibling died. This suggests that both resource-dependant brood reduction and the use of younger siblings as insurance chicks were occurring.

Data also suggested a potential negative impact on the elder siblings if brood reduction failed to occur, with higher rates of mortality observed in a-chicks whose younger siblings survived. However, data can be interpreted as poor elder sibling fitness resulting in decreased ability to outcompete younger siblings and increased likelihood of mortality, thereby allowing for increased b- and c-chick survival. The relationship up the brood hierarchy warrants further experimental investigation in order to understand fully whether younger siblings do negatively impact older sibling survival if they remain in the nest past the critical point when brood energy demands outstrips resource availability or reaches the limits of parental provisioning.

While the onset of brooding with the laying of the first egg puts younger siblings at a disadvantage, female Common Terns do alter the sex ratio of third chicks towards a female bias (e.g. Fletcher & Hamer 2004). Female chicks often show higher survival rates than the males, with female Common Tern chicks showing an 8% increase in fledging success compared to males (Gonzales-Solis et al. 2004). It is proposed that by increasing the survival chances of the youngest sibling, female terns are both increasing the likelihood that the chick will survive to replace an older sibling should one perish and increasing the chick's fledging chance should conditions be favourable for three chicks to be raised to fledging age.

Differences in the degree of asynchrony between siblings was also observed and corresponded with rates of sibling survival (although degree of asynchrony was not found to impact chick survival). The degree of hatching asynchrony was greater between first and second chicks for Arctic Terns than for Common Terns, and Common Terns showed greater asynchrony between second and third chicks than between first and second. Larger hatching asynchrony may facilitate removal of insurance chicks when they are no longer needed by increasing the impact of the brood hierarchy, while smaller hatching asynchrony ensures that in normal conditions younger siblings can compete successfully with their elders.

The breeding ecology of Arctic and Common Terns appears to be fairly distinct. It is suggested that the norm is for Arctic Terns to hatch 2 chicks and fledge 1 unless conditions are good, while Common Terns hatch 2 or 3 chicks and fledge 2 unless conditions are of one extreme or the other. By manipulating the degree of asynchrony

and the sex of younger offspring, adults can increase or decrease the effect of the brood hierarchy and therefore the likelihood of chick survival. A brood hierarchy is valuable for preserving elder sibling fitness and survival. However, by decreasing the age difference or biasing the sex ratio of younger siblings toward female chicks, adults are, to a certain extent, compensating for the disadvantage of being a younger sibling and therefore giving them a better chance of survival should conditions be favourable.

There is a need to study further the way in which hatching asynchrony and sex ratios within the brood impact chick survival both up and down the brood hierarchy. Little information is available on the sex ratios and subsequent survival of Arctic Tern chicks and it would be interesting to see if Arctic Terns bias the sex ratio of second chicks toward female offspring in a similar way to the third chicks in Common Tern broods. Manipulating the hatching asynchrony among first, second and third chicks and investigating the impact on survival throughout the brood would help in the understanding of the impact of asynchrony.

9.2 Provisioning behaviour

Both species provisioned chicks primarily with Sandeel, with Clupeid as the next largest prey group. A decline of Sandeel in the diet usually corresponded with an increase in Clupeid, implying that when availability of main prey is low, birds turn to the next most available prey species. Arctic Terns returned to the nest as a faster rate than Common Terns but brought back a higher proportion of the less energy rich Sandeel, and smaller sizes of both Sandeel and Clupeid. This resulted in a lower rate of energy delivery to the nest despite their higher provisioning rate.

Arctic and Common Terns on Coquet Island have access to the same foraging grounds and prey resources, so differences in their provisioning behaviour indicate differences in foraging strategies. While superficially very similar birds, Arctic Terns are lighter with proportionally larger wingspan than Common Terns (Robinson 2005) and with a lower skull to beak ratio (Brown et al. 1987). It is possible that Arctic Terns are better adapted to foraging on smaller prey than Common Terns, preferentially selecting smaller over larger prey. As their smaller prey yields less energy, Arctic Terns need to forage at higher rate than Common Terns to maintain energy delivery to chicks.

Differences in the provisioning behaviour of these two species have been observed before (Pearson 1968; Lemmetyinen 1976; Chapdelaine et al. 1995; Uttley 1989; Frick & Becker 1995; Robinson et al. 2001) and have been linked to a greater vulnerability of Arctic Terns to change and sub-optimal conditions.

With the on-going development of smaller GPS loggers (which now meet the 5% of body weight limit given by the BTO) research into the specific movements of terns around the breeding colony is already underway and is likely to become an integral part of foraging research. Data collected through loggers will greatly help our understanding of the differences between the two species and will show whether they arise from utilisation of different foraging habitats or from differences in the way they exploit similar habitats. These data will also highlight areas of high importance to foraging birds and hopefully aid in the establishment of Marine Protected Areas and other marine reserves.

Foraging behaviour of both species showed slight variation with the diurnal and tidal cycles. There was a peak in Arctic Tern provisioning in the early morning, but otherwise little diurnal pattern in provisioning and energy delivery was observed. Variation in diet was more marked, with increased presence of the nocturnally active prey in early morning and late evening provisioning, and a corresponding decline in numbers of the diurnal Sandeel.

Tidal patterns in foraging behaviour have been recorded in both species (Dunn 1972; Boecker 1967 in Becker et al. 1997; Frank 1992; Noordhuis & Spaans 1992; Frick & Becker 1993; Steinen et al. 2000; Gonxalez-Solis et al. 2001; Garcia & Jelicich 2005), but here only Arctic Tern provisioning rates changed with the state of the tide, with increased foraging associated with the ebb tide. As the tide line recedes, small fish either migrate out with it or become trapped in pools. It is proposed that this makes them easier targets for Arctic Terns.

The state of the tide did not have a large influence on the diet of either species, although Shrimp were only significant in the diet of Arctic Terns at high tide and Pipefish in that of Common Terns at low tide. Common Terns caught significantly fewer Sandeel at low tide, when it is suggested that they exploit other prey in the Coquet River.

Differences in the impact of the tide on the foraging behaviour of Arctic and Common Terns imply differences in their foraging grounds, and suggest that Arctic Terns may forage closer to the shoreline around Coquet Island or in areas more affected by tidal streams. The use of GPS loggers should show if and how foraging habitat use changes with time and tide.

While much yearly fluctuation in diet was observed over the course of the study, there was a clear decline observed in the proportion of Sandeel brought to the nest by adult birds. Both species, but especially Arctic Terns, are highly reliant on Sandeel for their chicks. A continued decline in Sandeel availability would seriously threaten future reproductive output.

9.3 Adult care of chicks

Adult behaviour changed as the chicks got older. Initially, parental presence at the nest was almost constant, and chicks were provisioned predominantly with small Sandeel. As the chicks grew, parental attendance declined, foraging effort increased and diet included larger prey items and a greater proportion of Clupeid (especially for Common Terns).

Brooding and foraging become mutually exclusive activities once the brood's energy requirements exceed what one parent can meet, and parent birds must make a choice between brooding and foraging depending on need of their chicks. It is likely that chick behaviour influences parental behaviour, with chicks calling to be either brooded or fed depending on the priority need at that time (Evans1994).

The reduction in parental attendance coincided with the increasing thermoregulatory capacity of chicks (Klassen 1989; Montevecchi & Vaughan 1989; Visser & Ricklefs 1993; Klassen 1994; Ostnes et al. 2001; Bakken et al. 2002). Similarly, the increase in foraging effort matched the increasing daily energy needs of growing chicks (Klassen 1989; Massias & Becker 1990; Klassen 1994). Once chicks are capable of thermoregulation at low cost, parental attendance at the nest can be thought of more as time not spent foraging than as time spent actively looking after chicks (Gabrielsen et al.1992; Robinson et al. 2001), and is indicative of foraging conditions.

As the chicks grew, adults met the increased energy demands in part by provisioning at a slightly increased rate but mainly by providing chicks with larger, more energy rich prey items. Less time spent at the nest suggests increased time spent locating suitable prey to match the increased food demands of the chicks.

Both species provisioned 2-chick broods, and Common Terns provisioned 3-chick broods, at a faster rate than 1-chick broods, and energy delivery per chick was generally maintained. This could imply that ability to provision chicks is not a limiting factor on brood size, and that adults can increase foraging effort to maintain provisioning per chick. However the majority of 3 chick broods had lost a chick before the energy demand of 3 chicks would have outstripped that of 2 chicks (Langham 1972).

While both species increased their provisioning effort in response to increased energy demands of the chick or brood, Arctic Terns appeared to be less able to do so than Common Terns. This is most evident when reviewing energy delivery rate to chicks depending on age. Arctic Terns reached maximum energy delivery when chicks were aged between 10 to 14 days, while Common Terns continued to increase energy delivery until chicks were at fledging age. It is proposed that Arctic Tern clutch size is limited by ability to successfully provision chicks, as they lack the capacity to increase foraging effort to maintain energy supply per chick when the energy demands of 3 chicks outstrip those of 2 chicks.

9.4 Impact of weather

Weather had a significant impact on provisioning of both species. Higher ambient temperatures were associated with more energy rich prey (increase in Clupeid and size of Sandeel), thereby increasing energy delivery to chicks. Precipitation had little effect, with only Common Terns showing a slight decrease in the energy delivered to the nest but no effect on provisioning rate, diet or size of prey. Wind speed had no effect on the provisioning behaviour or diet of either species. However, data from parental attendance suggested that adults were investing more time foraging when wind speed increased in an effort to maintain provisioning rate. The cost of thermoregulation increases with wind speed, so it was expected that parents would devote more time to brooding when conditions were windy. Instead, attendance at the nest declined significantly with

increased wind speed, implying that birds were giving priority to foraging notwithstanding the increased need for brooding.

Weather conditions have an effect on the thermoregulation of chicks. Declining ambient temperature results in lower body temperature, even for older chicks although the difference is less. Increasing wind speed results in a large increase in thermal conductivity and a consequent decline in body temperature (Chapple 1979; Bakken et al. 2002). Heat loss increases when down and feathers are exposed to precipitation (Nye 1964; Webb & King 1984; Macafferty et al. 1997). Even if provisioning is maintained under different weather conditions, net energy for growth and development may vary depending on the difference between energy consumed and energy used for thermoregulation.

Weather had little impact on parental attendance at the nest site when chicks were either very young or of almost fledging age, but did impact attendance at nests containing chicks between these ages. When chicks are small, parental attendance needs to be almost constant; weather conditions have little impact on attendance. Once chicks are feathered and fully able to thermoregulate, parental attendance is very low, and normal weather conditions are unlikely to have a significant impact on chick thermoregulation. However, between the ages of 5 to 14 days chicks are developing their ability to thermoregulate and may be left alone at the nest for extended periods, though they still benefit from brooding (Klassen 1989). It is at this age, therefore, that weather conditions are most likely to influence adult attendance at the nest.

9.5 Seasonal differences and their impacts

During the five years of this study, significant yearly variation was seen in Common Tern clutch size and in productivity, and in chick mortality of both species. RSPB data on mean yearly clutch size (1992 through 2010) and productivity (1991 through 2010) were highly correlated between the species, indicating that conditions in the sea around the breeding colony were influencing both species.

Variations in clutch size are associated with maternal condition and conditions at the breeding site at the time of laying (Nisbett 1977; Erikstad et al. 1993; Gonzales-Solis et al. 2004; Gladbach et al. 2010; Descamps et al. 2011). It is proposed that Common

Terns lay 2 or 3 eggs depending on conditions. Although no inter-annual variation was detected for Arctic Terns between 2006 and 2010, the correlation with Common Terns over the longer time frame suggest some effect of year on the number of eggs laid.

Much attention has been focused on conditions during the chick rearing period and subsequent breeding success. If, as suggested, conditions at the breeding site at the time of laying impact number of eggs, then that will in turn affect productivity. If conditions are poor at the time of laying then there are fewer potential fledglings regardless of conditions during the chick rearing period. If conditions are good during laying then females are likely to increase clutch size resulting in more chicks hatching. If conditions remain good then this potentially results in more fledglings. However, if conditions then deteriorate there may be a negative impact on the overall brood fitness if parents are unable to adequately provision larger broods.

Productivity and chick mortality also showed yearly variations. Years of high productivity were associated with low rates of second-hatched chick mortality and vice versa, as expected in brood reducing species. First-hatched chick mortality varied very little between years, with mortality rates remaining low unless the season was particularly poor. First-hatched chicks control primary access to food brought to the nest (Braun & Hunt 1983; Hunt & Evans 1997; Smith et al. 2005) and can react to a decline in provisioning by increasing the proportion of food they consume. When this happens, the impact of food shortages down the brood hierarchy increases. Thus the survival of younger siblings shows greater sensitivity to food shortages than that of their elders in part due to the impact of the brood hierarchy.

Starvation is a common cause of chick mortality (Langham 1972; Quillfeldt 2001; Buber et al. 2004), and yearly differences in foraging conditions can explain differences in productivity and chick survival (Corxall et al. 1999; Buber et al. 2004; Wanless et al. 2005). Low productivity was mainly associated with years of poor quality food, although rate of delivery was also important. The relationship was not always clear, with some apparently ‘good’ provisioning years being associated with poor productivity. However, once parental attendance was taken into consideration it became apparent that years of low productivity were associated with high foraging effort, as implied by low parental attendance, suggesting low availability of prey. It was found that differences in parental attendance between two years of apparently similar

provisioning behaviour can indicate whether adults are foraging to suit chick needs or foraging at maximum capacity to offset low availability of prey.

This study shows clearly the need to consider multiple aspects of a breeding season before drawing conclusions. Feeding conditions do appear to be the main factor impacting productivity but observing provisioning behaviour alone may not provide an accurate picture. Incorporating differences parental attendance gives information on parental pressure to provide for chicks, and examining sibling mortality within the brood allows a better and more rapid understanding of the severity of the situation (e.g. if a-chicks are dying then conditions are very poor).

Changing yearly conditions can also impact recruitment into the population, adult condition, and over-winter adult survival. If conditions are poor during the chick rearing period then fledglings are likely to be of lower mass than those fledging during a good season (Croxall et al. 1999; Suryan et al. 1999; Buber et al. 2004), and low mass at fledging could negatively impact post-fledging survival. In terms of adult survival, raising chicks is costly, with both sexes losing weight as the season progresses (Barret et al. 1985; Monaghan et al. 1989); if conditions are poor then adults are likely to lose more weight than when conditions are favourable (Monaghan et al. 1989). As long lived seabirds, Terns are unlikely to invest in a single breeding season to significant detriment of future ones; therefore if conditions are severe and adult fitness declines to a critical level adults may abandon chicks. Even in non-extreme conditions, adult fitness at the end of the breeding season is likely to impact their chances of surviving the migration. Therefore the impact of a 'bad' season is likely to be far reaching, with lower fledgling survival resulting in lower recruitment and lower adult survival leading to fewer adults returning to breed in subsequent years.

Yearly productivity on Coquet corresponds fairly closely to the patterns seen throughout the British Isles (Mavor et al 2007). This implies that while there may well be localised factors impacting breeding at specific sites, there is an over-arching pattern in breeding success. Thus if conditions continue to decline we are at risk of losing breeding Terns throughout Britain and not just from certain high risk areas.

9.6 Within season chick mortality

Young chicks were susceptible to poor weather conditions. Poor weather conditions are associated with increased costs of thermoregulation and risk of hypothermia (Klassen et al. 1989; Visser & Ricklefs 1993) and low weight gain in chicks (Dunn 1975; Becker & Specht 1991). However, once chicks are large enough to maintain stable body temperature at low energy cost, the direct impact of weather conditions becomes negligible.

Wind speed had the most impact on chick mortality. It has been shown that the impact of high wind speed on chicks is most likely through the energy spent on thermoregulation: both through the direct effect of wind on chicks and through reducing the time adults spend brooding (due to increased time spent foraging), therefore further increasing thermoregulatory costs. As a result, chicks are more susceptible to hyperthermia and are expending more energy on thermoregulation but unlikely to be receiving more food to compensate. Wind can therefore cause mortality directly (hypothermia) or reduce chick fitness, making them more vulnerable to future hardships.

It should be noted that analysis did not look at interactions between different weather phenomena. It is likely that interaction would increase the negative effects. For example, while precipitation on its own had no effect on chick mortality, if combined with high winds it is likely to magnify the effect of wind on chicks' thermoregulatory cost by reducing the insulation effect of feathers. As was seen in 2007 with the high chick mortality due to a single storm event, the combination of cold, wind and rain can be deadly however fit chicks are before exposure.

As expected, feeding conditions influenced chick mortality throughout development, with an increased impact on second-hatched. Increased provisioning rate was associated with increased survival, but the quality of prey brought back to the nest was also important. It is suggested that parent birds may not have the capacity to increase foraging effort sufficiently to compensate for low energy prey. Higher survival rates were seen in chicks which experienced better conditions during early development, indicating that a good start increases capacity to overcome later hardship.

This analysis provided very valuable information about the factors effecting chick mortality. Of particular interest was the long term effect of conditions experienced early in development. This is important when considering post-fledging mortality and recruitment back into the breeding population. Others have shown that chicks raised under poor feeding conditions fledge at a lower mass than those raised under good conditions (Osterblom et al. 2001; Weimerskich et al. 2001). How long do the negative impacts of poor conditions last and how do they impact post fledging survival?

This also shows the importance of the timing of events. While provisioning needs to remain good throughout development, the impact of poor weather declines as chicks develop. Unfortunately there were insufficient data for analysis of late stage mortality in any chick other than Arctic Tern a-chicks, although this in its self suggests that once chicks have survived past 20 days then the risks of mortality are significantly reduced.

Analyses from this chapter also support the conclusions proposed in Chapter 4 with regard to the effect of the brood hierarchy and the roles siblings play within the brood. A-chick mortality is fairly low and constant throughout development, as expected for the elder sibling in a brood hierarchy. The younger siblings show higher rates of mortality and a larger dependence on feeding conditions, as expected in a brood reducing species. The similarity between Arctic Tern b- and Common Tern c-chicks supports the theory that these siblings have a similar purpose within the brood and that they are fairly frequently removed from the brood when feeding rates decline.

9.7 Causes for concern

Both species are vulnerable to adverse changes in prey populations and in weather conditions. If there is a decline in prey abundance, availability or quality, then this will impact reproductive output for the season and have long term impacts on recruitment and even adult survival. The observed decline of Sandeel in the diet throughout the five years of the study is of special concern due to the high reliance of both species, but especially of Arctic Terns, on Sandeels for chick provisioning. Both species' chicks showed sensitivity to weather conditions, with a significant link between windy conditions and high chick mortality. While temperature and precipitation did not greatly affect chick survival, severe storms were linked with high mortality whatever the

previous conditions. If climate change continues to cause increases in the frequency and severity of summer storms, then its impact on chick mortality is likely to increase.

All data suggest that while both species are vulnerable to changing conditions during the breeding season, Arctic Terns appear to be especially sensitive and show greatly reduced reproductive output when conditions are sub-optimal. Provisioning behaviour linked with parental nest attendance implies that Arctic Terns are investing a higher level of effort in foraging than Common Terns but do not provide their chicks with as much energy. The low nest attendance seen in Arctic Terns implies that they are already foraging at, or close to, maximum capacity and are therefore unable to increase foraging effort should prey availability decline.

Why the difference in sensitivity between the two species? While there is significant overlap in the breeding ranges of Arctic and Common Tern, on Coquet Island Arctic Terns are around the southern limit of their geographic breeding range while Common Terns are in the middle (Hagmeijer & Blaire 1997). It is possible that Arctic Tern breeding strategy is better suited to more northerly climes, with adults struggling to raise chicks successfully at the limits of their breeding range. If this is the case and climate change continues to increase SSTs then we are likely to see a northerly contraction of the Arctic Tern breeding range as southerly breeding colonies become increasingly unsustainable. However, this does not explain why some of the highest rates of breeding failure are seen in the Northerly colonies on the Shetlands and Orkneys.

Instead, it is suggested that the differences in the foraging behaviour of the two species account for the increased sensitivity of Arctic Terns to prey abundance. If Arctic Terns are indeed limited by the size and type of prey they prefer (see 9.2) then they will be much more vulnerable to any changes in the stocks, be it overall availability or distribution of age classes. Common Terns appear to be much more able or willing to adapt their prey choices in response to availability. In addition, their lower foraging rate means they are better able to increase foraging effort than Arctic Terns (who appear to be already foraging at or near maximum capacity). These two factors mean that the Common Tern is much better able to cope with changes in the availability or type of prey available than the Arctic Tern, although both are vulnerable when prey is scarce.

Arctic and Common Terns are fairly long lived species with multiple breeding seasons and a few poor or failed breeding seasons should not greatly impact population size. If, however, reproductive output remains low, then population size will decrease as there will be insufficient new recruits to offset adult deaths. We are already recording a decline in tern breeding populations around the UK, and both species are classified 'amber' in terms of conservation concern within the UK. The Seabird Monitoring Programme combined data from Operation Seafarer (1969-1970), the Seabird Colony Register (1985-1988) and Seabird 2000 (1998-2002) with data from sample colonies in 2000-2011 to estimate the changes in the population index of seabirds breeding in the UK. Both Arctic and Common Terns showed decline in breeding population numbers since 1969 (JNCC 2012). Almost more concerning is that since 1969, of the eight inshore surface-feeding seabird species regularly breeding in the UK, six have declined (only the Black-Headed Gull and Little Tern have increased, the latter probably as a result of extensive conservation efforts). UK breeding seabird populations as a whole have declined by 9% in the last decade, suggesting large scale and widespread decline in the breeding conditions around the British Isles.

9.8 Using breeding ecology to monitor change

Breeding success and chick provisioning behaviour are often used to measure the quality of a season and changes between seasons. Listed below are seven indicators which can be used to gauge different aspects of a breeding season and help to highlight areas of concern.

1) **Clutch size:** a good indicator of conditions at the time of laying but not a good predictor of the outcome of a season.

2) **Productivity:** gives an accurate overview of whether a season was successful or not in terms of reproductive output.

3) **Percentage mortality:** likely to be less accurate than productivity as influenced by clutch size, therefore years with relatively high percentage mortality may still maintain productivity.

4) **Mortality of siblings:** high mortality of a-chicks is a good indicator that the season is especially poor, while b-chick survival is sensitive to less extreme fluctuations in food supply so can be used to gauge the quality of a season. Easily monitored throughout the season therefore can highlight when conditions have changed, and the impact of events such as storms.

5) **Provisioning behaviour:** while provisioning rate can be a good indicator of what feeding conditions are like at sea, it does not show the whole picture. There is a need to incorporate information about the quality of prey and level of parental foraging effort before sound conclusions can be drawn.

6) **Parental attendance:** a very useful, simple and sensitive tool for gauging the level of pressure adults are under when provisioning their chicks. Especially useful when comparing years with similar provisioning rates but different productivity. Parental attendance also provides an immediate warning that conditions have changed, without the time delay seen between conditions deteriorating and chicks dying.

7) **Chick biometrics:** not used in this study but show how conditions are affecting chick fitness.

While individually each of these tools provides information about a breeding season, it is only when using several in combination that one can begin to understand how and why a season progressed as it did, and be able to draw conclusions about how and why conditions impacted breeding success as they did. Such combined data sets allow changes to be monitored more accurately across breeding seasons, highlighting trends and giving better identification of any aberrant years.

Little is as yet known about the impact of climate change on the marine environment and weather patterns, and there is an urgent need to increase our understanding of the impact of these changes on marine animals. Seabirds provide an accurate and sensitive bio monitor of the marine environment. Their study provides valuable information on the changes occurring throughout the marine environment, and may help highlight areas of particular concern.

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