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**Prey selection, foraging effort and breeding
performance of Arctic (*Sterna paradisaea*)
and Common (*Sterna hirundo*) Terns**

Wylie Horn

University of Glasgow

1995

Candidate's Declaration

I declare that the work recorded in this thesis is entirely my own unless otherwise stated. No part of this work has been submitted for any other degree.

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Chapter 1 Introduction

1. Introduction

1.1 Why study seabirds and their prey?

Scientific studies of seabirds are of intrinsic interest in that they further our understanding of the natural world. In addition, with some seabird species, there are important conservation issues that need to be addressed. Furthermore, seabirds are potentially very useful indicators of the health of the marine environment and can provide important information that would otherwise be very difficult to obtain due to logistic and financial constraints.

The UK contains internationally important concentrations of breeding seabirds. Breeding failures amongst Arctic terns *Sterna paradisaea* from 1984 until 1990 in one of their most important breeding grounds in Shetland caused widespread concern. Shetland previously held 40% of the British breeding population of Arctic terns (Thomas 1982). Of all seabirds, terns are the most constrained in their time and energy budgets during the breeding season. They are restricted to the inshore area, normally bring only one prey item to the nest at a time, and they have very short foraging ranges (Pearson, 1968). Various studies have shown that they are temporally tightly constrained during the breeding season as a consequence of these and other factors (see Uttley, 1991 for a review). This makes them an ideal species to study due to their particular sensitivity to changes in prey abundance. This issue was identified as one of the most important conservation issues in the UK at that time. The cause of the decline in the breeding success of the Shetland colonies was the decreased availability of lesser sandeels *Ammodytes marinus* during these years.

The Shetland situation highlighted our lack of understanding of the relationship between marine birds such as terns and their fish prey populations. It has also highlighted the need to study the way in which terns exploit fish prey in areas where food supply is currently good, such as Coquet Island, in order that the effects of changes in fish stock, and in the pattern of exploitation of fish by man, on seabird populations can be predicted.

1.2 What are the costs to adults of chick rearing ?

In order to understand how seabirds provide useful information on the marine environment, we need to understand how they respond to changing environmental conditions. This requires an understanding of their life history strategies. The focus of attention is generally on their breeding strategies since it is really only during the breeding season, when birds are tied to land-based colonies, that they can easily be intensively studied. In monogamous birds, mutual participation in chick rearing is typical (Lack 1968). Evolutionary theory predicts that both participants in a monogamous pair aim to maximise lifetime reproductive success. Each individual investment can be seen in terms of fitness costs and benefits (Burger 1987). Any current benefits of increased reproductive success will be countered by the costs of achieving them. In long-lived birds such as terns life-history theory predicts that there will be upper limits to the reproductive effort that they are willing to make in a single season and the pattern may differ between males and females (Goodman 1974). Allocation of the investments is divided between courtship and display, the production of eggs, incubation, chick brooding, chick provisioning and nest defence. Differences between the sexes in the extent of parental care over the course of the breeding season may occur (Wiggins and Morris 1987). The costs may vary according to prevailing environmental conditions, food supply, predation risk, and brood size. These "costs" may have several consequences resulting from variation in the age of onset of breeding, time of breeding, clutch size, hatching success, chick growth and chick survival and fledging success (Uttley 1991).

1.3 Are seabirds good indicators of fish stocks?

Several authors have drawn attention to the usefulness of seabirds as indicators of changes in the marine environment (Furness & Ainley, 1984; Cairns, 1987; Monaghan *et al.*, 1989). Indeed seabirds have been used for some very specific monitoring tasks (e.g. Watanuki *et al.*, 1993). A close correlation between fish stock abundance near breeding colonies and seabird breeding numbers and success has been identified by several authors (Safina, Burger, Gochfeld & Wagner 1988; Monaghan, Uttley & Okill 1989a). This close correlation may give an early indication of changes to fish stocks (Monaghan and Zonfrillo, 1986). As mentioned above, species such as terns which have short foraging ranges and spend a greater proportion of time foraging during the breeding season than larger seabirds (Pearson, 1968) are particularly likely to be sensitive to changes in prey abundance. This is particularly the case where the range of prey items is limited (Uttley 1991). Where two closely related species are breeding in close proximity and utilising the same fish stocks they may respond differently to differing food availability, giving different indices of fish stocks and availability (Uttley 1991). A highly significant correlation exists between the recruitment of 0-group sandeels *Ammodytes marinus* estimated on 1st July each year and the number of Arctic tern *Sterna paradisaea* chicks ringed in the same year in Shetland (Monaghan *et al.* 1989a). Similarly, elegant tern *Sterna elegans* breeding productivity was strongly correlated with anchovy *Anchovetta anchovetta* abundance for 1979 to 1983 in colonies in California (Schaffner 1986). More subtle changes may be detected through monitoring of fish brought in to the breeding colonies. In colonies in northern Norway in a period when the supply of capelin *Mallotus villasus* was depleted, seabirds caught a higher proportion of sandeels than initially anticipated. This study also postulated the existence of a previously unknown stock of capelin which the seabirds in the study area were exploiting (Barrett and Furness 1990). The recent improvement in the breeding performance of Arctic terns in Shetland reflects an improvement in the availability of sandeels.

However, seabirds may have different dietary preferences which may alter for example in relation to changing chick requirements, or where more than one prey species is available. Consequently for normally synchronously laying species such as Arctic terns an experimental approach is required to

study dietary changes. This enables the provisioning of chicks of different ages to be studied at the same time, and chicks of the same age to be studied at different times.

1.4 The need to conserve fish stocks around seabird colonies

Where seabirds are feeding upon fish of species and size for which there is also a commercial fishery direct competition for the same resource may occur (Furness 1982). Declines in commercially fished species for whatever reason have had an effect on the diets of seabirds (Montevecchi et al 1988; Monaghan et al 1989b). Where alternative prey are not available this may have a serious deleterious effect upon breeding productivity, as evidenced by the very poor breeding performance of Arctic terns in Shetland from 1984– 1990, that was a consequence of a decline in the availability of lesser sandeels of a size normally utilised by breeding terns. The Shetland situation highlights a more general problem of paucity of data on key prey requirements for breeding seabirds. Lack of data on seabird breeding success and fish stock abundance in previous periods has been problematical for researchers studying declines in breeding success.

1.5 Aims of this study

Previous studies of breeding terns have found temporal variation in prey selection by adults provisioning their chicks (Uttley 1991). This may have been a consequence of changes in prey availability or may have been the outcome of selection by foraging adults of energetically more profitable prey. Studies in Shetland during the 1980s highlighted the importance of fish within particular size classes to breeding Arctic terns. In years when sandeels of a particular size were scarce breeding failure occurred. This work was carried out in a situation where the prey spectrum was limited to the lesser sandeel. To further investigate these findings this project had several aims listed below.

1. To examine the diet and foraging behaviour of Arctic and common terns *Sterna hirundo* in a situation where a broader spectrum of prey was available.
2. To examine, by both observational and experimental studies, changes in the diet of Arctic and common tern chicks in relation to age and to investigate whether these are a consequence of changes in prey availability, prey profitability, or are a consequence of changing chick requirements.
3. To investigate the relationships among foraging profitability, brood size, adult body weight and breeding success in male and female terns.
4. To investigate differences between the foraging strategies of Arctic and common terns
5. To study variation in the growth of Arctic and common tern chicks in relation to brood size and year.
6. To investigate breeding success in relation to the status of the pair bond.

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Chapter 2 Methods

2 Methods

Data used in the following chapters were collected using similar methods. To avoid unnecessary repetition of methodology the major methods are set out here. Where methods, or statistical techniques are specific to a particular chapter details are recorded in the methods section of the appropriate chapter.

Arctic and common terns are ground-nesting colonial breeders. This makes the collection of data on breeding chronology, egg and clutch size, and chick measurements relatively easy. Where nesting density is sufficient, data on foraging effort and chick provisioning may be gathered by watching breeding pairs from a hide.

2.1 Study site

Coquet Island is a small island off the north-east coast of England ($55^{\circ} 37' N, 1^{\circ} 32' W$), Terns re-colonised the island in 1958, after an absence of seventy-six years. Further historical details of use of the island as a breeding colony by terns may be found in Langham (1967).

There have been marked changes in the composition of the vegetational communities on the island within the last 35 years. Currently the island is dominated by Yorkshire fog, *Holcus mollis*, stinging nettle, *Urtica dioica*, and bugloss, *Lycopsis arvensis*. The island has been an RSPB nature reserve since the late 1960's, and the RSPB actively manages the island, primarily by controlling the numbers of breeding pairs of herring *Larus argentatus* and lesser black-backed *Larus fuscus* gulls with a culling programme. The RSPB also has a policy of strimming areas of thick vegetation and spraying these with herbicide in an attempt to maintain suitable nesting areas for breeding Arctic and common terns. Consequently a proportion of nests of both species are in positions where they are readily visible from a hide.

In the six year period before this study began numbers of breeding pairs of Arctic terns fluctuated between 450 and 560 on Coquet island. Numbers of breeding common terns varied from 525–730 pairs during the same period (Unpublished RSPB reports). The island is considered to be of national importance for its particularly diverse community of breeding seabirds, and is especially noted for its population of breeding Roseate terns *Sterna dougallii*. Numbers of breeding pairs of

this species have increased steadily from 18 pairs in 1985 to 30 pairs in 1994. In addition Sandwich terns *Sterna sandvicensis* regularly breed on the island with a breeding population of between 1000 and 1500 pairs. Other notable species are black-headed gulls *Larus ridibundus*, with a breeding population of 2–3,000 pairs, an estimated 9,000 pairs of puffins *Fratercula arctica*, and 300 pairs of Eiders *Somateria mollissima*. The island has recently been colonised by kittiwakes *Rissa tridactyla* with 12 pairs attempting to nest in 1991 (Unpublished RSPB reports).

There are no ground predators on the island. The resident population of rabbits *Oryctolagus cuniculus* fluctuates in size as a consequence of infrequent but recurrent outbreaks of myxomatosis. The rabbits have a small detrimental effect on the reproductive success of terns, as they supplement their calcium intake by nibbling off the wings and legs of young tern chicks. During the two years of this study the main predators of tern eggs and chicks were black-headed gulls (see later chapters for details).

The lighthouse on Coquet Island was automated in 1990. It had previously been manned. Any nest found within the lighthouse compound by Trinity lighthouse staff had previously been removed for safety reasons. The concern was that nesting terns might block the air intakes on incoming jet-engined helicopters. The removal of this human interference affected the distribution of nest sites within the study plot in 1991, and particularly in 1992.

Arctic terns were studied during the breeding season from mid-April to early August in 1991 and 1992. This period encompassed the courtship, egg incubation and chick rearing periods of the breeding cycle. Common terns were also studied in 1992 during this period, but in 1991 they were studied during the courtship and incubation periods only. The area had previously been used from 1987–89 for monitoring of breeding performance of Arctic terns on Coquet island for comparison with birds from colonies in Orkney and Shetland, which were experiencing greatly reduced breeding success at that time (Monaghan *et al.*, 1989). In 1991 this area was found to be reasonably clear of vegetation early in the breeding season and was again selected as the main Arctic tern study plot. RSPB wardens had strimmed the area and sprayed it prior to the arrival of breeding terns in late April. The following year there was a reduction in the number of pairs nesting in the study plot as pairs translocated to the lighthouse compound. However, sufficient numbers remained within the plot and so the same plot was retained. Forty-two birds which had been colour-ringed in

1991 returned to the study plot in 1992, and 26 of these birds bred. This enabled a direct inter-year comparison of prey selection, breeding performance, pair and nest site fidelity, using paired data. In both years subsidiary plots were established in order to increase the sample of data on the timing of breeding, breeding performance, and chick growth were collected.

There was no equivalent research conducted on breeding success of common terns in the late 1980s on Coquet. Consequently there was no established study plot for this species. A site which had been strimmed and sprayed by the RSPB on a regular basis for several years was selected as a study site for its combination of good visibility of the nests and the density of nesting pairs it contained. A number of adult common terns were trapped in 1991. For similar reasons to those listed above I decided to use the same main study plot in 1992 for common terns.

Subsidiary plots were established for common terns also.

Uttley (1991) listed various important criteria to consider in the choice of tern study plots: topography, drainage, vegetation, exposure, the abundance and density of nesting terns, likely age and breeding experience of terns and predator pressure. Although the same study plots were chosen in both years for the reasons listed above, other possible study areas on the island were regularly monitored during the pre-laying period. This was necessary due to the unpredictable nature of nest site establishment by terns where pre-laying birds move from area to area before finally settling on one nest site. Had insufficient breeding pairs become established in the main study plots it would have been possible to move to one of these other plots.

The study plots were required to have a sufficient number of visible, active nests to enable accurate recording of the prey selection and foraging effort of adult birds. In total, 77 and 36 pairs of Arctic terns nested within the study plot in 1991 and 1992 respectively. In total, 53 and 40 pairs nested within the common tern study plot in 1991 and 1992 respectively. Of these 48 and 21 nests were used for collecting data on foraging economics for Arctic terns in 1991 and 1992 respectively. In all, 25 and 40 common tern nests were watched in 1991 and 1992. A sub-sample of between 10 and 15 nests were observed during watches. Only nests that were no more than 30 metres from the hide were used in recording details of prey selection and foraging effort. All common tern nests studied in both years were no more than 14 metres from the hide. Nests which were further than 30 metres from the hide were too distant to accurately identify prey items brought to the nest.

One factor which detrimentally affected visibility in the study plots later in the season was the growth of vegetation within the study colony, especially Bugloss which was the dominant plant within the Arctic tern study plot, while Yorkshire fog was the dominant plant within the common tern study plot. Early in the season both these plants were short and close to the ground. Visibility of the chosen nests was unaffected. Later the growth of these plants obscured the view of events at these nests. Where necessary lines of sight were created by pruning vegetation with garden shears. Only the minimum amount necessary to ensure visibility was cut and as much of the natural vegetation cover as possible was left standing to ensure that nests did not become unnaturally visible to black-headed gulls which were the main aerial predators. In 1992 this process was augmented by an additional pre-season strimming of the Arctic and common tern study plots.

2.2 Study species

Arctic and common terns breed in temperate areas and have a limited period in which to breed before deteriorating weather, changes in daylength (leading to a reduction in the daylight hours available for foraging), and changes in food availability necessitate departure for their wintering quarters (Cramp and Simmons, 1985). Species such as terns which have short foraging ranges and which spend a greater proportion of time foraging during the breeding season than larger seabirds (Pearson, 1968) are particularly likely to be sensitive to changes in prey abundance. Furthermore as they are long-lived and iteroparous, and often return to the same breeding colonies in consecutive years they make an ideal study species to use in examining reproductive costs and how these may affect reproductive success and pair and site fidelity.

2.3 Marking and sexing individuals

Several elements of this study required having individually recognisable birds, particularly to distinguish members of each pair. Both Arctic and common terns show little if any sexual dimorphism. This means it is generally not possible to distinguish individual members of a pair without some artificial means of marking at least one bird. Occasionally a plumage, or physiognomic, aberration enabled me to distinguish one member of a pair from the other. However,

in most cases it was necessary to mark birds with picric acid. This dye bonds to protein molecules within the feather and does not fade on contact with either salt-water or sunlight. It is lost at the marked birds' next moult.

Birds were dye marked using Picric acid: Small squares of flat sponge were cut into regular squares 3cm x 3cm in size. These were soaked in a solution of picric acid dissolved in absolute alcohol and placed on the edge of the nest scrape. Birds which I attempted to mark would either settle quickly back onto the nest and the sponge, or else they would show reticence in returning to incubate their clutch, and eventually pick up the soaked sponge in their bill, fly off with it and drop it in vegetation nearby, before re-settling on the nest. With perseverance the majority of birds were marked successfully. After a bird was marked, the sponge was removed and any sand in the nest scrape which had absorbed the dye was covered with fresh sand to prevent inadvertent marking of the marked bird's partner after a changeover. Careful notes were taken of the position of picric marks on the plumage, especially in the limited number of cases where two birds in a pair were marked inadvertently. Blue sponge, which appeared green when soaked with the dye, has been found to be the colour of sponge which birds were least likely to remove from the nest (Uttley 1991, this study).

There was no evidence that eggs which were in contact with picric acid suffered any reduced hatching success. However care was taken to minimise contact between eggs and picric acid as picric is toxic, and eggshell is porous. Sitting birds shift position in response to changes in wind direction (Skipnes 1983, Uttley, 1991). When birds changed over incubation duties and sat in the same orientation in relation to the wind they would have been similarly marked had I not removed the sponge to avoid this. This ensured that both birds were not similarly marked. The majority of birds were marked using these methods.

Picric marks alone made identification difficult as marks were localised on the belly, flanks, and the leading edge of the wings of marked birds. These areas were not always readily visible from the hide. In the second year of the study picric marks were augmented, on birds which had been trapped for weighing, with white tippex marks on the crown of their heads. These faded over the chick rearing period but sufficient white flecking remained visible on the crown of the marked birds to enable individuals in a pair to be distinguished throughout. Colour rings placed on Arctic terns in

1991 aided identification of birds in 1992. Additionally birds were marked on the mantle, and upper breast, with more picric acid when they were trapped for weighing. Birds were marked as soon as laying began. Birds were sexed on the basis of observations of both courtship feeding, which continued for several days after laying, and of copulation. Reverse courtship feeding was seen during the chick rearing period but never during the courtship phase in either year of the study.

2.4 Assessment of hatching, fledging, and breeding success

In 1991 a hide was put in position during the courtship phase of breeding. During the second year of the study it was put in place prior to the return of breeding terns in late April. Birds were observed from the hide using 8x30 binoculars from the courtship phase until the chicks fledged. Terns may commence incubation immediately after laying the first egg in a clutch, and this was readily apparent from their behaviour. Brief daily checks of nests not clearly visible from the hide ensured newly laid eggs were not missed. The position of nests was marked in both years by bamboo canes with numbered colour flags attached. When the first egg was laid nests were checked daily. Nests were checked for fresh eggs for 10 days after the last egg was laid. Eggs were marked "A", "B", or "C" with indelible marker ink according to laying sequence, and weighed with a 50 g Salter spring balance to the nearest 0.5g. Length and breadth of the eggs were measured using Vernier callipers to the nearest 0.1 mm. The balance was calibrated regularly using a calibration weight. Egg volume was calculated using the formula: Volume =

Nests were checked every 2–3 days throughout incubation to monitor egg loss. I attempted to restrict visits to the colony to once per day, and to as short a period as practicable. In practice this meant visits to the colony were restricted to 15 minutes during incubation. Visits of 30 minutes were necessary to weigh and measure chicks during chick rearing. Visits were never made either to check nests nor to weigh and measure eggs during rainy or excessively windy periods.

Groups of nests were observed throughout incubation, with each nest being watched at least every other day. Early in the incubation period, birds would occasionally leave eggs unattended for several hours. Only those nests where eggs were unattended for several days in succession were classified as deserted.

Hatching success was calculated for each nest as the number of eggs hatched per clutch. Fledging success was calculated as the number of chicks that reached twenty days old per hatched egg within the clutch. Breeding success was calculated as the number of chicks that reached twenty days old per nest.

Arctic and common tern chicks are semi-precocial and several days after hatching they are able to move from the nest scrape and seek cover to avoid aerial predators. In a situation such as that found within the study plots on Coquet, where vegetation becomes tall and lush by the time the chicks hatch, it would have been extremely difficult and very disruptive to the colony as a whole to relocate chicks for repeat weighing and measuring. Any attempt to do so would, in all likelihood, have led to an increase in chick mortality through increased risk of hypothermia for chicks which have wandered and could not be relocated by their parents, and thus could not have been brooded. An additional risk to wandering chicks was of attack by other adult terns within the colony when chicks inadvertently wandered into their nesting territory. These attacks may be fatal (pers obs.). Another substantial problem was that chicks may not have been relocated at all. The ultimate fate of such chicks would thus have been unknown. Consequently any data collected on fledging success would have been inaccurate.

For these reasons it was necessary to use chicken wire nest surrounds. These have been used successfully in previous studies of terns (Uttley 1991). Individual nests were surrounded with 13 mm gauge chicken wire. This was small enough to prevent chicks becoming trapped and injured. An area of at least 4 m² was enclosed by the wire. Whenever possible some natural cover was retained within the enclosed area for chicks to hide in and shelter under. If there was no natural cover within the enclosure an artificial shelter made of stone, brick and/or wood or a halved drainage pipe was placed within its confines. Enclosures were placed around nests during the latter half of the second week of incubation to allow adults to become habituated to them. The majority of adults quickly did so. In several cases adults appeared confused by the barrier and attempted to get to the nest by walking through it. However even these birds eventually learned to fly in to the nest scrape.

At 18 days after the first egg had been laid nests were checked daily for newly hatched chicks or evidence that hatching had begun. Notes were taken on which eggs were "starred" (showing small cracks in the eggshell) or "pipping" (egg tooth showing through the eggshell) as

these eggs would hatch within the next few days. In both years the average incubation period for both species was 22 days. Chicks were weighed as soon as possible after hatching, but not if they were still wet from the egg. These chicks were weighed on the following day to reduce any possible detrimental effects of chilling. Chicks were marked with colour coded leg flags attached to the tarsus in such a way as to allow its unrestricted growth. This enabled repeat measurements of the same individuals to be made. Chicks were ringed at 16–18 days old with BTO metal rings. Chicks were weighed and measured every 2 or 3 days. Weight was taken using 50g and 200g "Salter" spring balances, which were regularly calibrated using calibration weights. They were weighed to the nearest gram. Maximum chord length was measured using a stopped metal rule to the nearest mm. Chord length was measured to the tip of the growing feather not including the downy tip of the wing. The presence or absence of chicks within the enclosures was recorded as 'found', 'not found', 'dead', or 'not checked' during these measuring bouts. These data supported by observations from the hides enabled an accurate record of chick survival to be maintained.

2.5 Measuring foraging parameters

Terns normally carry single prey items for their chicks horizontally in their bill. With practice these can be identified to species level and, size estimated in relation to head and bill length. The relative ease of identification and measurement of fish make bio-energetic modelling of reproductive effort much simpler than for species of sea bird which carry prey back to their offspring in the crop and regurgitate it at the nest site.

Sandeels, sprats *Sprattus sprattus*, and rockling *Cilia mustela* all have distinctive body forms and with practice could be readily distinguished in the parents bill. Individual items were recorded as sandeel, sprat/clupeid, rockling, shrimp etc. Rockling were only specifically recognised as a constituent of Arctic tern chick diet during the latter stages of the 1991 breeding season. Where fish were obviously not sandeels, but could not be specifically identified, they were classified simply as non-sandeels. Fish size was estimated in relation to bill, and head and bill, length of Arctic and common terns and placed into one of four size categories (0–4 cm, 4–8 cm, 8–12 cm, and >12 cm). The 0–4 cm 'needle' sandeels are easily distinguished from small 4–8 cm group sandeels by their

translucent and very thin appearance. On the few occasions where more than one prey item was brought to the nest the sizes of both prey items were recorded. During 1992 when two observers were involved, regular comparisons of their size class estimates were made to ensure data was comparable. This was done by using fish that were dropped by incoming terns. These were collected and measured and a sample of these same fish were held by the tail by one observer at set distances (5–35 metres) from the other observer. This person was not informed of the actual length of the fish, and made an estimate of its length. The two measures of fish length were then compared.

Foraging rate was recorded by noting the number of arrivals and departures that an individual bird made within a given watch period. Watch periods varied from 1 hour 30 minutes to four hours, and were distributed through all daylight hours from 4 a.m. to 10 p.m. in both years. Watches were randomised in an attempt to ensure that different periods of the day were adequately represented in the data set. For each arrival at the nest site the following information was recorded: watch date; watch period; watch duration; time of arrival; time of departure; prey type; prey size; presentation number; prey fate (fed to chick, eaten by self, kleptoparasitised, taken away, unknown add to this list if necessary); time to fate ; time present; nest status (courtship, incubation, 1 chick, 2 chick, 3 chick , failed, unknown); bird mark status(marked, unmarked, female, male, unknown).

I followed the approach used by Pearson (1968), Uttley (1991), and others in using time away from the nest as an approximation of foraging trip duration. It was not possible to record other activities such as preening, bathing, or roosting away from the colony, but if one assumes that these activities occupy a standard proportion of a tern's activity budget, using time away from the nest seems a reasonable compromise measure of foraging trip duration.

2.6 The need for an experimental approach in studying provisioning of tern chicks.

Colonial breeding Arctic and common terns generally lay their eggs synchronously. Previous studies on Coquet island have demonstrated that in certain years Arctic terns feed their young on sandeels during the first week of chick life, then subsequently on sprats (Monaghan *et*

al., 1989 Unpublished RSPB reports, Langham, 1967). It is necessary in determining prey selection criteria to distinguish between date effects, which may result from differences in prey availability, from chick age effects which may be indicative of preferential selection by the adult terns. In order to investigate whether this switch was a consequence of prey availability or whether the Arctic terns were selecting as a consequence of prey suitability, I delayed the hatching of a sub-sample of eggs for up to one week. These eggs were stored for up to seven days under controlled conditions before they were replaced in the same scrapes they came from.

Both age and accumulated breeding experience are known to affect the breeding performance of sea-birds. In general young birds have been found to lay later, lay smaller clutches, and have lower hatching and fledging success than older birds. To ensure that birds selected for egg storage experiments were of similar quality to other control birds I attempted to ensure that birds were selected from the period of peak laying. However, in 1991 this was not possible for Arctic terns due to a prolonged and asynchronous laying period (27 days). As a sample of nests had to be left unmanipulated to enable study of foraging effort, and as egg storage was an untried technique for terns, I erred on the side of caution and left the first 20 pairs which laid eggs unmanipulated. Only after these sites were established were clutches from subsequent pairs taken into storage. In total, eight Arctic tern clutches were taken into storage in 1991. Only these clutches were laid in scrapes which were visible from the hide. Although this gave rise to problems of pseudoreplication this was unavoidable. If eggs had been taken from the first sites and stored eggs had subsequently been found to be unviable I would have been left with no nests with which to observe details of chick provisioning. Furthermore I also wanted to wait for later birds which may have been more representative of the colony as a whole. Numbers nesting within the Arctic tern study plot were much higher in previous years. This also led me to expect more birds to lay in the later period. This did not happen and hence I was left with the sample size listed above for my experimental group in the first year of the study. The unexpectedly low numbers of Arctic terns nesting within the study plot in 1991 led to the decision to restrict the egg storage experiments to common terns in 1992. Thirteen common tern clutches were taken into storage in 1992. Observing common terns during the chick rearing period had the additional benefit of allowing inter-specific comparisons of breeding performance, prey selection, and foraging economics.

2.7 Egg storage techniques

Eggs were taken from nest scrapes as soon after they had been laid as possible. Dummy eggs made of modelling clay and painted to resemble tern eggs were placed in the nest scrapes at the same time. No egg was removed from the nest more than twenty-four hours after it had been laid. Eggs were marked with their nest number and laying sequence using a marker pen. They were placed immediately into re-sealable polythene bags. These were placed in an insulated polystyrene box and surrounded with cotton wool and taken to the storage container. This was an egg tray inside a gas-powered refrigerator. The bags containing the eggs were placed on this tray. Care was taken to ensure that the eggs stood in a vertical orientation. The fridge acted as a controlled temperature chamber. Temperature was recorded at six-eight hourly intervals and never fell outside the ideal range previously stated. Eggs were turned daily to mimic egg rolling by incubating adults within the nest scrape. After the storage period was complete eggs were returned to the scrapes from which they had been taken and dummy eggs removed at the same time. No terns deserted as a consequence of this procedure. Details of numbers of terns in the control and experimental groups are given in chapter 6.

2.8 Measurement of adult masses

During both field seasons, remotely operated weighing balances (See Monaghan *et al.*, 1989 for technical details) were used to obtain masses of free-living adult terns. In 1991 only weights of Arctic terns were obtained using these balances. In 1992 weights of common terns were also obtained using the electronic balances. The biometrics and weight of Arctic terns caught in nest-traps for colour-ringing were recorded in 1991. These weights were added to the data set of weights obtained from the electronic balances. Unfortunately during 1992 the remote weighing system suffered technical failure and I had to rely solely on nest-trapping to obtain records of the adult Arctic and common tern mass.

During the egg storage experiment I attempted to weigh adults from the control and experimental groups at the end of their respective incubation periods and when their chicks were

between 14 and 18 days old. This was done to assess whether the extra days of incubation resultant from eggs being placed in storage led to a decline in body weight. Change in body mass was used as an indicator of body condition. Where body measurements of the same bird were obtained body mass was corrected for body size.

2.9 Statistical analyses

Analyses were performed using procedures described in Sokal and Rohlf (1981), Noru.is (1990), and Siegel and Castellan (1988).

All tests of significance were made using two-tailed test statistics. Means are given \pm standard error. Medians are given \pm the semi-inter-quartile range or \pm the inter-quartile range. Where box plots are used the dark line represents the median, the box outline the inter-quartile range, and the upper and lower bars the range.

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Chapter 3 Factors affecting maintenance of the pair bond in Arctic terns

3.1 Introduction

In this chapter I use data collected during two field seasons to examine annual survival rate in Arctic terns. This was not one of the original aims of this study but as some adult Arctic terns were colour-ringed in 1991 a limited analysis was possible. The selective advantages of high annual survival to Arctic terns are discussed in relation to the spatial and temporal variation in the ambit (Hunt and Schneider, 1987) in which they exist. Haury *et al.* (1978) defined ambits as "the sphere of action of individuals over days, weeks, lifetimes". Possible explanations for the high proportion of non-breeding adults in 1992 are presented.

Data were collected on the identity of birds within a pair in both field seasons. Breeding success was compared using paired data to assess what effect breeding success in the previous year had upon re-appearance at the colony, breeding success in the following year, and on pair fidelity. The effect of pair fidelity, or its absence, upon laying date, clutch size, hatching success, and fledging success was examined to assess the relative benefits of remaining with the same partner or divorcing. The growth rate of chicks which fledged from nests with changed and unchanged parents were compared with the colony average growth rates of chicks which fledged in 1991 and 1992. Growth rate of the chicks was used as a proximate measure of parental provisioning ability, whilst recognising the limitations of this approach discussed later.

Nest site position was mapped in both years to investigate the role that nest site fidelity might have in maintenance of the pair bond.

3.1.2 What are the implications of high annual adult survival?

Seabirds generally have high annual adult survival, whilst annual reproductive output is low (Furness and Monaghan, 1987). Various authors have attempted to relate this K-selected life history pattern to variability in several ecological parameters, especially food supply, and adult/juvenile survival probability. However other aspects of the environment such as nest site availability, and social

constraints may have a profound effect upon seabird life histories in general and upon annual survival in particular.

In a stimulating paper Ricklefs (1990) attempted to relate seabird life histories to characteristics of the marine environment and ways in which seabirds exploit marine resources. In particular Ricklefs argued that certain aspects of life history theory are inadequate explanations for known facts of seabird biology. He stressed the need for an understanding of the interplay between population demography, the environment, and adaptation in interpreting seabird life histories. Furthermore in examining pelagic seabird life histories the point was stressed that long life and low reproductive rate, whilst undoubtedly reflecting characteristics of the marine environment, are not unique to seabirds. The occurrence of low mortality outwith the breeding season may favour modification of effort in a particular breeding attempt in order to maximise the total number of breeding attempts. Although this generalisation referred to pelagic seabirds particularly they seem appropriate for other long-lived seabirds such as terns.

A related issue is the age at which seabirds first make a breeding attempt. If birds have matured to the extent that they are capable of breeding and do not do so an explanation for this phenomenon is required. The costs of attempting to breed before the necessary foraging skills have been developed may be so great as to preclude early breeding (Ricklefs, 1990). Spatio-temporal variation in food resources over several geographical scales over periods similar to the adolescent periods of seabirds may necessitate a learning period during which prospective breeders gain the necessary knowledge to reduce foraging costs to a level which enables breeding to commence. For example Ollason and Dunnet (1978) found that in Fulmars, birds which bred for the first time at six years of age had higher subsequent mortality rates and hence a reduced lifetime reproductive success in relation to birds that bred for the first time at nine years old.

It is likely that fluctuations in the marine environment play a key role in shaping seabird life histories. Both delayed age at first breeding and high adult annual survival may be explained by the selective advantages these life history attributes give seabirds in ensuring sufficient lifetime reproductive success in response to stochastic variations due to climate, oceanographic processes over several scales, and food supply.

3.1.3 Factors affecting pair fidelity

Where breeding individuals vary in quality there may be a selective advantage in mate choice (Trivers, 1972). Quality is an often used but poorly defined parameter. Halliday (1983) defined quality as : " a variety of properties of individual animals, including resources that they actually or potentially hold, their abilities as parents and their genotypes". Furthermore he listed several criteria for mate choice which would produce fitness benefits. These were:

1. Choice for high fecundity or fertility
2. Choice for immediate gains and parental abilities
3. Choice for resources and for high male status
4. Choice for mate complementarity
5. Choice for good physical condition

However, mate choice may have costs as well as benefits (Halliday, 1983). The prospective breeding bird must find a compromise between the costs of finding a high quality mate, and possibly missing out on the opportunity of breeding, with the benefits a high quality mate would bring. However the time investment involved in mate choice may be constrained especially for palearctic and Arctic breeding species such as Arctic and common terns which, due to their long range migrations and the short period when climatic and foraging conditions are suitable, have a restricted temporal opportunity for breeding. Indeed it has been suggested that the costs of assessing the genotype of prospective mates may be so high that an individual may do better to choose a mate at random (Halliday, 1983). Where breeding organisms return annually to the same breeding sites these search costs may be reduced as both partners return to the same nest site and/or breeding area.

These factors may in turn be affected by age and accumulated breeding experience. This leads to the related issue of maintenance of the pair bond, and what selective advantages keeping the same partner for several breeding seasons may have.

For long-lived iteroparous species such as seabirds, which have the potential for several reproductive attempts, complementarity of partners may assume particular importance. Coulson found that partners within pairs of kittiwakes had individual incubation schedules of 1,2,3 or 4 hours. Pairs which did not exhibit complementarity in incubation period suffered reduced hatching success.

Furthermore pairs which remained together over two seasons tended to show enhanced breeding success as a consequence of their accumulated breeding experiences (Coulson 1980).

3.1.4 Definitions of re-pairing

It is important to distinguish between perennial and seasonal pair bonds. Species which have high annual survival rates such as seabirds may exercise choice both seasonally and perennially. Throughout this chapter I have used the conventions defined by Rowley (1983). Under this scheme re-pairing after the death or disappearance of a partner is termed mate-replacement. Pairs which do not re-unite are said to have divorced. The divorce rate is calculated as the percentage of pairs that survived between any two years who do not re-unite. Individual birds which divorce may either re-mate or remain solitary.

3.1.5 Existing data on pair fidelity in birds

Data are scant and mainly restricted to seabirds. Many long-lived iteroparous breeding seabirds exhibit site fidelity to the nesting colony once established as breeders. This, allied to the fact that some seabirds nest in dense, easily accessible colonies, explains their predominance in studies of pair fidelity. The following discussion makes the assumption that the individuals in a pair do not arrive back at the colony at the same time. Presumably for pairs which re-unite the benefits of re-pairing with the same partner outweigh the potential cost of missing a breeding opportunity if its partner does not re-appear. Such data as there are suggest that old established pairs produce more young than new ones (Rowley, 1983). The success of pairs in the previous breeding season may also affect mate choice in the current breeding attempt. For example Coulson (1966) found that kittiwakes that had failed in their breeding attempt in the previous year were more likely to divorce.

The age of birds within a partnership may be particularly important (Coulson & Horobin, 1976). These age-related advantages are presumably related to physiological and behavioural characters associated with age (Rowley, 1983). Of particular importance in this respect is the advantage age brings to birds such as seabirds which live in an environment that is subject to fluctuations on several temporal and spatial scales. Birds which have accumulated experience of the different breeding, foraging, and migratory conditions that arise as a consequence of these

fluctuations may be at an advantage over younger breeders that have as yet not experienced these varied conditions. Established pairs may have the advantage over younger competitors (Rowley, 1983). Established pairs may achieve better nesting sites (Rowley, 1983). The considerable time saving gained by mating with a previously known partner may also be of considerable importance.

3.1.6 Mechanisms of maintenance of the pair bond

There are a number of possible selective advantages to re-uniting with the same partner. Rowley (1983) lists factors which assist re-uniting. These are :

1.

a. The courtship investment.

Presumably there is some cost in seeking out a known partner from a range of potential partners. Parker (1983) has suggested that where this cost is high it may pay a bird to mate at random rather than miss out on breeding at all. However life history theory would predict modifications to this hypothesis as birds would trade-off current investment with future benefits which might accrue from remaining with the same partner.

b. Increased egg size with age.

Egg size has been found to increase with age for several species. Although there may also be seasonal effects on the quality of the egg, and hence the resources available to the chick during development, it is generally accepted that egg size reflects the resources available to the chick. Ultimately this has an important bearing on chick survival.

c. Clutch size varying with age in several species of seabird (Coulson, 1972, Mills, 1973).

Older birds may lay larger clutches at least until a period of reproductive senescence sets in with extreme old age. As members of a pair become older it may pay them to remain with the same partner for the maintenance of consistently high reproductive success, determined in part by clutch size.

d. Earlier laying date with increasing age or experience.

In gannets *Sula bassana*, for example, age and persistence of the pair bond affect laying date (Nelson, 1966). Laying date is earlier in the season with increasing age and longevity of the pair bond (Nelson, 1978). Early laying may be important to colonially breeding seabirds for several

reasons. Climatic and foraging conditions may only be suitable for breeding for a limited period. In late season the re-establishment of stratification in the water column leads to a decline in mixing in the water column. This in turn causes a decline in productivity, and hence a decline in the available prey. Early breeders may find better nest sites and may be of higher quality (Wooller and Coulson, 1977). Late layers may be out of synchrony with the majority of the colony increasing the predation risk to these birds (Ryder, 1980).

e. Foraging efficiency

Dunn (1972) found that young Sandwich terns were less efficient foragers than older birds. The status of female nutrition prior to egg formation, and its importance to the size of the eggs and clutch, is well documented (Perrins, 1970). Rowley (1983) suggests that it is the increased foraging efficiency of the older females which enables them to lay down the necessary reserves for egg formation sooner and consequently lay their eggs earlier.

f. Hatching success

Hatching success may improve with age due to increased fertility for physiological or behavioural reasons. As birds in a pair grow older they may become more experienced at mating leading to increased viability of the resultant eggs (Rowley, 1983). Improved incubation technique with increased age has been recorded for the gannet (Nelson, 1966).

g. Chick rearing

Both chick weight at fledging and fledging success may improve with increased age of the parents (Ainley and Schlatter, 1972, Ryder, 1980).

2. Quality of nest sites

In some seabirds sites in the centre of the breeding colony tend to be more productive. Pairs may gradually attain more favourable sites within the colony with increasing age (Coulson, 1972; Coulson and Deans, 1980). Sites in the centre of a kittiwake colony studied by Coulson (1972) for 25 years were more productive. Pairs at the centre of this colony also suffered a lower rate of divorce than those on the edge. Consequently maintenance of the pair bond may lead to a better nest site.

3. Familiarity of partners

Individuals which are already paired at the beginning of the breeding season or which pair up with their previous partners soon after arrival at the breeding colony are therefore likely to be at a distinct advantage compared to individuals which may incur a time cost seeking a partner.

All of these individual components of reproductive success may be enhanced through maintenance of the pair bond synergistically.

3.1.7 Reasons for failure to re-unite.

Rowley (1983) lists two reasons why it is not always practical or possible for birds to re-unite: longevity and life style. Where a bird has an annual survival probability of 0.85, the probability of two birds returning to the breeding colony is only 0.72. Obviously the lower the annual survival rate, the lower will be the probability that both birds in a pair survive. In species with relatively low annual survival the benefits of breeding with a known partner may be outweighed by the costs of waiting for a dead mate to return. Even for species such as terns which have high annual adult survival the costs of waiting may assist in explaining why some birds swap partners even when their partner eventually turns up.

Rowley (1983) designates gulls into a category he defines as site faithful opportunists meaning that they roam widely post breeding season in search of good feeding conditions and return to a traditional nest site during the breeding season. Mortality and divorce rate may be higher amongst nomads or migrants than species which remain in the same area throughout their life. Another interesting hypothesis that Rowley proposes is that the constancy of the pair bond in albatrosses may be the consequence of the long period that these species spend "Keeping company" before breeding. He suggests that during this period birds assess the quality of prospective partners and change partners frequently. Young Adélie penguins *Pygoscelis adeliae* split and divorce more frequently than older birds (Le Resche and Sladen, 1970). First breeding attempts are functionally an extension of the keeping company period and may explain some of the splitting and divorcing that is observed.

The majority of experimental evidence accumulated to date suggests that reproductive success is greatest where birds re-mate with the bird they successfully bred with in the previous year, but the ease with which this re-mating is done varies from species to species. Natural

selection does not favour pair fidelity for those species which suffer high annual adult mortality. For longer lived birds such as seabirds the evidence is contradictory, with no discernible pattern being apparent in divorce rates amongst species with seemingly similar ecology. Coulson (1966) found that in kittiwakes re-mating was linked to breeding success in the previous breeding season. A similar effect on re-mating was found in Manx shearwaters *Puffinus puffinus* (Brooke, 1978). No such trend was found in a study of little penguins *Eudyptula minor* (Reilly and Cullen, 1981). It may be that the timing of breeding failure is an important determinant of whether a bird re-pairs or not. If the nesting attempt fails at the egg stage it may be that the absence of further reinforcement of the pair bond as a consequence of rearing a brood of chicks may weaken it and make re-pairing more likely. Rowley (1983) suggests that it is this rather than a specific assessment of breeding capacity which achieves a re-sorting of partners. Divorce may be a result of birds trying to re-mate, thus a bird may be successful in one year but may still change partners in a subsequent year if it assesses the new partner to be of higher quality than its previous partner. Finally, Rowley suggests that the consequence of these hypotheses is that the major part of the addition to any population is from a relatively few successful pairs. These pairs achieve this status over several years during which they may : " (1) re-sort partners until compatibility is attained, (2) improve their breeding performance by experience, and (3) enhance their breeding opportunities by achieving better nest sites". Within any one species the relative importance of these three factors will vary.

3.2 Methods

3.2.1 General

A total of 49 breeding Arctic terns, representing 20 pairs, 2 triplets and 6 individual members of pairs, were trapped on the nest in 1991 using hinged lid traps which fitted on top of the chicken wire enclosures which surrounded individual nests. No birds abandoned incubation or chick rearing as a result of being caught. Appearance or non-appearance of these individuals at the colony in 1992 was recorded. This enabled a minimum survival estimate to be calculated for the year 1991 to 1992, assuming that terns which did not return to the colony had died. Individual colour ring combinations enabled identification of 1991 pairs which remained the same in 1992 and those pairs which changed

partners. Data on the egg dimensions, clutch volumes, hatching success, and breeding success of both groups were recorded. The relative breeding success of the two groups was compared.

Only 8 birds of known age were trapped at the nest during the two field seasons of this study. No analysis of age related correlations in pairing was possible. Seven of the known age birds had been ringed as chicks on the Farne islands. The other was ringed as a chick on Coquet island. These birds ranged in age from 5 years old to 28 years old. The 28 year old individual was a member of a pair which successfully reared one chick in 1991. 3 birds greater than 20 years old bred in 1991. A further three birds ranging in age from 13 – 17 years old also made breeding attempts. The longevity of these breeding birds accentuates the need for studies on a much longer time scale than this one.

3.2.2 Foraging rate/Chick growth

It was not possible to watch the same pairs in both years due to the differing position of nest sites. Consequently an inter-year comparison of the foraging rate of changed and unchanged pairs and an examination of the spectrum of prey fed to their chicks was not possible. However chick growth data were collected for all nests within this sample where chicks hatched in either year. These data were used to test the hypothesis that changing partner might affect chick growth. Chick growth is likely to be proximately related to the prey selection and provisioning rate of the parents. Growth rates were calculated for all chicks which fledged and for chick ages between 0 and 20 days old for a sample of 33 nests (40 chicks) in 1991 and 51 nests (55 chicks) in 1992 using forced entry linear regression (Noru.is SPSS 1992) with chick age as the forced independent variable. Individual growth rates for nests within the two categories were calculated using the same technique. Where two chicks fledged from the same nest, individual growth rates were calculated and an average taken. Per nest growth rates were compared with the colony average growth rate .

3.3 Results

3.3.1 Annual adult survival

Of the 49 adults trapped in 1991, 42 were seen on at least one occasion around the study plot from 11th May to 19th July in 1992. The assumption was made that non-attendance at the colony in 1992 was equivalent to the death of that bird. This gave an annual adult survival rate of 85.7%. This did not differ significantly from the average adult survival rate of $86.7 \pm 2.0\%$ which Coulson and Horobin (1976) found for Arctic terns in the Farne islands between 1965 and 1967 ($\chi^2_1=0.002$, $P>0.05$, $n_{\text{Farne}} = 218$, $n_{\text{Coquet}} = 49$).

Whether or not an Arctic tern which made a breeding attempt in 1991 fledged a chick in 1991 had no statistically significant effect upon whether it re-appeared in 1992 (Table 3.1, Fisher's Exact test two-tailed = 0.51 or upon whether it bred in 1992 (Fisher's Exact test two-tail = 1.0, Table 3.2). 49 adults were colour ringed in 1991. However data on fledging success were only available for 47 of these.

Table 3.1 The effect of Arctic tern fledging success in 1991 on re-appearance at the colony in 1992

	Absent 1992	Present 1992
Did not fledge a chick in 1991	1	4
Fledged at least one chick in 1991	5	37

Table 3.2 The effect of Arctic tern 1991 fledging success upon breeding attempts in 1992

	Did not breed 1992	Bred 1992
Did not fledge a chick in 1991	1	3
Fledged at least one chick in 1991	12	25

3.3.2 Pair fidelity and divorce

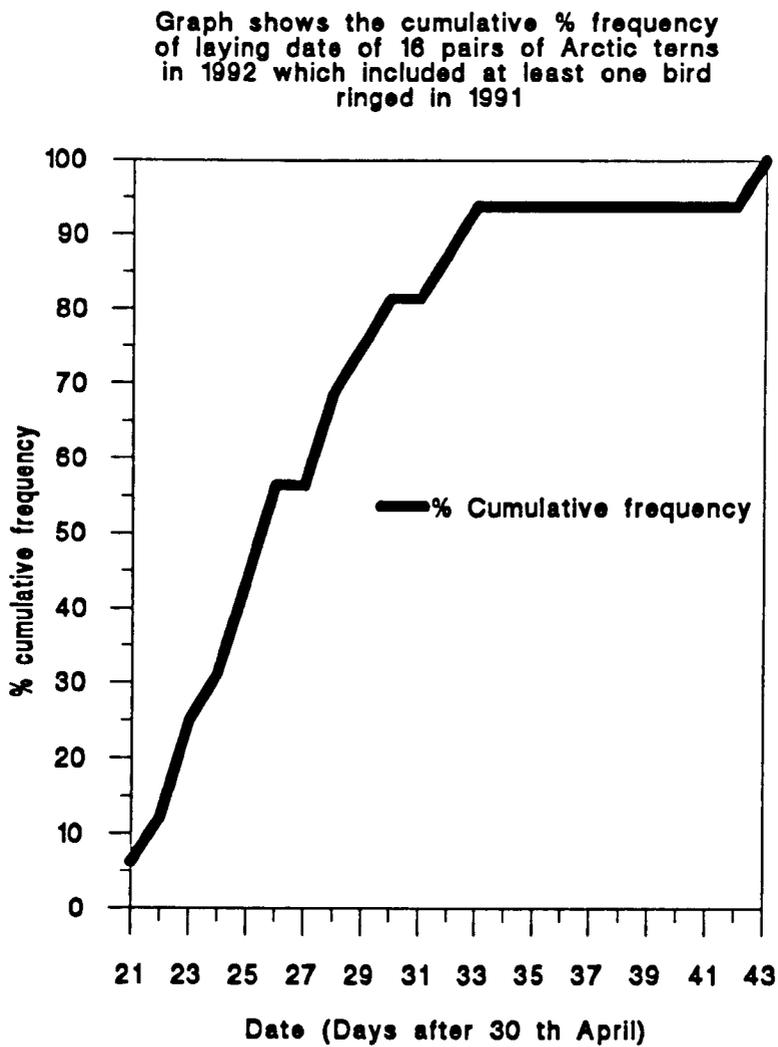
Whether a bird fledged at least one chick in 1991 had no effect upon whether a bird changed partners that year (Table 3.3, Fisher's Exact test two-tail = 0.692, $n_{\text{pairs 1992}} = 13$), but the sample size of pairs is very small.

Table 3.3 The effect of Arctic tern 1991 fledging success upon pair fidelity in 1992

	Unchanged pairs 1992	Changed pairs 1992
Fledged at least one chick in 1991	8	4
Fledged no chicks in 1991	1	0

Of the 42 returning adults, 26 made breeding attempts. Systematic searches of the study colony failed to find any evidence of breeding attempts by the remaining 16 returning birds. These birds were seen at regular intervals throughout the breeding season around the study plot. Regular but non-systematic searches of other areas on the island where these individuals could conceivably have been breeding failed to find any evidence of breeding attempts. Figure 3.1 shows a cumulative frequency of laying dates for the 26 birds which made a breeding attempt. The 16 birds that did not breed were seen around the colony on dates after 100% of those birds which were proven to have

Figure 3.1 Cumulative frequency of laying date of the Arctic terns ringed in 1991 that were proven to have made a breeding attempt in 1992 (number of birds=26)



bred had laid clutches. It seems likely that at least the majority of these birds did not make a breeding attempt in 1992. This represents a non-breeding proportion of 38.1% of the population.

3.3.2.1 Effect of mate change upon breeding success

There was no significant difference in clutch size in 1991 and 1992 for the eight pairs which did not change partners between years (Wilcoxon matched pairs signed ranks test, two-tailed $z = -1.34$, $P = 0.18$, $n_{\text{pairs}} = 8$). All pairs within the colony nested earlier in 1992 than in 1991 (*see chapter 5*). This was reflected also in the earlier laying date of unchanged pairs in 1992 (Wilcoxon matched pairs signed ranks test, two-tailed $z = -1.96$, $P = 0.05$). Neither hatching success nor fledging success between the two years varied for this group (Hatching success: Wilcoxon matched pairs signed ranks test, two-tailed, $z = -1.10$, $P = 0.27$; Fledging success: Wilcoxon matched pairs signed ranks test, two-tailed, $z = -1.60$, $P = 0.11$).

Clutch size did not vary significantly for pairs which changed partner in 1992 (Wilcoxon matched pairs signed ranks test, two-tailed, $z = 0$, $P = 1.00$). All six pairs which included at least one bird which had changed partner nested earlier in 1992 (Wilcoxon matched pairs signed ranks, two-tailed, $z = -2.2$, $P < 0.03$). As for the unchanged pairs, this reflected the earlier nesting trend in the rest of the colony in 1992. There were no significant inter-year differences in either hatching success, or in fledging success (Wilcoxon matched pairs signed ranks test, two-tailed, hatching success $z = -1.34$, $P = 0.18$; fledging success, $z = -0.91$, $P = 0.36$).

The pair changes between 1991 and 1992 are shown below (Table 3.4).

Table 3.4 Details of Arctic tern pair changes in 1992

Bird identity		1991 nest number	1991 partner	1992 partner		Nest number in 1991 of 1992 partner	1992 nest number
Left leg	Right leg			Left leg	Right leg		
ST DB	BTO	43 male	Absent	LG ST	BTO	73	9
WH LB	BTO	53 female	Present not proven to breed	Unringed	Unringed	Unknown	8
BTO	ST WH	55 unknown sex	Present not proven to breed	BTO	ST LG	70	12
BTO	ST LG	70 unknown sex	Bred x unringed nest 13	BTO	ST WH	55	12
BTO	DG WH	70 unknown sex	Bred x BTO ST WH Nest 55	Unringed	Unringed	Unknown	13
LG ST	BTO	73 unknown sex	Present not proven to breed	ST DB	BTO	43	9

Where birds changed partners to individuals of known 1991 identity (4 cases) they did so with individuals which had been members of pairs which bred at sites (43,73,55,70) close to their 1992 partner's 1991 nest site. Pairs 55 and 70 swapped partners in 1992. One of each pair from nest 43₁₉₉₁ and nest 73₁₉₉₁ bred together. These nests were 2 and 2.25 metres apart respectively in 1991.

3.4 Chick growth rate

In neither year were the differences in growth rates of chicks reared by adults who changed partners significantly different from the differences from the colonial average growth rate or growth rates of

chicks reared by parents who remained with the same partner. (1991 median difference in chick growth rate of changed partners = 0.19, $n=5_{\text{pairs}}$; median difference in chick growth rate of unchanged pairs = 0.257, $n=7_{\text{pairs}}$; 1992 median difference in growth rate from changed partners = 0.128, $n=4_{\text{pairs}}$; median difference in growth rate of unchanged pairs = 0.3219, $n=6_{\text{pairs}}$ 1991 Mann-Whitney U test $U = 15$, $P>0.05$; 1992 Mann-Whitney U test $U = 11$, $P>0.05$).

3.5 1992 Pairing data for Arctic terns colour-ringed in 1991

Data collected in 1992 are shown in Table 3.5 below.

Table 3.5 1992 pairing data for 49 adult Arctic terns ringed during summer 1991. The legend below outlines the various categories which the code numbers refer to along with further 1991 nest numbers where these data are helpful.

Category															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
No.	19	3	1	1	2	1	1	3	8	1	2	3	1	1	2

Legend:

1. Bred same ((19), Nests 15,27(-1 from 3 trapped at the nest in 1991), 42 (triplet), 44,47,48,57,77,80)
2. Bred possibly with the same partner, 1991 partner wasn't trapped and colour-ringed ((3), Nests 46, 58, 66)
3. Bred with a new partner which had been colour-ringed as a member of a different pair in 1991, 1991 partner absent ((1), Nest 43)
4. Absent, partner re-paired with 1991 colour-ringed bird ((1), Nest 43)
5. Bred with a new unringed partner in 1992, 1991 partner present did not breed ((1), Nests 53)
6. Present did not breed, 1991 partner re-paired with unringed bird ((1), Nest 53)
7. Bred with a new partner which had been colour-ringed in 1991, partner present did not breed ((2), Nests 55, 73)
8. Present did not breed. 1991 partner paired to 1991 colour-ringed bird ((2), Nests 55 & 73)
9. Bred with a new unringed partner, 1991 partner paired with a partner colour-ringed in 1991 ((1), Nest 70)

10. Bred with a new partner colour-ringed in 1991, 1991 partner paired with new unringed partner ((1), Nest 70)
11. Present did not breed, partner absent from the colony in 1992 ((3), Nests 22, 76, 79)
12. Absent, partner present in colony in 1992 but did not breed ((3), Nests 22, 76, 79)
13. Present did not breed, 1991 partner also present and did not breed ((8), Nests 52, 56, 60 75)
14. Absent remaining two from triplet trapped on the nest in 1991 bred with the same partner ((1), Nest 27)
15. Both partners absent from colony in 1992 ((2), Nest 74)

These data enabled me to calculate rates of splitting and divorce for this sample of 42 terns which returned to the colony in 1992. Following Rowley (1983) I have limited the following to consideration of pairs/triplets where all members of the breeding unit were individually identifiable ($n_{\text{birds}}=39$, $n_{\text{nests}}=22$). Categories 3, 4, 11, 12 and 15 refer to splitting (*sensu* Rowley, 1983: Pairs which have ceased to exist because one (or both) members died or otherwise disappeared). Category 1 refers to pairs which have reunited (*sensu* Rowley 1983: pairs which have re-mated with the same partner). Categories 5, 6, 7, 8, 9, and 10 refer to divorced pairs (*sensu* Rowley, 1983: pairs in which both partners have survived but which have not reunited and have chosen a new partner). Category 13 is a category which is not included in Rowley's scheme; pairs where both members of the pair survived between years but the pair did not breed. Percentages of pairs in the various categories are shown below in comparison with other species (Table 3.6, other species taken from Rowley, 1983).

Table 3.6 Data on pair fidelity for several seabirds a : Figure in bold indicates % mortality in species where data for 'splitting' were not available.

Number of breeding pairs							
Species	In year one	Split ^a n, (%)	In year two				References
			both alive n, (%)	reunited n, (%)	divorced n, (%)	non- breeding pairs n, (%)	
Arctic tern <i>Sterna paradisaea</i>	22	5,(23)	17, (60)	9, (41)	4,(18)	4, (18)	This study
Adélie Penguin <i>Pygoscelis adeliae</i>	277	(40)	165	138	(16)	-	Penney, 1968
Rock-hopper penguin <i>Eudyptes chrysocome</i>	25	(44)	14	13	(7)	-	Warham, 1963
Yellow-eyed Penguin <i>Megadyptes antipodes</i>	737	(27)	539	442	(18)	-	Richdale, 1957
Little Penguin <i>Eudyptula minor</i>	158	(12)	139	115	(17)	-	Reilly and Cullen, 1981
Wandering Albatross <i>Diomedea exulans</i>	64	(17)	53	53	(0)	-	Tickell, 1968
Waved albatross <i>Diomedea irrorata</i>	310	(5)	-	272	-	-	Harris, 1973
Laysan albatross <i>Diomedea immutabilis</i>	341	(3)	330	323	(2)	-	Rice and Kenyon, 1962
Buller's albatross <i>Diomedea bulleri</i>	-	-	400	400	(0)	-	Richdale and Warham, 1973
Northern Fulmar <i>Fulmarus glacialis</i>	-	-	443	422	(5)	-	Ollason and Dunnet, 1978
Northern Fulmar <i>Fulmarus glacialis</i>	54	(2)	53	51	(4)	-	Macdonald, 1977
Fairy Prion <i>Pachyptila turtur</i>	223	(56)	98	96	(1)	-	Richdale, 1965
Sooty shearwater <i>Puffinus griseus</i>	83	(77)	32	19	(41)	-	Richdale, 1963
Manx shearwater <i>Puffinus puffinus</i>	-	-	175	158	(17)	-	Brooke, 1978
Northern Gannet <i>Sula bassana</i>	149	(23)	126	96	(15)	-	Nelson, 1978
Masked Booby <i>Sula dactylatra</i>	56	(25)	42	23	(45)	-	Kepler, 1969
South Polar skua <i>Catharacta maccormicki</i>	294	(9)	267	263	(1)	-	Wood, 1971
Glaucous-winged gull <i>Larus glaucescens</i>	13	(23)	10	7	(30)	-	Vermeer, 1963
Silver gull <i>Larus novaehollandiae</i>	153	(10)	138	125	(9)	-	Mills, 1973

Silver gull <i>Larus novaehollandiae</i>	50	(18)	41	40	(2)	-	Nicholls, 1974
Black-legged kittiwake <i>Rissa tridactyla</i>	458	(11)	408	295	(38)	-	Coulson, 1966

The high combined percentage for split and divorced categories (42 %) compares with 41 % of pairs which reunited. This is at variance with the view that Arctic terns form monogamous pair-bonds which tend to persist (Cramp & Simmons., 1985). Unfortunately the study site was not strimmed in the pre-breeding season in 1993. Consequently the maintenance of the pair bonds could not be followed in to the third year. Data which I managed to collect on return of ringed birds in summer 1993 were limited to 10 birds. Of these two were observed during the courtship feeding display. For this pair we may at least be certain that an attempt to form a pair bond was made. The two birds were colour-ringed as a pair in 1991. In 1992 one of the birds from this pair divorced and re-paired with another bird colour-ringed in 1991 whose partner was absent in 1992. The other bird from this pair was present in the colony in 1992 but was thought not to have made a breeding attempt. From this it appears that neither the initial pairing nor new pairings are fixed, and both are subject to change. This provides limited evidence, for either random mating or for pairings based upon the kind of cost-benefit assessment mentioned earlier in this chapter. The fact that 41% of pairs re-united makes totally random mating less likely, and supports the latter conclusion.

3.6 Nest site fidelity.

The locations of the nest sites within the study plot in 1991 and 1992 were mapped to the nearest 0.5 metres in 1991 and the nearest 0.25 metres in 1992. Differences in nest position between years were calculated using Pythagoras' theorem and are listed in Table 3.7 (Same partners in both years) & Table 3.8 (different partners in both years)

Table 3.7 Differences in Arctic tern nest position between years for pairs which retained the same partner in 1991 and 1992

1991 nest number	1992 nest number	1991/1992 difference in nest position (metres)
27	3	3.01
57	6	1.06
80	16	0.25
47	22	0.35
42	24	2.69
44	25	0.25
77	27	21.51
48	66	17.56
15	91	22.53

Table 3.8 Differences in Arctic tern nest position between years for pairs that changed partners in 1992

1991 nest number	1992 nest number	1991/1992 difference in nest position (metres)
43	9	2.5
53	8	2.5
55	12	4.8
70	12	6.6
70	13	4.8
73	9	4.1

There was no difference on average between pairs which remained the same and pairs which changed partners in the distance nest sites moved between 1991 and 1992 (Mann-Whitney U test $U = 22$, P two-tailed corrected for ties = 0.55).

3.7 Discussion

3.7.1 Determinants of maintenance of the pair bond.

3.7.1.1 Age/Previous breeding performance

The annual survival rate found in this study was similar to that found in two previous studies conducted on the Farne islands, and falls within the known range for Arctic terns. This study found no effects of breeding performance in the preceding year upon re-appearance at the colony or upon whether a breeding attempt was made in the following breeding season. Similarly breeding performance in 1991 was apparently unrelated to divorce in 1992. Where birds did change partners no apparent difference in laying date, clutch size, hatching success, or fledging success was found between the group which changed partner and the group which remained with the same partner. It may be that pairs which changed partners were younger birds which were still in the process of assessing the relative worth of prospective lifetime partners. The long term nature of the pair bond in terns may have been over-stated in the past. Few studies have followed the same pairs for more than a few years. Only studying pairs over the full extent of their reproductive period would establish the relative importance of the various components of mate choice. Age of partner is known to be of importance in mate selection in birds. Improvements in breeding success with age have been attributed to: selection of older and more experienced mates (Mills, 1979; Coulson and Thomas, 1980; Pugsek, 1983), occupation of more favoured sites (Nelson, 1978; Haynes and Blokpoel, 1980; Pugsek and Diem, 1983), earlier laying (Perdeck and Cave, 1992; most studies), larger clutches (most studies), larger eggs (Richdale, 1957; Coulson *et al.*, 1969; Mills, 1973, 1979; Davis, 1976; Thomas, 1983), higher hatching success (Richdale, 1957; Chabrzyk & Coulson, 1976; Nelson, 1978; Haynes & Blokpoel, 1980; Pugsek & Diem, 1983; Thomas, 1983), and higher fledging success (Nelson, 1978; Pugsek & Diem, 1983; Thomas 1983) all in (Nisbet *et al.*, 1984). For example Coulson and Horobin (1976) found a close association in the respective ages of 29 pairs of known age trapped on the Farne islands. They found that clutch size, egg volume, hatching success, and fledging success all varied with the age of the parents. Maxima in both clutch size and egg volume were found amongst middle-aged birds, with breeding success being highest in older

birds. Similar age-related trends have been recorded amongst common terns in colonies in the eastern United States (Nisbet *et al.*, 1984).

3.7.1.2 Nest site fidelity

There was no evidence within this study for mate changing being associated with the large changes in nest site location found amongst a colony of Bridled terns *Sterna anaethetus* in southwestern Australia (Dunlop and Jenkins, 1992). Age related differences in survival rates might affect return rates of terns to the colony and hence pair fidelity .

3.7.1.3 Annual survival rate

Age related effects on annual survival rate have been recorded for several species of seabird. Survival of breeding adults was found to be age-related in a colony of Californian Least Terns *Sterna albifrons*, with young breeders aged two and three years showing lower return rates than adults equal to or greater than four years (Massey *et al.*, 1992). In a 34 year study of kittiwakes adult survival was found to be related to sex, time-period, breeding experience and nest position (Aebischer and Coulson, 1990). This study did not provide sufficient data to address this question.

3.7.1.4 Mate quality

In the absence of any data on age related mate choice and its effect on pair fidelity, and the lack of any simple relationship between breeding performance in a preceding year and its effect upon pair fidelity in the following year what other alternative mechanisms may explain the observed pattern of fidelity and divorce. What follows are examples from the literature which generate hypotheses which could be tested in a larger, more long-term study. Where birds changed partners but their partner from the previous year was present within the colony active mate choice may have been occurring. Means of assessing mate quality in terns are subtle unlike other species with more elaborate secondary sexual characteristics (Buchholz, 1991). It has recently been suggested that for another migratory species , the bar-tailed godwit *Limosa lapponica*, prospective partners assess the quality of birds returning from the winter quarters during the pre-breeding period on the basis of breeding plumage quality (Piersma and Jukema, 1993). Such a scenario seems plausible for Arctic terns also, where the cost of the return flight from the Antarctic could conceivably lead to active

mate choice based upon some measure of quality on return to the breeding colony, although which cues potential mates might use is a matter of conjecture.

Few studies have been of sufficient duration to examine the benefits of mate retention over several breeding seasons. One study found that half of all male and female short-tailed shearwaters *Puffinus tenuirostris* had only one breeding partner during their lives, with a maximum of seven partners. Maintenance of pair bonds varied with age and sequentially. Increasing total breeding experience and increasing familiarity with a particular partner were both related to increased reproductive performance. In both sexes 74% of birds retained their mate from previous years, 10% took a new mate after their previous mate had died and 16% divorced their living mate. Divorce was more likely if a pair failed to produce young in the preceding season; impending divorcees were also absent during a pair bond more often than birds retaining their mates. (Bradley *et al.*, 1990).

It would be interesting to have some record of whether birds ever returned to a previous partner after a breeding attempt with another but only long-term studies on a much larger scale than this one would be able to establish whether this happens. The hypothesis is that the costs and benefits of breeding with the same individual might fluctuate throughout the life span of an individual. This might explain the pattern of couplings which we observe.

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Chapter 4 Variations in adult Arctic and common tern body mass

4.1 Introduction

Life history theory has its foundations in a basic premise that : " selection will adjust the amount of immediate reproductive effort in such a way that the cost in physiological stress and personal hazard will be justified by the probability of success" (Williams, 1966, quoted in Stearns 1992). A further refinement of this premise suggests that long-lived iteroparous species trade-off current and residual reproductive value during breeding attempts in such a way that they maximise their lifetime fitness. This is one of many possible trade-offs for life-history traits, (See Stearns 1992, p. 79 for a comprehensive list) only a few of which have been examined in any detail. Terns have a high expectation of survival from one breeding season to another. Consequently they have several opportunities to breed. It seems plausible that natural selection will have shaped reproductive behaviour in response to this, and that breeding adults may modify their investment in a particular breeding attempt as a consequence. In this chapter, the relationship between current reproductive effort and parental body condition, which may be related to lifetime reproductive success through adult survival, is examined.

Foraging behaviour allied to other activities determines the amount of energy acquired and connects physiological ecology with life history evolution (Stearns 1992). Some aspects of individual physiology are set by phylogenetic constraint. They are lineage specific. Examples are digestive efficiency, excretion and basal metabolism. Other aspects of individual physiology and behaviour vary between individuals and are the parameters used in studying trade-offs. Examples of these are : "the amount of food eaten, the efficiency with which it is collected, the proportion of net power devoted to activity, the surplus power available for growth and reproduction, and the policy used to allocate that surplus..." (Stearns, 1992). Foraging rate as used in this paper is an index of foraging effort which has some utility in understanding the constraints on life history variation. Ideally one would choose to have some direct measurement of the surplus energy devoted to reproduction but even where the resources necessary to do such measurements are available it is very difficult in practice to obtain a large enough sample of individuals. Terns are temporally and

energetically constrained during their breeding attempts (Pearson, 1968). This makes them ideal for investigating reproductive investment and its effects upon adult condition.

4.2 Methods

Breeding adult Arctic and common terns were studied in 1991 and 1992. Changes in the body masses of breeding adult Arctic terns were examined in both 1991 and 1992, and those of common terns in 1992. A sub-sample of nests ($n = 10\text{--}15$ per watch: Total 1991 : $n_{\text{ nests Arctic}} = 77$; $n_{\text{ nests common}} = 52$; 1992: $n_{\text{ nests Arctic}} = 36$; $n_{\text{ nests common}} = 40$) were watched from a hide using 8x30 binoculars throughout the breeding season. All observed nests were within 30 metres of the hide. Observational watches were between 2 and 4 hours length ($\text{mean}_{1991} = 3.3$ hours $\text{min} = 1.5$, $\text{max.} = 4$, $n_{\text{ watches(chick rearing)}} = 62$; $\text{mean}_{1992} = 3.4$ hours $\text{min} = 1.5$, $\text{max.} = 4$, $n_{\text{ watches(chick rearing)}} = 44$) and were randomised throughout the daylight hours. Adults were individually recognisable through a combination of picric and tippex marks on their plumage, or colour rings. The rate of delivery of prey to the chick was used as an index of parental breeding effort. Only individually recognisable birds were included in rate calculations since the same prey item was sometimes presented to the chick more than once and, only the first presentation of a prey item at the nest was included. Rate expressed as the number of prey items delivered to the nest per hour was calculated within each watch period, and corrected for current brood size to give the number of items per chick per hour. Current brood size was known for all observed nests. These values were then used to calculate a mean foraging rate per day.

Exact egg laying dates were known for the majority of sites. Where laying date was unknown it was estimated as hatching date minus the colony average incubation period of twenty-two days in both years for both species. The stage of the breeding cycle was therefore known for each site watched.

In 1991 adult Arctic tern body mass was monitored at a sub-sample of the study nests using remotely operated weighing devices as previously used by Monaghan *et al.* (1989). These were placed near nest sites where adults used them as perches. Where repeated measurements were made

of the mass of a particular individual on the same day a mean of these masses was calculated. Daily individual masses were used to calculate a mean per stage of the breeding cycle.

In 1992 adult Arctic and common terns were trapped and weighed, generally once during late incubation and once during mid-late chick rearing to examine overall mass changes (Table 4.1).

Table 4.1 Dates of weighing and sample sizes for Arctic terns and common terns in 1992

Species	Total range Days since laying (Total n)	Late incubation range (n)	Late chick rearing range (n)
Arctic	2-46 (51)	14-22 (25)	37-43 (17)
Common	10-50 (102)	14-22 (23)	37-43 (27)

No birds deserted as a consequence of this procedure. Hatching, fledging, and breeding success of pairs where at least one of the pair was trapped and weighed did not vary significantly from pairs where neither adult was trapped and weighed (Table 4.2 & 4.3).

Table 4.2 Hatching, fledging and breeding success of Arctic and common tern pairs where at least one breeding adult was trapped compared to sites where no breeding adults were trapped. Medians (Inter-quartile range)

Species/trapped/untrapped (n)	Hatching success Median (IQR)	Fledging success Median (IQR)	Number of chicks fledged Median (IQR)
Arctic/trapped (20)	1 (0)	0.5 (0.5)	1 (1)
Arctic/not trapped (58)	1 (0.5)	0.5 (0.63)	1 (1)
Common/trapped (27)	1 (0.33)	0.33 (0.5)	1 (1)
Common/not trapped (19)	1 (1)	0.33 (0.67)	0 (2)

Table 4.3 Mann–Whitney U tests of hatching, fledging, and breeding success of Arctic and common tern pairs where at least one individual was trapped compared to sites where no adults were trapped.

Species	Hatching success Z (probability)	Fledging success Z (probability)	Breeding success (Number of chicks fledged) z (probability)
Arctic	-0.81 (P=0.42)	-0.16 (P=0.87)	-0.35 (P=0.73)
Common	-1.26 (P=0.21)	-0.23 (P=0.82)	-0.17 (P=0.87)

All statistical tests are two-tailed, and were done using SPSS for Windows version 5. Variables were tested for normality using boxplots created by the SPSS for Windows EXPLORE function. Where variables were non-normally distributed, non-parametric procedures were used.

4.3 Results

4.3.1 Arctic tern foraging rate

Foraging rates (number of trips per nest per chick per hour) were calculated for each day of the 22 day chick rearing period (days since laying 23–45). (These data are examined in more detail in chapter 6). In 1991 foraging rate (grouped by week of the chick rearing period) did not vary significantly with increasing chick age (Kruskal–Wallis one-way ANOVA H_2 corrected for ties = 1.26, $P=0.53$, Figure 4.1). In contrast, in 1992 there was a highly significant increase in foraging rate throughout chick rearing.

Figure 4.1 1991 Arctic tern foraging rate by chick age group

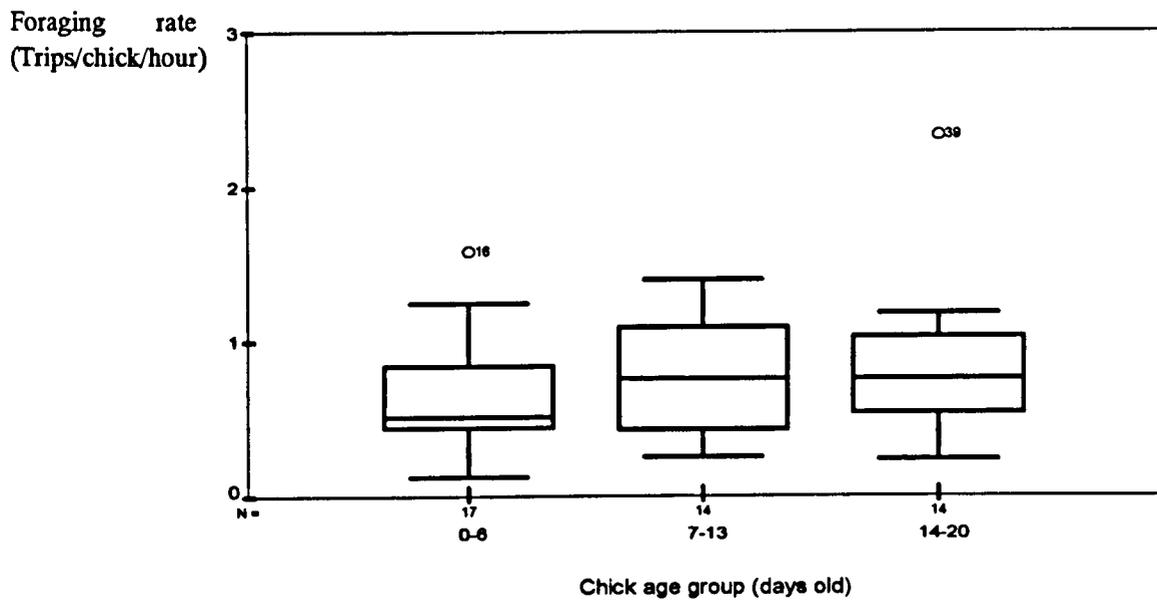


Figure 4.2 1992 Arctic tern foraging rate by chick age group

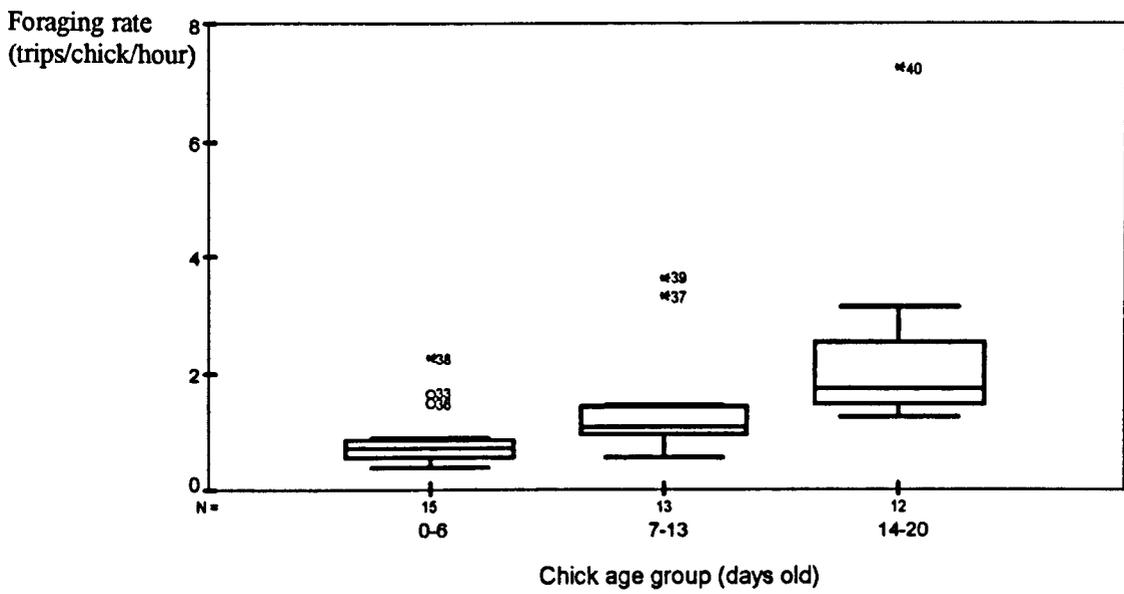


Table 4.4 Arctic tern 1991 foraging rate (Medians are given with 25% and 75 % percentiles).

Chick age group (days old)	Foraging rate (trips/chick/hour ⁻¹)
0-6 (n=17)	0.51 (0.45, 0.85)
7-13 (n=14)	0.76 (0.43, 1.09)
14-20 (n=14)	0.76 (0.53, 1.04)

In 1992 the foraging rate corrected for brood size increased with increasing chick age (Kruskal-Wallis one-way ANOVA H_2 corrected for ties=16.55, $P=0.003$, Table 4.5, Figure 4.2). A post-hoc multiple comparison found that the only significant difference was between the foraging rates of adults provisioning chicks aged less than 6 days old compared to chicks ages 14-20 days old.

Table 4.5 Arctic tern 1992 foraging rate (Medians are given with 25% and 75 % percentiles).

Chick age group (days old)	Foraging rate (trips/chick/hour ⁻¹)
0-6 (n=15)	0.71 (0.57, 0.86)
7-13 (n=13)	1.08 (0.96, 1.43)
14-20 (n=12)	1.74 (1.47, 2.54)

4.3.2 Common tern foraging rates

Prey delivery rate at different chick ages was significantly different in 1992 (Kruskal-Wallis one-way ANOVA H_2 corrected for ties=13.37, $P=0.0012$, Table 4.6, Figure 4.3). As for Arctic terns the data were aggregated to give means of means for each chick age group. Once again the only significant difference in foraging rate was found between age groups 1 and 3.

Figure 4.3 1992 common tern foraging rate by chick age group

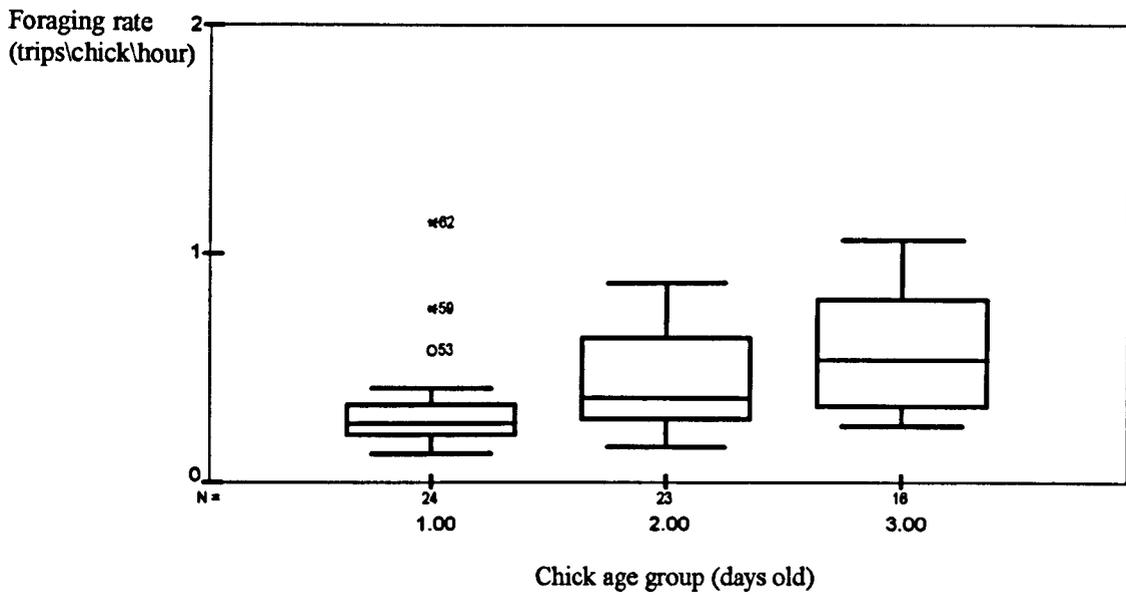


Table 4.6 Common tern 1992 foraging rate (Medians are given with 25% and 75 % percentiles).

Chick age group (days old)	Foraging rate (trips/chick/hour ⁻¹)
0-6 (n=24)	0.26 (0.21, 0.34)
7-13 (n=23)	0.38 (0.28, 0.64)
14-20 (n=16)	0.55 (0.33, 0.80)

4.3.3 Changes in adult body mass.

Overall adult Arctic tern body masses were significantly lower in 1991 than in 1992 (Table 4.7, Mann-Whitney U-test $z_{\text{corrected for ties}} = -5.39$, $P < 0.0001$, $n_{1991} = 216$, $n_{1992} = 51$, Figure 4.4).

Table 4.7 Median body masses of Arctic terns in 1991 and 1992

Year	Median body mass	Semi-inter quartile range	Inter-quartile range
1991	96	90-100.4	85-105.5
1992	105	102-107	100-110

The pattern of body mass changes in adults during 1991 began with an initial increase in mass during incubation, a rapid decline during the first two weeks of chick rearing followed by an increase (Figure 4.5). Adults were significantly lighter during the first 10 days of chick rearing than in the last ten days of incubation (Table 4.5, one-way ANOVA on mean adult body mass per stage of breeding cycle, $F_{2,25} = 5.36$, $P = 0.011$). Late-incubation and late-chick rearing masses were recorded for seven individual Arctic terns, in 1992. The individual pattern of mass loss was consistent with the overall trend, all individuals showing a decline. (Wilcoxon matched pairs test, $Z = -2.20$, $P = 0.03$, Table 4.8).

Figure 4.4 Arctic tern inter-year comparison of all recorded adult body masses

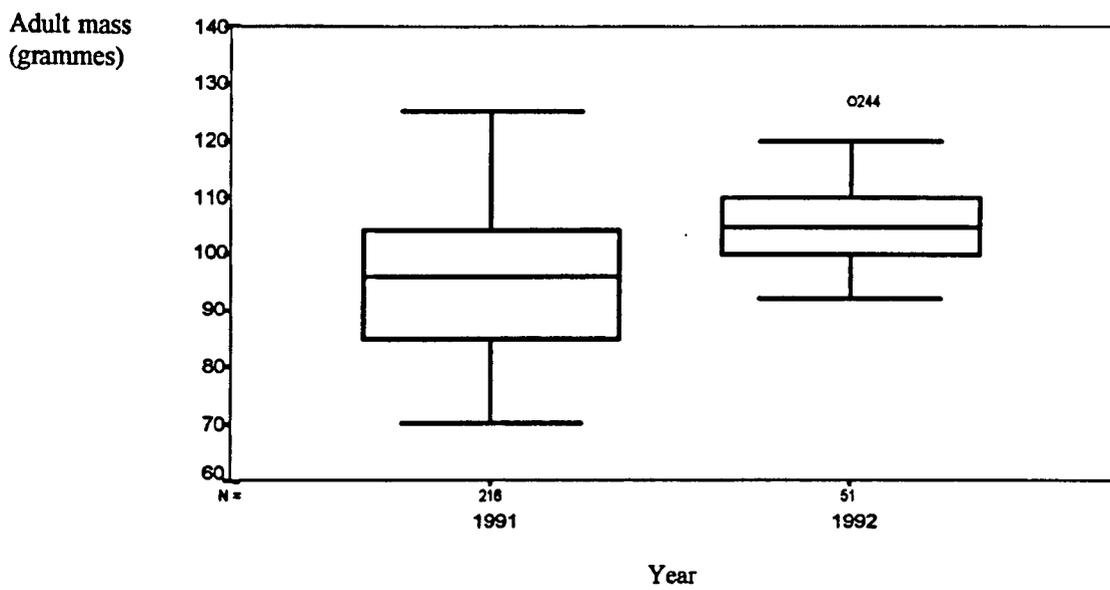


Figure 4.5 1991 Arctic tern pattern of adult body mass variation

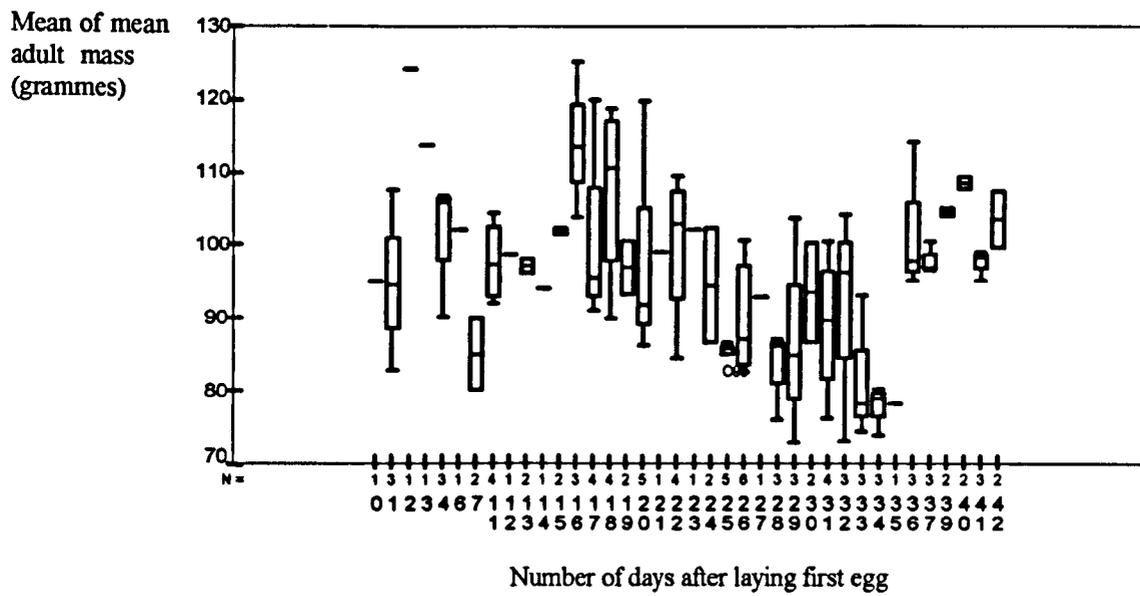


Table 4.8 Mean Arctic tern adult body masses for different sites and years. Population means are based on mean values for individuals. Sample sizes are in parentheses

Location (year)	Last ten days of incubation	First ten days after chicks hatch	Last ten days of chick rearing
Shetland (1987)	109.8 ± 2.8 (7)	107.8 ± 1.9 (6)	-
Shetland (1988)	104.3 ± 2.0 (8)	95.9 ± 1.1 (11)	-
Orkney (1988)	113.9 ± 2.8 (5)	113.2 ± 3.9 (7)	-
Coquet (1987)	126.0 ± 1.5 (4)	113.4 ± 2.8 (12)	-
Coquet (1991)	100.1 ± 2.7 (11)	88.6 ± 2.1 (12)	91.1 ± 4.7 (5)
Coquet (1992)	108.5 ± 1.7 (21)	104.9 ± 1.9 (9)	103.4 ± 1.9 (16)

Data for Arctic terns in 1992 were less extensive than in 1991. Each individual was weighed on two occasions. While adult body mass declined slightly overall during the breeding period ($r_s = -0.30$, $P=0.035$, Figure 4.6) it was not significantly different in the pre- or post-egg hatching period (Table 4.9, Mann-Whitney U-test, $z_{\text{corrected for ties}} = -1.92$, $P=0.546$). Mean adult body mass during the pre-egg hatching period was 108.2 ± 1.6 grammes, while that during the post-egg hatching ten day period was 103.6 ± 1.4 grammes.

Similar data were recorded for common terns in 1992 when body mass was examined in relation to days since laying. There was a highly significant decline in adult body mass during the breeding period ($r = -0.42$, $P<0.0001$, Figure 4.7). This was due to a significant decline in adult body mass during the chick rearing period (Incubation $r = 0.11$, $P=0.55$), Chick rearing $r = -0.52$, $P<0.0001$). Adult body mass was significantly less towards the end of the chick rearing period than late in incubation (Table 4.9, Mann-Whitney U-test, $z_{\text{corrected for ties}} = -2.18$, $P= 0.029$)

Figure 4.7 1992 common tern pattern of adult body mass variation

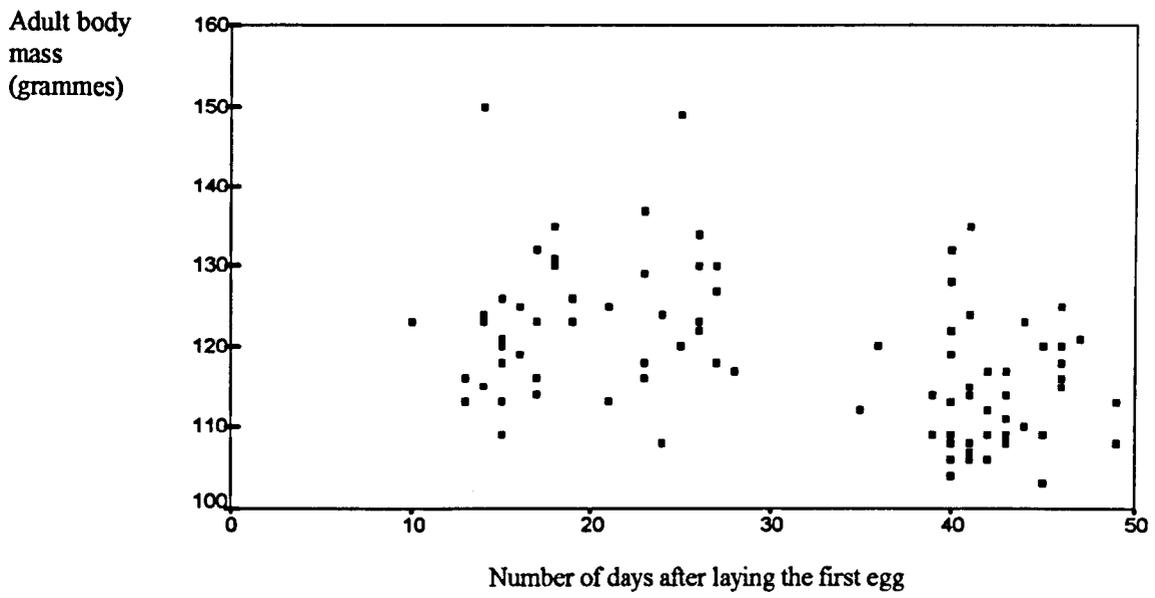


Table 4.9 Adult common tern body mass by period of breeding cycle

Period	Adult body mass (\pm s.e.)
Late incubation	122.7 \pm 1.5, n=30
Late chick rearing	118.4 \pm 1.5, n=44

Late incubation, and late chick rearing adult body masses were obtained for 20 individuals. As with the Arctic terns these individuals showed a consistent decline in mass (Figure 4.8 Wilcoxon matched pairs signed ranks test, $Z=-3.81$, $P=0.0001$, $n=20$).

Although fewer birds were trapped and weighed during the first ten days of chick rearing, there was a sufficient number were to allow a comparison by stage of the breeding cycle similar to that done for the Arctic terns in 1991 (Table 4.10).

Table 4.10 Mean individual adult common tern body masses calculated for stage of the breeding cycle and breeding area/year; sample sizes are in parentheses

Location (year)	Last ten days of incubation	First ten days after chicks hatch	Last ten days of chick rearing
Coquet (1992)	122.7 \pm 1.5 (29)	125.1 \pm 2.3 (17)	113.9 \pm 1.3 (33)

Late in chick rearing, adult body mass was significantly less than during the first ten days of chick rearing, and the first ten days after chick hatching (one-way ANOVA on adult body masses $F_{2,76}=13.53$, $P<0.0001$, followed by Bonferroni multiple range test, Figure 4.9).

4.3.4 Individual patterns of mass loss

A series of records of mass during the breeding period were obtained for four individuals from two pairs in 1991 using the remotely operated weighing devices. (Figure 4.10 and Figure 4.11). Both members of these pairs showed a rise in mass during incubation, followed by a decline during

Figure 4.8 1992 Arctic tern body masses in late incubation and late chick rearing

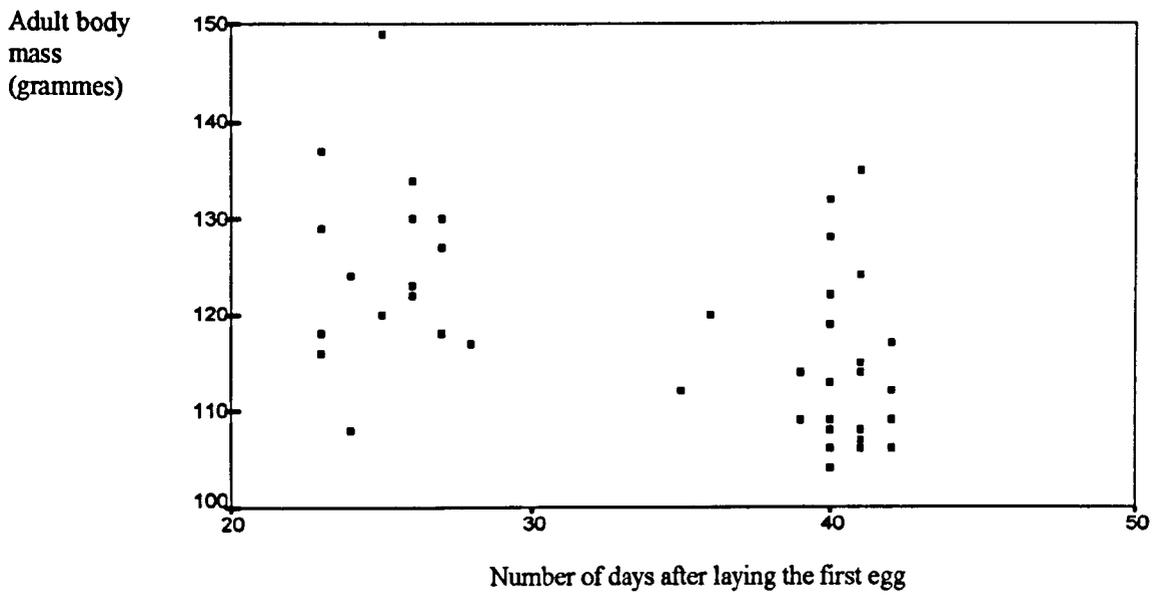


Figure 4.9 1992 common tern body masses in late incubation and late chick rearing

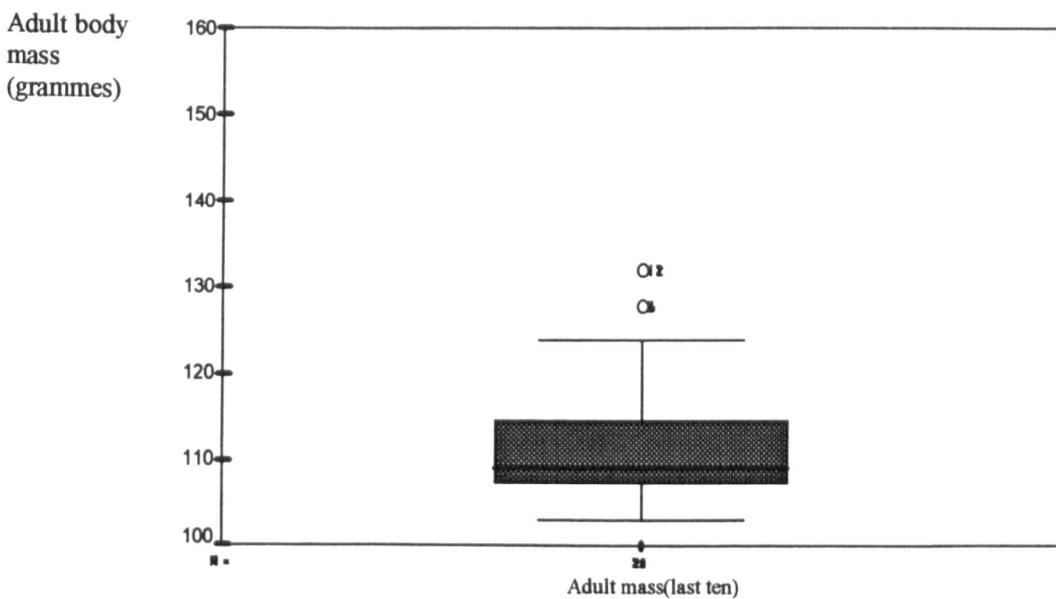
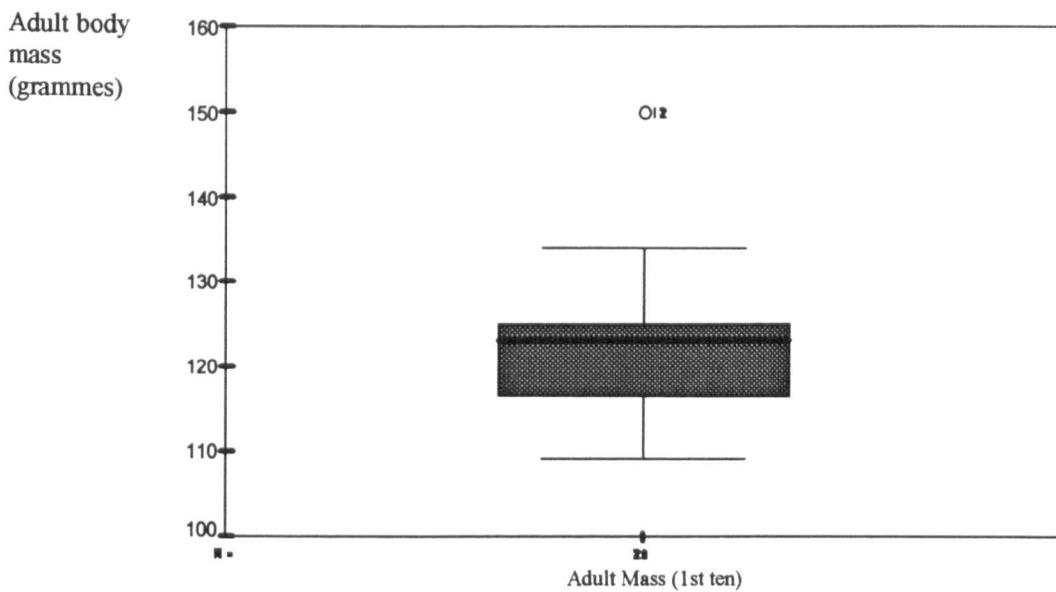


Figure 4.10 1991 Arctic tern individual patterns of mass variation of a pair

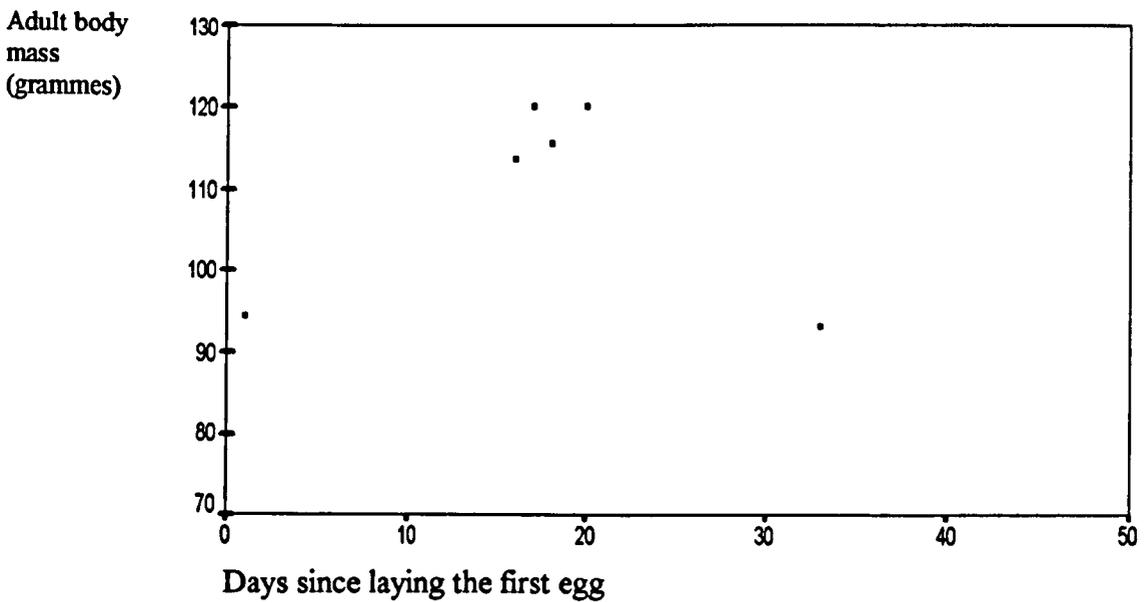
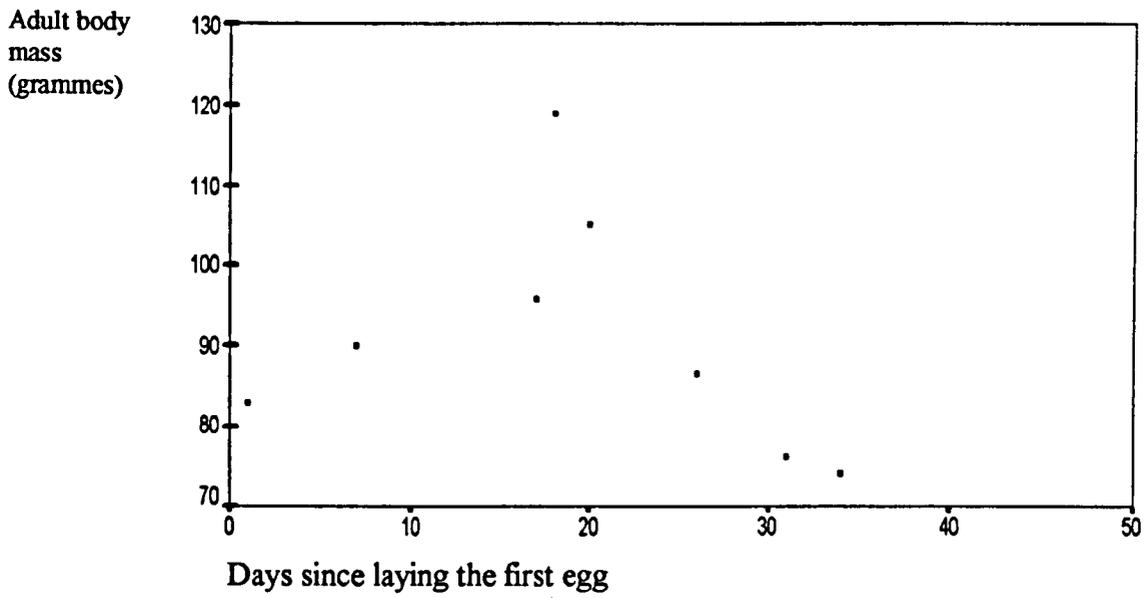
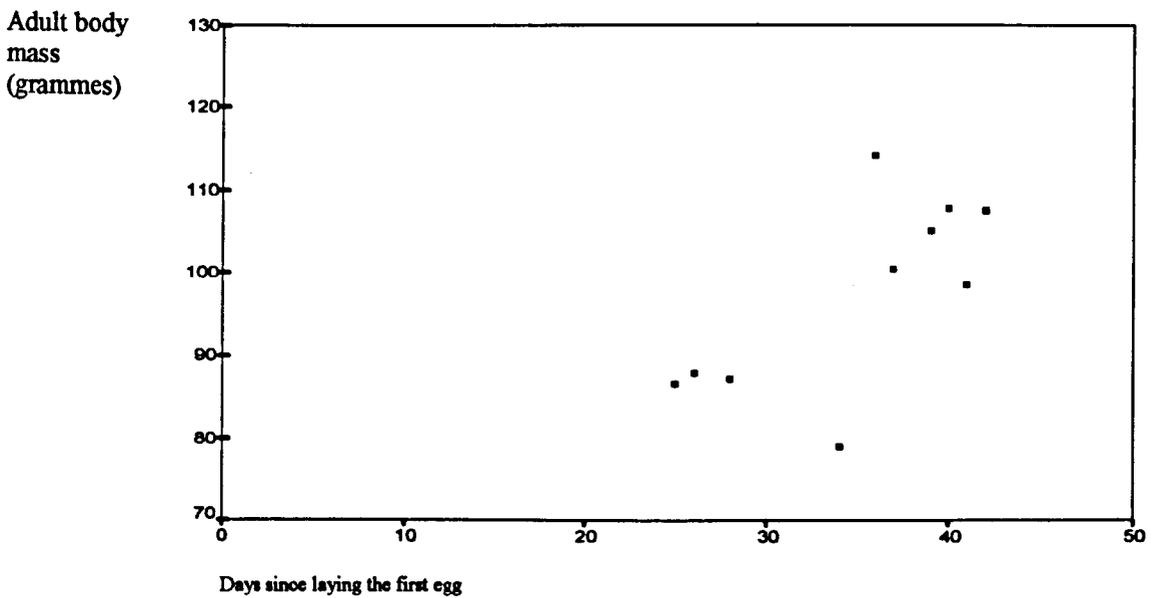
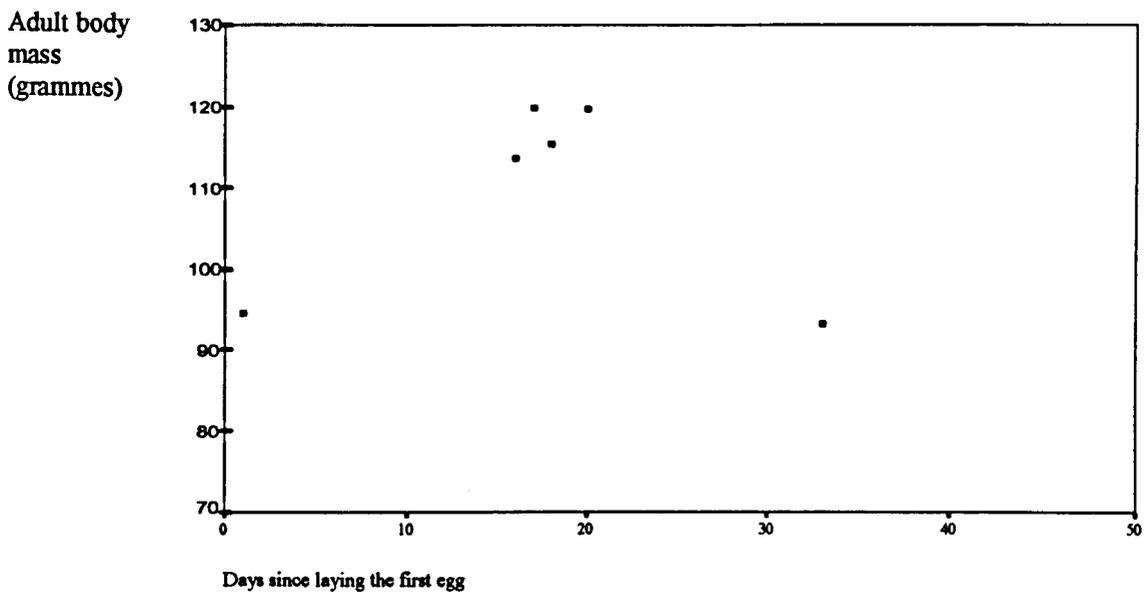


Figure 4.11 1991 Arctic tern individual patterns of mass variation of a pair



chick rearing. Members of pair "b" were measured only during late chick rearing but showed an increase.

4.4 Discussion

4.4.1 General

Several studies have used adult body mass as a means of assessing the reproductive effort of breeding seabirds and as the proximate factor determining the decision to persist with a breeding attempt or not (e.g. Monaghan *et al.*, 1992). However other studies have suggested that adult body mass may vary during a breeding attempt, serving to reduce the energetic costs of provisioning the brood (e.g. Gaston & Jones, 1989; Croll, Gaston & Noble, 1991). Two alternative hypotheses have been proposed by Jones (1994) to explain the non-linear loss of mass of adult alcids during a breeding attempt. The first of these, the stress hypothesis, suggests a steady decline in adult body mass throughout chick rearing as a consequence of increased adult foraging effort. This in turn is determined by increased chick growth requirements. The second of these, the programmed anorexia hypothesis (PAH), predicts an abrupt change, or abrupt changes, in adult body mass as a consequence of a change in adult's own feeding behaviour leading to a decline in adult body mass. The postulation is that such a drop in mass reduces energetic flight costs during a period when adult seabirds experience a marked increase in their foraging costs as result of their eggs hatching.

4.4.2 Comparing the stress and programmed anorexia hypothesis for terns.

The foraging performance of Arctic terns in 1991 was relatively poor with no increase in foraging rate with increasing chick age. Both species showed a decline in body mass in 1991 followed by an increase when feeding large chicks. Arctic tern mass declined until day 35 of the chick rearing period in 1991 (Figure 4.5) and then increased towards the end of chick rearing, when adults may have been increasing their mass in preparation for migration. Data were less complete in 1992, but adult Arctic terns body mass did decline during the period from late incubation until late chick rearing. Due to the less complete coverage of days upon which adult masses were recorded in 1992 I was unable to ascertain whether adult mass increased in the late incubation period in this year as it

had in 1991. Adult common tern body mass increased during the first ten days of chick rearing in 1992 when foraging rate presumably increased due to the requirement to feed newly hatched chicks. This also suggests that the PAH may be less appropriate than the stress hypothesis in explaining the observed non-linear variations in adult body mass of terns during the chick rearing period. Indeed, Jones suggests that the PAH may have specific advantages for the alcids compared to the gulls (*and presumably their close relatives the terns Sternidae*, my italics), due to the extraordinary energetic demands of flight in this group caused by the need to optimise both the use of wings for flight and for under-water flapping when foraging.

The two hypotheses are not mutually exclusive. Abrupt losses of mass during critical periods of high energetic demands on the adults which are due to stress could have short-term beneficial consequences of decreasing the energetic costs of foraging. However unlike the situation amongst breeding alcids reported by Jones (1994) mass loss in Arctic terns in 1991 was not abrupt but continuous throughout the chick provisioning period and followed by an increase at its end. As it increases when foraging demands are high, it is unlikely that mass loss was due to programmed anorexia.

4.4.3 Comparison with previous data for Arctic terns.

Monaghan *et al.* (1992) suggested, in reference to a postulated mass threshold affecting the decision to persist with a breeding attempt or not, that : "... such a threshold will be selected to produce the best trade-off between an individual's current and future reproductive potential, and as such is likely to vary (my italics) between individuals. While agreeing with this postulation Avery *et al.* (1992) criticised a threshold value of 105 g which figure in Monaghan *et al.* (1992) paper inferred had wider applicability than was actually suggested by the text. However the text actually stated that the threshold value was liable to change with the quality of the individual. Breeding Arctic terns with body mass as low as 82 g have been trapped in Shetland during a period of markedly decreased breeding success (Avery *et al.*, 1992). Such low mass may have had an effect upon adult survival , as was found for the Great skua during the same period of food shortage (Hamer, Furness & Caldow, 1991), although the recent substantial recovery in the size of the breeding population of Arctic terns in Shetland suggest that this could be an erroneous assumption if

the same birds were breeding during the decline and the recovery. It is possible that the recovery in numbers may have been due to large scale immigration from elsewhere into the Shetland breeding population. However my own data, and Avery *et al.* (1992) data support the notion that certain adults may persist with a breeding attempt in the hope that environmental conditions will improve. Indeed the Arctic terns studied in 1991 on Coquet island may have delayed the onset of their breeding attempt in response to poor conditions. Although nothing is known about prey availability around Coquet in either year and hence nothing can be said with any certainty about how this may have affected reproductive decisions made within a season by the breeding terns, the weather in early 1991 led to the abandonment of 33% of the nests within the study plot. Furthermore, egg-laying occurred over a period of 27 days which is extremely protracted for terns, and suggestive of a delay in the onset of breeding to acquire further reserves (Drent and Daan, 1980, Monaghan *et al.*, 1992).

Arctic terns with body masses of lower than 90 grammes persisted with their breeding attempts in 1991. It is also of more general interest that Arctic terns in an area where breeding performance did not suffer the same drastic declines recorded elsewhere in their distribution during the late 1980's had similarly low adult body masses. These were lighter even than those reported by Avery *et al.* (1992) which they believed may have been the lightest recorded anywhere in the world. Mass of adult terns is likely to differ with body size. Unfortunately insufficient data were available for adult terns of known mass to control for this factor in this study. Future comparisons should attempt to control for body size.

The availability of prey around Coquet island is unknown. Until more complete data on adult mass and prey availability are available we should remain cautious in our interpretations of changes in adult mass.

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Chapter 5 Breeding performance of Arctic and common terns

5.1 Introduction

Many factors have been found to affect the breeding performance of seabirds in general, and terns in particular, including age of breeding adults (e.g. Coulson & Horobin, 1976; Nisbet, Winchell, & Heise, 1984; Becker & Specht, 1991; Croxall, Rothery & Crisp, 1992), food supply during the breeding season (e.g. Safina & Burger, 1988; Monaghan, Uttley, Burns, Thaine & Blackwood, 1989; Uttley, Monaghan & White, 1989; Uttley, 1991), weather (e.g. Becker & Finck, 1985; Becker, Finck & Anlauf, 1985; Anlauf & Becker, 1986; Mlody & Becker 1991, Aebischer, 1993), seasonality (e.g. Diamond & Prys-Jones, 1986), nesting density (e.g. Becker & Finck, 1986), predation from a variety of sources both of eggs and nestlings (Nisbet & Walton, 1984; Morris & Wiggins, 1986; Uttley, Monaghan & Blackwood, 1989; Shealer & Kress, 1991; Burness & Morris, 1993), human interference (Carvacho, Rios, Leon, & Escofet., 1989; Forbes, Robertson, Ogilvie & Seddon, 1992), parental quality (Nisbet 1978), egg size (Nisbet, 1978; Davis, 1975; Bolton, 1991), hatching asynchrony (Gauzer, 1989), lunar cycles (Smith, 1990), tidal effects (Becker & Specht, 1986), the effect of neuro-toxins (Coulson & Horobin, 1976; Nisbet, 1983), environmental pollutants (Becker, Schuhmann & Koepff, 1993), and inter-specific competition (Safina *et al.*, 1988; Weimerskirch & Stahl, 1988). Although these effects have often been considered individually it is more likely that breeding performance is a synergistic consequence of them all. However it is rarely possible to examine all of these in a single study, and their importance will vary between years and study sites.

In this chapter various measures of the breeding performance of Arctic and common terns in 1991 and 1992 on Coquet Island are compared, and the recorded inter and intra-year differences found are discussed with reference to life-history theory.

One of the most important predictions of life-history theory is that where there is a cost of reproduction in long-lived iteroparous breeders, reproductive effort during a single breeding season will have been shaped through natural selection to optimise lifetime reproductive success (Drent & Daan, 1980; Reznick, 1985; Winkler & Wilkinson, 1988 & see Stearns, 1992 for a comprehensive list of possible trade-offs during breeding). Depending on environmental conditions and thereby the

reproductive effort required clutch size may be modified between years. Additionally migratory species may be affected by constraints which delay laying until after the period when the optimal clutch size is greatest (Crick, Gibbons & Magrath, 1993). Obviously in such a short-term study as this it is not possible to adequately study inter-year costs in terms of worsened body condition and decreased survival of adults which have bred, although investigating intra-year effects on adult body condition is more feasible (see earlier chapters) and may give some insight into the trade-offs through which variation in lifetime reproductive success is mediated.

Throughout the following chapter a cost of reproduction is assumed, and the breeding performance of both species (Arctic and common tern) is considered. Costs incurred during a single breeding season may reduce residual reproductive value with advancing age (Hamer & Furness, 1991). One consequence of this is that individuals are expected to optimise reproductive effort within a breeding season (Winkler & Wilkinson, 1988). By observing animals during the breeding season insights into the behavioural means by which any optimisation of breeding performance may occur may be obtained.

For long-lived seabirds, such as terns, the evidence for optimisation of lifetime reproductive success is mixed. Amongst the factors implicated in affecting reproductive "decisions", weather and food supply are some of the most important. Obviously these two are closely related for surface foragers like Arctic and common terns which are known to be affected profoundly by weather effects upon their foraging behaviour (Dunn, 1975; Taylor, 1983). Weather may affect foraging behaviour directly or through changing the availability of prey (Becker, Finck & Anlauf, 1985). Seabirds are affected by long (e.g. El Niño type perturbations of marine ecosystems) and shorter term fluctuations in prey availability. These may affect annual breeding success and birds may optimise their reproductive investment in response to changes in prey availability resulting from these short and long term fluctuations.

Monaghan *et al.*, 1989, state that: "Food supply is therefore likely to act as a proximate factor influencing the reproductive "decisions" of individuals in any one year. Such decisions could affect many aspects of breeding effort, such as whether to attempt breeding, the timing of laying, clutch and egg size, foraging performance and the probability of desertion ". These decisions may be envisaged as a series of opportunities to either persist with or abandon one breeding attempt.

Through studying the modifications in a bird's reproductive effort we may gain insights into the validity of life history theory.

Ideally one would wish to manipulate prey availability directly through experimentation, as Welham & Ydenberg (1993) did for black terns *Chlidonias niger* breeding and feeding within a freshwater ecosystem. In practice this is rarely possible for seabirds, primarily for logistical and economic reasons. This leaves the researcher the option of studying the same birds breeding in the same place in different years. If prey availability or weather differs between the two years one is left with a natural experiment, albeit one without rigorous controls. Prey availability to foraging seabirds may vary considerably between years with consequent effects on the foraging behaviour of diving and surface feeding seabirds (Hamer *et al.*, 1993; Uttley *et al.*, 1994). Ideally one would wish to have concurrent data on the abundance and distribution of the major prey populations, but this is also rarely possible for most studies. However because some of the birds observed in both years were known to be the same birds and consequently of the same quality, differences in their breeding performance and foraging behaviour (see later chapters) will reflect differing conditions, and any differences between individuals within one year may reflect differences in quality.

5.2 Methods

All the relevant methods used in collecting the data described in this chapter are contained in chapter two. Significant differences were found between the fledging and breeding success of Arctic terns for clutches that were re-lays and those which were not in 1991. No pairs of Arctic terns re-laid in 1992. Consequently re-lays from 1991 were not included in comparisons of hatching, fledging, or breeding success of Arctic terns between years. Re-lays are also excluded from the intra-year comparisons in 1991 of hatching, fledging, and breeding success including comparisons of the egg volume of fledged and failed eggs.

In 1992 hatching success of stored eggs was significantly lower than for the control group (Mann-Whitney U-test, $z_{\text{corrected for ties}} = -3.01$, $P = 0.003$). This group was excluded from the inter-year comparison of hatching success, and from the 1992 intra-year comparisons of hatching, fledging and breeding success, including comparisons of the egg volume of fledged and failed eggs.

For all other analyses no significant differences were found between stored egg or re-lay sites, and data from these sites are included.

In 1991 no pairs of common terns within the study sample re-laid, and no eggs were taken into storage. Eggs were stored in 1992 but no significant differences were found for any of the measured breeding parameters between these and the control group. Consequently data collected for the stored egg group are included in the following analyses.

A marked advantage of the study site was the absence of any mammalian predators, which can severely affect breeding success in ground-nesting seabirds (Uttley, Monaghan & Blackwood, 1989; Burness & Morris, 1993).

Landings on Coquet island by the public are prohibited so the effects of human disturbance on breeding performance are limited to those incurred during observation and the collection of breeding data. The only predation of eggs and chicks was by black-headed and, to a much lesser extent, lesser black-backed and herring gulls.

Hatching success was calculated as the number of eggs that hatched divided by the number of eggs that were laid in a clutch. Fledging success was calculated as the number of chicks that reached twenty days old per egg that hatched. Breeding success was defined as the number of chicks that reached twenty days old per pair.

Levene's test for equality of variance was used prior to any use of parametric statistics. All post-hoc multiple comparisons are constrained at the 0.05 level.

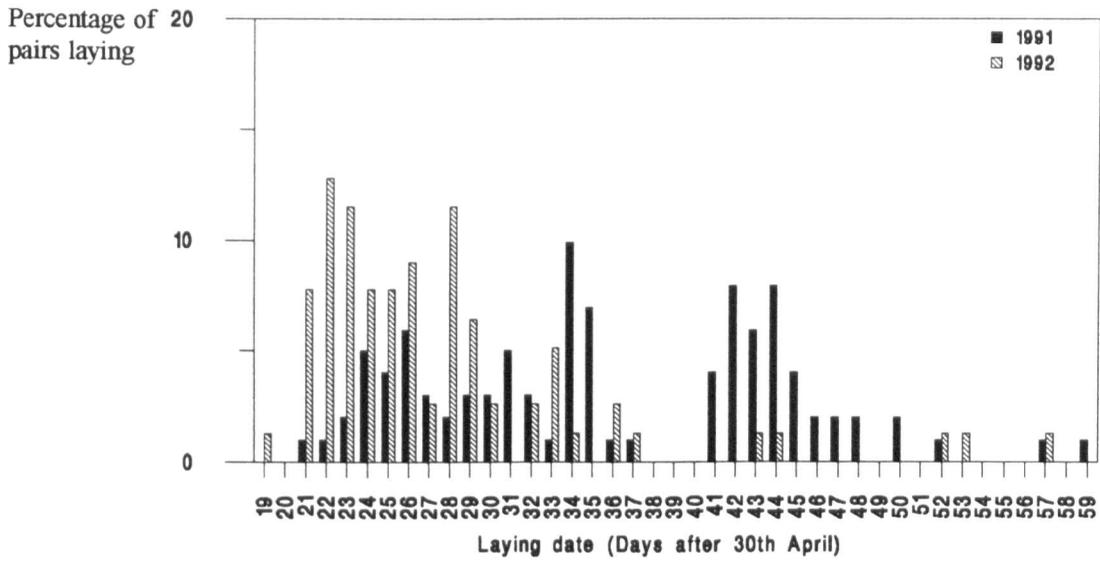
5.3 Results

5.3.1 Arctic tern

5.3.1.1 Laying period

The median laying date of the first egg within the study plot was significantly later in 1991 than in 1992 (Mann-Whitney U-test, $z_{\text{corrected for ties}} = -6.86$, $P < 0.00001$, Table 5.1; Figure 5.1). The greater spread in 1991 reflected a later, more protracted and asynchronous laying period in that year than in 1992. The range in laying date in 1991 was from 21st May–28th June (38 days) compared to 19th May–26th June in 1992. More importantly the majority of birds laid over an eight

Figure 5.1 Arctic tern laying periods in 1991 and 1992



day period in 1992. In 1991 laying was more spread out. As the distribution of the dates was non-normal no statistical test was appropriate.

Table 5.1 Median Arctic tern laying dates plus 25 % and 75 % percentiles, and the overall average laying dates in 1991 and 1992.

Year	25 % of clutches started	Median laying date	75 % of clutches started	Number of clutches
1991	29th May	4th June	12th June	101
1992	23rd May	26th May	29th May	78

5.3.1.2 Courtship prey

There was no significant difference in the proportions of sandeels and non-sandeels fed by male Arctic terns to females during courtship between 1991 and 1992 (χ^2_1 corrected for continuity = 3.28, n.s., Figure 5.2).

The size of sandeels fed to females during courtship feeding varied significantly between 1991 and 1992 ($\chi^2_3 = 12.48$, $P < 0.01$ with a greater proportion of sandeels in the 8–12 cm size class in 1991).

There was no significant difference in the proportions of different size classes of non-sandeels fed to female Arctic terns in either year ($\chi^2_1 = 0.1$, n.s., size categories collapsed in to <8 and >8 cm).

5.3.1.3 Clutch size

On average Arctic terns laid a clutch of 1.7 eggs in 1991 and 1.9 eggs in 1992. Median clutch size was significantly smaller in 1991 than in 1992, with a significantly higher proportion of one egg clutches (χ^2_1 corrected for continuity = 10.84, $P = 0.0001$, Table 5.2). There were significantly more clutches of two or greater in 1992 than in 1991.

Figure 5.2 1991 & 1992 Arctic tern courtship prey

Arctic tern composition of diet during courtship 1991 and 1992
(1991, n=227; 1992, n=92)

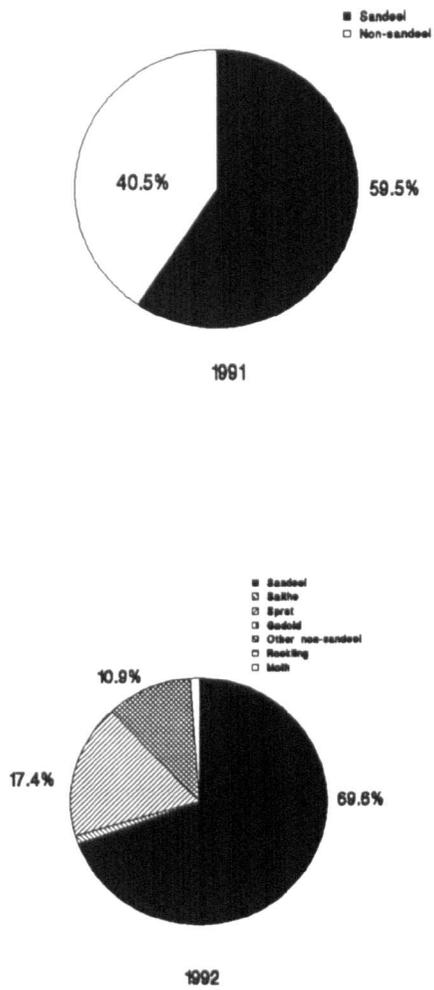


Table 5.2 Percentages of Arctic tern clutches of different size laid in 1991 and 1992.

Year	Percentage of c/1	Percentage of c/2	Percentage of c/3	Total n
1991	35.6	60.4	4.0	101
1992	13.3	84.0	2.7	75

5.3.1.4 Egg dimensions and volume

The lengths and breadths of "a" and "b" eggs did not differ significantly between the two years (Length "a": student's t-test $t_{s173}=-0.42$, $P=0.68$; Breadth "a": student's t-test $t_{s173}=-1.46$, $P=0.15$; Length "b": student's t-test $t_{s127}=-1.44$, $P=0.15$; Breadth "b": student's t-test $t_{s127}=-1.16$, $P=0.25$, Table 5.3). Individual egg volumes did not differ significantly between years ("a" egg volume: student's t-test $t_{s173}=-1.45$, $P=0.15$; "b" egg volume: student's t-test $t_{s127}=-1.74$, $P=0.08$, Table 5.3).

Table 5.3 Length, breadth and volume of Arctic tern eggs in 1991 and 1992

Year	Egg	Length Mean±s.e. (mm)	Breadth Mean±s.e. (mm)	Volume Mean ± s.e (cm ³).	Number of eggs
1991	a	40.9±0.2	29.4±0.1	16.94±0.15	97
1992	a	41.0±0.2	29.6±0.1	17.24±0.14	78
1991	b	39.9±0.2	29.0±0.1	16.14±0.16	63
1992	b	40.3±0.2	29.2±0.1	16.50±0.13	66
1991	c	41.2±0.5	29.8±0.3	17.59 ± 0.35	4
1992	c	39.4±0.3	29.4±0	16.35 ± 0.12	2

Egg volume has been found to affect the fledging success of some seabirds in some years (Parsons, 1970). In both years the volumes of eggs from which birds fledged successfully were compared with those from which birds did not fledge successfully. In 1991 the egg volumes of the two groups did not differ significantly (student's t-test $t_{s152}=1.60$, $P=0.11$, Table 5.5). However in

1992 eggs which resulted in successful fledging had a significantly larger volume than unsuccessful ones (student's t-test $t_{s149}=2.00$, $P=0.047$, Table 5.6).

A fuller comparison of the volumes of eggs which resulted in fledged young with those that did not is shown below (Tables 5.5 & 5.6). The classification follows that used by Horobin (1971) where "c1" is a single egg clutch, "c2/1" the first egg of a two egg clutch, "c2/2" the second egg of a two egg clutch, "c3/1" the first egg of a three egg clutch, "c3/2" the second egg of a three egg clutch, and "c3/3" the third egg of a three egg clutch. A dash marks instances where there were no eggs in a particular category.

Table 5.5 The volumes of Arctic tern eggs from which young fledged compared to those which did not in 1991. Sample sizes are in parentheses.

Egg category	Mean volume ± s.e. (c.c.) Fledged	Mean volume ± s.e. (c.c.) Failed	student's t value	Degrees of freedom	Probability
c1	16.78±0.30 (10)	16.62±0.47 (21)	0.22	29	0.83
c2/1	17.66±0.25 (16)	17.34±0.19 (41)	0.93	55	0.36
c2/2	16.87±0.45 (5)	16.23±0.18 (49)	1.13	52	0.26
c3/1	-	17.08±0.63 (4)	-	-	-
c3/2	-	18.17±0.52 (4)	-	-	-
c3/3	-	17.30±0.59 (4)	-	-	-
All	17.25±0.19 (31)	16.79±0.14 (123)	1.60	152	0.11

Table 5.6 The volumes of Arctic tern eggs from which young fledged compared to those which did not in 1991. Sample sizes are in parentheses.

Egg category	Mean volume ± s.e. (c.c.) Fledged	Mean volume ± s.e. (c.c.) Failed	student's t value	Degrees of freedom	Probability
c1	17.04±1.24 (3)	16.69±0.49 (8)	0.32	9	0.75
c2/1	17.86±0.23 (32)	17.41±0.18 (36)	1.58	66	0.12
c2/2	16.76±0.28 (18)	16.76±0.16 (48)	0.02	64	0.98
c3/1	17.15±0.20 (2)	-	-	-	-
c3/2	16.40 (1)	17.43 (1)	-	-	-
c3/3	-	16.59±0.13 (2)	-	-	-
All	17.41±0.18 (56)	17.00±0.11 (95)	2.00	149	0.047

5.3.1.5 Clutch volume

Clutch volume was significantly larger in 1992 due to the higher proportion of two egg clutches in that year (Clutch volume 1991 compared to 1992 Mann-Whitney U-test, $z_{\text{corrected for ties}} = -2.83$, $P=0.005$, Table 5.7).

Table 5.7 1991 and 1992 Arctic tern clutch volumes

Year	Median Clutch volume (25%, 75% percentiles).	Number of clutches
1991	31.57 (17.54, 34.25)	97
1992	33.71 (31.54, 35.09)	78

The volume of "a" eggs from clutches of different size were compared to examine whether clutch size significantly affected egg volume. This comparison was limited to clutches of one and two eggs due to the small sample of three egg clutches in both years. In 1991 the volume of eggs in

single egg clutches were significantly smaller than the volumes of the first egg in two egg clutches (student's t-test, $t_{891}=-2.55$, $P=0.01$, Table 5.8). There was no statistically significant difference in 1992 (student's t-test, $t_{374}=-1.78$, $P=0.08$, Table 5.8).

Table 5.8 Egg volume of single Arctic tern eggs and first eggs from clutches of two in 1991 and 1992.

Year	Clutch size	"a" egg volume (c.c.) \pm s.e.	Number of clutches
1991	1	16.45 \pm 0.30	33
1991	2	17.23 \pm 0.15	60
1992	1	16.61 \pm 0.49	10
1992	2	17.35 \pm 0.14	66

5.3.1.6 Hatching, fledging and breeding success

These parameters are as defined in chapter 2. Medians and inter-quartile ranges for hatching, fledging and breeding success are shown below (Table 5.9).

Table 5.9 Median hatching, fledging, and breeding success of Arctic terns in 1991 and 1992

Year	Median Hatching success	25 %	75%	Median Fledging success	25%	75%	Median Breeding success	25%	75%
1991	0.5 (n=83)	0	1	0.5 (n=43)	0	1	0 (n=83)	0	1
1992	1 (n=74)	1	1	0.5 (n=65)	0.33	0.5	1 (n=74)	0	1

Average hatching success was 0.46 in 1991 and 0.82 in 1992. On average fledging success was 0.49 in 1991 and 0.50 in 1992. Average breeding success was 0.35 in 1991 and 0.74 in 1992. There were very highly significant differences between median hatching success (Mann-Whitney U-test, $z_{\text{corrected for ties}} = -4.89$, $P < 0.00001$) and median breeding success (Mann-Whitney U-test,

$z_{\text{corrected for ties}} = -4.46$, $P < 0.00001$) between the two years. However median fledging success was not significantly different (Mann-Whitney U-test, $z_{\text{corrected for ties}} = -0.13$, $P = 0.90$).

5.3.2 Common tern

5.3.2.1 Laying date

Median laying dates for the first egg in a clutch did not differ significantly between 1991 and 1992 (Mann-Whitney U-test, $z_{\text{corrected for ties}} = -0.3301$, $P = 0.74$, $n_{1991} = 51$; $n_{1992} = 32$, Table 5.10, Figure 5.3 & 5.4).

Table 5.10 Median and average laying dates of common terns in 1991 and 1992, with inter-quartile range

Year	25 % of clutches started	Median laying date	75 % of clutches started	Average laying date	Number of clutches
1991	25th May	27th May	29th May	27th May	50
1992	25th May	28th May	29th May	29th May	32

5.3.2.2 Courtship prey

The proportions of sandeels and non-sandeels fed to female common terns did vary significantly between 1991 and 1992 (χ^2_1 corrected for continuity = 14.62, $P < 0.001$, Figure 5.5). Female common terns were fed significantly more sandeels of greater than 8 cm length in 1991 compared to 1992 (χ^2_1 corrected for continuity = 14.15, $P < 0.001$, Figure 5.6). Female common terns were fed significantly more 0-4 cm non-sandeels and significantly fewer 8-12 cm non-sandeels in 1991 than in 1992 ($\chi^2_3 = 52.98$, $P < 0.001$, Figure 5.6). Rockling formed the overwhelming majority of non-sandeels in the 0-4 cm size category. No rockling larger than 6cm was brought to the colony in either year. Sprats constituted the majority of non-sandeels fed to females in both years.

5.3.2.3 Clutch size

On average pairs of common terns laid clutches of 2.75 in 1991 and 2.80 in 1992. In both years of the study the majority of birds laid three egg clutches and median clutch sizes did not differ significantly (Mann-Whitney U-test, $z_{\text{corrected for ties}} = -0.8652$, $P = 0.3869$, $n_{1991} = 50$, $n_{1992} = 32$, Table

Figure 5.4 1992 Common tern laying dates

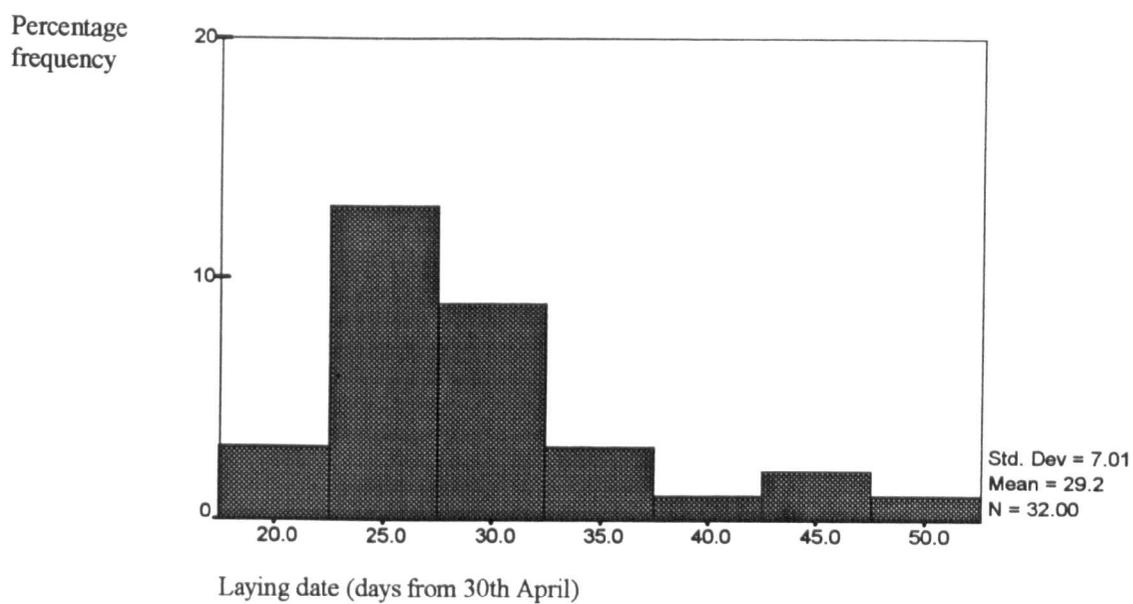


Figure 5.5 Proportions of sandeels and non-sandeels in common tern courtship prey in 1991 & 1992

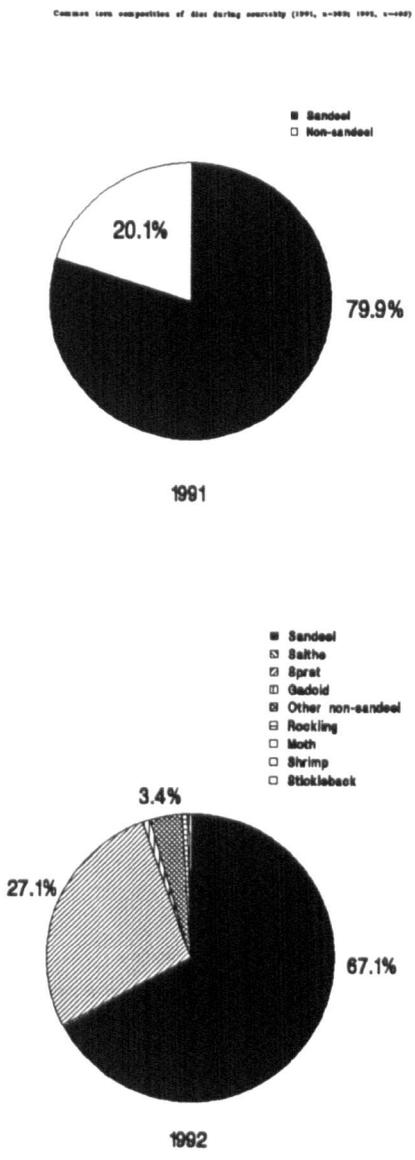
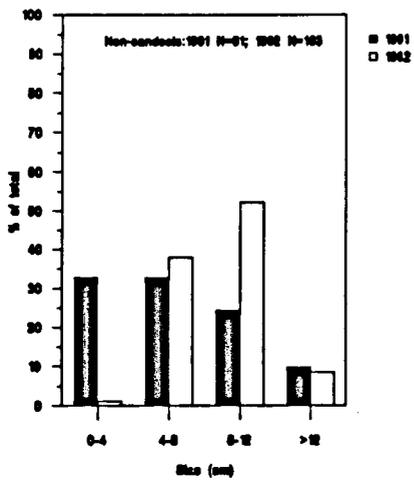
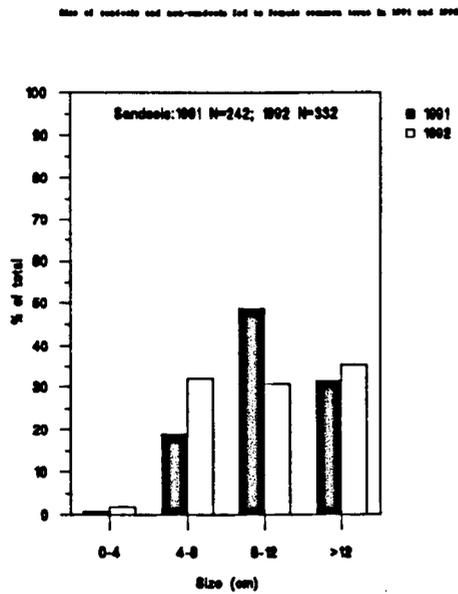


Figure 5.6 Proportions of sandeels and non-sandeels of different size classes in common tern courtship prey in 1991 & 1992



11). There was no difference between the two years in the proportions of clutches of two or fewer eggs, and of three eggs, ($\chi^2_1=1.15$, $P=0.28$).

Table 5.11 Percentage of common tern clutches of different size in 1991 and 1992

Year	Percentage of c/1	Percentage of c/2	Percentage of c/3	Total n
1991	3.9	11.8	84.3	51
1992	4.4	20.0	75.6	45

5.3.2.4 Egg dimensions and volume

Due to the substantial number of tests the level of significance was set at $\alpha=0.01$. No significant differences were found between any of the egg dimensions or volumes between years (Length "a": student's t-test $t_{s94}=-0.95$, $P=0.34$; breadth "a": student's t-test $t_{s94}=-0.43$, $P=0.67$; length "b": student's t-test $t_{s90}=-1.27$, $P=0.21$; breadth "b": student's t-test $t_{s90}=1.70$, $P=0.09$; length "c": $t_{s76}=-2.44$, $P=0.02$; breadth "c": student's t-test $t_{s76}=1.56$, $P=0.12$; Volume "a": student's t-test $t_{s94}=-0.81$, $P>0.05$; volume "b" egg: student's t-test $t_{s90}=0.62$, $P=0.54$; volume "c" egg: student's t-test $t_{s76}=0.45$, $P=0.66$, Table 5.12).

Table 5.12 Volumes of common tern a, b and c eggs in 1991 and 1992.

Year	Egg	Mean length (c.c.) \pm s.e.	Mean breadth (c.c.) \pm s.e.	Mean volume (cubic centimetres) s.e.	Number of eggs
1991	a	41.13 \pm 0.24	30.29 \pm 0.11	18.14 \pm 0.19	51
1992	a	41.46 \pm 0.26	30.41 \pm 0.25	18.46 \pm 0.36	45
1991	b	40.71 \pm 0.20	30.34 \pm 0.10	18.00 \pm 0.17	49
1992	b	41.09 \pm 0.22	30.06 \pm 0.13	17.84 \pm 0.20	43
1991	c	40.60 \pm 0.24	29.78 \pm 0.13	17.30 \pm 0.20	44
1992	c	41.41 \pm 0.22	29.30 \pm 0.31	17.13 \pm 0.34	34

The volume of those eggs that produced chicks that fledged were compared with those that did not (Table 5.13).

Table 5.13 Egg volumes of successful and unsuccessful common tern eggs in 1991 and 1992

Year	Egg volume (Fledged) ±s.e.(c.c.)	Egg volume (Failed) ±s.e.(c.c.)
1991	18.39±1.37 (n=39)	17.87±1.49 (n=110)
1992	18.82±1.34 (n=33)	17.97±1.93 (n=93)

Egg volume significantly affected the probability of fledging successfully in 1992 but not in 1991. (1991 student's t-test $t_{s147}=189$, $P=0.06$; 1992 student's T-test $t_{s124}= 2.34$, $P=0.021$).

	Sum of squares	Degrees of freedom	Mean Square	F	Significance of F
Main effects	16.14	2	8.07	4.59	0.011
Fledged	10.97	1	10.97	6.24	0.013
Year	1.95	1	1.95	1.11	0.29
Fledged * Year	0.03	1	0.03	0.02	0.89
Explained	16.56	3	5.52	3.14	0.03
Residual	529.32	301	1.76		
Total	545.88	304	1.80		

The two-way ANOVA shows that between years there was no significant difference in the egg volumes of eggs that resulted in fledged chicks compared to those that did not, and within each year the egg volumes of eggs that resulted in fledged chicks were significantly different compared to those that did not.

The fledging success of eggs within different categories were compared to further examine the influence of egg volume on fledging success

Table 5.14 Egg volumes of successful and unsuccessful common tern eggs in 1991

Egg category	Mean volume ± s.e. (c.c.) Fledged	Mean volume ± s.e. (c.c.) Failed	student's t value	Degrees of freedom	Probability
c1	-	18.18±1.25 (3)	-	-	-
c2/1	17.77±0.23 (3)	16.55±1.20 (4)	0.85	5	0.44
c2/2	-	17.44±0.77	-	-	-
c3/1	18.58±0.37 (18)	18.35±0.27 (26)	0.52	42	0.60
c3/2	18.27±0.32 (14)	18.26±0.23 (30)	0.04	42	0.97
c3/3	18.37±0.81 (4)	17.46±0.21 (40)	1.27	42	0.22
All	18.39±0.22 (39)	17.87±0.14 (110)	1.89	147	0.061

Table 5.15 Egg volumes of successful and unsuccessful common tern eggs in 1992

Egg category	Mean volume ± s.e. (c.c.) Fledged	Mean volume ± s.e. (c.c.) Failed	student's t value	Degrees of freedom	Probability
c1	18.23 (1)	17.49 (1)	-	-	-
c2/1	17.47±0.22 (3)	17.89±0.70 (8)	-0.36	9	0.73
c2/2	-	17.35±0.39 (11)	-	-	-
c3/1	19.01±0.40 (16)	19.05±0.78 (18)	-0.04	32	0.97
c3/2	18.99±0.34 (11)	17.86±0.25 (23)	2.65	32	0.01
c3/3	18.62±0.42 (2)	17.68±0.23 (32)	1.02	32	0.32
All	18.82±0.23 (33)	17.97±0.20 (93)	2.34	124	0.021

5.3.2.5 Clutch volume

The total clutch volumes did not differ between years (student's t-test, $t_{94}=0.93$, $P=0.354$, Tables 5.16) because in both years the majority of pairs laid clutches of three eggs.

Table 5.16 1991 and 1992 clutch volumes for common terns

Year	Clutch volume \pm s.e.	Number of clutches
1991	50.37 \pm 0.13	50
1992	49.53 \pm 1.90	32

5.3.2.6 Hatching, breeding and fledging success

On average pairs of common terns had a hatching success of 0.82 in 1991 and 0.76 in 1992. Average fledging success per pair was 0.32 in 1991 and 0.37 in 1992. Average breeding success was 0.75 in 1991 and 0.76 chicks fledged per pair in 1992. There were no significant differences in median hatching, fledging, or breeding success between the two years (Table 5.17 & 5.18).

Table 5.17 Median hatching, fledging, and breeding success of common terns in 1991 and 1992

Year	Median Hatching success	25 %	75%	Median Fledging success	25%	75%	Median Breeding success	25%	75%
1991	1 (n=51)	0.67	1	0.32 (n=46)	0	0.5	0.75 (n=51)	0	1
1992	1 (n=32)	0.67	1	0.29 (n=29)	0.33	0.5	0.88 (n=32)	0	1

Table 5.18 Mann-Whitney U-test $z_{\text{corrected for ties}}$ statistics for the comparisons of hatching, fledging, and breeding success of common terns between 1991 & 1992.

Breeding parameter	Mann-Whitney $z_{\text{corrected for ties}}$ statistic	Probability
Hatching success	-0.0299	0.9818
Fledging success	-1.0665	0.2862
Breeding success	-0.8283	0.4075

5.4 Intra-year variation in Arctic and common tern breeding parameters

5.4.1 Arctic tern 1991

To investigate seasonal effects on breeding parameters the breeding season was split into three periods in both years. These were from 21st May – 1st June (12 days), 2nd June – 13th June (12 days), and 14th June – 16th June (3 days). Due to the differing spread of laying dates in the two years it was not possible to have the statistical ideal of three periods of equal size.

5.4.1.1 Variation in clutch size with date.

Clutch sizes became significantly smaller with advancing calendar date (1991 Kruskal-Wallis one-way ANOVA $H_2=6.65$, $P=0.04$; 1992 Mann-Whitney U-test, $z=-2.57$, $n=74$, $P=0.01$, Table 5.19).

Table 5.19 Arctic tern median clutch size with 25% and 75% percentiles. Sample sizes are given in parentheses.

	Clutch size (Median, 25% and 75% percentiles) Percentages of clutches in each size class are shown in italics	Clutch size (Median, 25% and 75% percentiles) Percentages of clutches in each size class are shown in italics
	Year	
Period	1991	1992
1	2 (2,2) (n=38) <i>23.7, 65.8, 10.5</i>	2 (2,2) (n=64) <i>9.4, 87.5, 3.1</i>
2	2 (1,2) (n=46) <i>41.3, 58.7, 0</i>	2 (1,2) (n=10) <i>40.0, 60.0, 0</i>
3	1.5 (1,2) (n=16) <i>50.0, 50.0, 0</i>	No three egg clutches in 1992

5.4.1.2 Egg dimension and volume.

Dimensions of eggs laid on different dates were compared to examine whether birds which laid later in the season laid smaller eggs. Egg size and egg volume may have an effect on fledging success. Only the breadth of the "a" and "b" egg differed significantly with period in 1991, but a post-hoc Bonferroni comparison found no differences between groups in either case. However, "b" egg volume was significantly greater during the first period than during the second. (One-way ANOVA length of "a" by period, $F_{2,93}=0.57$, $P=0.57$; one-way ANOVA breadth "a" by period, $F_{2,93}=1.54$, $P=0.22$; one-way ANOVA volume of "a" egg by period $F_{2,93}=0.99$, $P=0.38$; one-way ANOVA length "b" by period, $F_{2,59}=0.61$, $P=0.55$; one-way ANOVA breadth "b" by period $F_{2,59}=3.46$, $P=0.04$; one-way ANOVA volume of "b" egg by period, $F_{2,59}=2.25$, $P=0.11$, followed by Bonferroni multiple comparison, Table 5.20).

Table 5.20 1991 Arctic tern egg dimensions and volumes by period (Sample sizes are given in parentheses, units are cm³).

Period	Length "a" Mean±s.e.	Breadth "a" Mean±s.e.	Volume "a" Mean±s.e.	Length "b" Mean ±s.e.	Breadth "b" Mean ±s.e.	Volume "b" Mean±s.e.
1	40.8±0.3 (n=38)	29.6±0.2 (n=38)	17.19±0.18 (n=38)	40.1±0.3 (n=27)	29.3±0.2 (n=27)	16.46±0.22 (n=27)
2	41.0±0.3 (n=42)	29.2±0.1 (n=42)	16.82±0.20 (n=42)	39.8±0.3 (n=27)	28.7±0.2 (n=27)	15.80±0.25 (n=27)
3	40.5±0.4 (n=16)	29.2±0.6 (n=16)	16.68±0.58 (n=16)	39.3±0.4 (n=8)	29.5±0.3 (n=8)	16.44±0.42 (n=8)

5.4.1.3 Clutch volume

The average volume of clutches laid during the first period was significantly greater than that of clutch volumes of clutches laid during the second and third period (One-way ANOVA clutch volume by period, $F_{2,94}=6.10$, $P=0.04$, followed by post-hoc Bonferroni comparison, Table 5.21).

Table 5.21 1991 Arctic tern clutch volume by period (Sample sizes are in parentheses)

Period	Clutch volume (Mean±s.e., c.c.)
1	30.74±0.16 (n=38)
2	26.35±0.12 (n=43)
3	24.90±0.24 (n=16)

5.4.1.4 Hatching, fledging, and breeding success

Hatching success was similar in all periods (Kruskal-Wallis one-way ANOVA $H_2=2.36$, $n=91$, $P=0.31$, Table 5.22). However fledging success improved throughout the 1991 breeding season with the greatest success coming in the final period (Fledging success: Kruskal-Wallis one-way ANOVA $H_2=9.76$, $n=49$, $P=0.008$). Breeding success followed a similar pattern (Breeding success: Kruskal-Wallis one-way ANOVA $H_2=8.51$, $n=91$, $P=0.01$).

Table 5.22 Arctic tern hatching, fledging and breeding success by period in 1991. Medians are given with the 25 % and 75 % percentiles. Sample sizes are in parentheses. Mean and standard error are in italics.

Period	Hatching success	Fledging success	Breeding success
1	0 (0,1) (n=38) <i>0.40 ± 0.08</i>	0 (0,0.5) (n=16) <i>0.19 ± 0.08</i>	0 (0,0) (n=38) <i>0.13 ± 0.06</i>
2	0.5 (0,1) (n=42) <i>0.56 ± 0.07</i>	0.5 (0,1) (n=27) <i>0.54 ± 0.09</i>	0 (0,1) (n=42) <i>0.45 ± 0.10</i>
3	0.5 (0,1) (n=11) <i>0.50 ± 0.15</i>	1 (1,1) (n=6) <i>0.83 ± 0.17</i>	0 (0,1) (n=11) <i>0.64 ± 0.24</i>

5.4.2 Arctic tern 1992

5.4.2.1 Variation in clutch size with date.

In 1992 the laying period was less protracted than in 1991. As a consequence of this only eggs and clutches laid during the first and second periods could be compared. Clutch size was significantly smaller during the second period than in the first (Mann–Whitney U–test, $z_{\text{corrected for ties}} = -2.57$, $P=0.01$, Table 5.23)

Table 5.23 1992 Arctic tern median with 25% and 75% percentiles clutch size by period. Sample sizes are given in parentheses. Means and standard errors are given in italics.

Period	Clutch size (Median, 25% and 75% percentiles)
1	2 (2,2) (n=64) <i>1.94 ± 0.04</i>
2	2 (1,2) (n=10) <i>1.60 ± 0.16</i>

5.4.2.2 Egg dimension and volume.

Neither egg dimensions nor egg volumes differed between the two periods in 1992. (Length "a" egg by period: student's t–test, $t_{872} = -0.34$, $P=0.74$; breadth "a" egg by period: student's t–test,

$t_{s72}=2.72$, $P=0.008$; volume of "a" egg by period: student's t-test, $t_{s72}=1.82$, $P=0.07$; length "b" egg by period: student's t-test, $t_{s60}=-0.33$, $P=0.74$; breadth "b" egg by period: student's t-test, $t_{s60}=0.86$, $P=0.39$; volume of "b" egg by period: student's t-test, $t_{s60}=0.42$, $P=0.68$, Table 5.24)

Table 5.24 Arctic tern 1992 Egg dimensions and volumes by period (Sample sizes are given in parentheses, units are cm^3).

Period	Length "a" Mean \pm s.e.	Breadth "a" Mean \pm s.e.	Volume "a" Mean \pm s.e.	Length "b" Mean \pm s.e.	Breadth "b" Mean \pm s.e.	Volume "b" Mean \pm s.e.
1	40.9 \pm 0.2 (n=64)	29.7 \pm 0.1 (n=64)	17.36 \pm 0.15 (n=64)	40.2 \pm 0.2 (n=57)	29.3 \pm 0.1 (n=57)	16.54 \pm 0.14 (n=57)
2	41.1 \pm 0.6 (n=10)	29.0 \pm 0.3 (n=10)	16.59 \pm 0.45 (n=10)	40.5 \pm 1.2 (n=5)	29.0 \pm 0.5 (n=5)	16.32 \pm 0.72 (n=10)

5.4.2.3 Clutch volume

Clutch volume during the first period was significantly greater than during the second period (student's t-test clutch volume by period, $t_{s72}=3.31$, $P=0.001$, Table 5.25).

Table 5.25 1992 Arctic tern clutch volume by period (Sample sizes are in parentheses, units are cm^3)

Period	Clutch volume (Mean \pm s.e.)
1	32.62 \pm 0.82 (n=64)
2	24.76 \pm 0.29 (n=10)

5.4.2.4 Hatching, fledging, and breeding success

None of these measures of breeding performance varied between the two periods (Hatching success, Mann-Whitney U-test, $z_{\text{corrected for ties}}=-0.30$, $P=0.76$; fledging success, Mann-Whitney U-test $z_{\text{corrected for ties}}=-0.98$, $P=0.32$; breeding success, Mann-Whitney U-test, $z_{\text{corrected for ties}}=-1.51$, $P=0.13$, Table 5.26).

Table 5.26 1992 Arctic tern hatching, fledging and breeding success. Medians are given with the 25% and 75% percentiles. Sample sizes are given in parentheses. Means and standard errors are in italics.

Period	Hatching success	Fledging success	Breeding success
1	1 (1,1) (n=61) <i>0.82 ± 0.04</i>	0.5 (0.5, 0.5) (n=54) <i>0.51 ± 0.04</i>	1 (0,1) (n=61) <i>0.79 ± 0.07</i>
2	1 (1,1) (n=10) <i>0.85 ± 0.11</i>	0.5 (0, 0.5) (n=9) <i>0.39 ± 0.14</i>	0.5 (0,1) (n=10) <i>0.50 ± 0.17</i>

5.4.3 Common tern 1991

Period 1 was from the 20th–27th May, period two was from the 28th May – 4th June, and period three was from 5th June–13th June.

5.4.3.1 Clutch size

Clutch size declined with period in both years. The decline was more pronounced in 1992 due to the more protracted season (1991 Mann–Whitney U–test clutch size by period $Z=-2.03$, $P=0.04$; 1992 $\chi^2_2=19.48$, $P=0.0001$, Table 5.27).

Table 5.27 Common tern 1991 & 1992 Clutch sizes by period. Medians are given with the 25% and 75% percentiles. Sample sizes are in parentheses.

Period	Clutch size (Median, 25% and 75% percentiles) Percentages of clutches in each size class are shown in italics	Clutch size (Median, 25% and 75% percentiles) Percentages of clutches in each size class are shown in italics
Year	1991	1992
1	3 (3,3) (n=30) <i>3.3, 3.3, 93.3</i>	3 (3,3) (n=16) <i>0, 0, 100</i>
2	3 (2,3) (n=21) <i>4.8, 23.8, 71.4</i>	3 (3,3) (n=9) <i>0, 11.1, 88.9</i>
3	-	2 (2,2) (n=6) <i>16.7, 66.7, 16.7</i>

5.4.3.2 Egg dimensions and volumes

Only the breadth of the "a" egg varied with period in 1991. All other egg dimensions and individual egg volumes showed no difference with date (Length of "a" egg by period: student's t-test, $t_{349}=-0.17$, $P=0.86$; breadth of "a" egg by period: student's t-test, $t_{349}=2.45$, $P=0.02$; volume of "a" egg by period: student's t-test, $t_{349}=1.49$, $P=0.14$; length of "b" egg by period: student's t-test, $t_{347}=-1.28$, $P=0.21$; breadth of "b" egg by period: student's t-test, $t_{347}=1.25$, $P=0.22$; volume of "b" egg: student's t-test, $t_{347}=0.20$, $P=0.84$; length of "c" egg by period: student's t-test, $t_{342}=-0.45$, $P=0.66$; breadth of "c" egg by period: student's t-test, $t_{342}=0.37$, $P=0.71$; volume of "c" egg by period: student's t-test, $t_{342}=0.02$, $P=0.98$, Table 5.28).

Table 5.28 1991 common tern Egg dimension and volumes by period Means are given \pm standard error.

Sample sizes are in parentheses. Units are cubic centimetres.

Period	Length "a"	Breadth "a"	Volume "a"	Length "b"	Breadth "b"	Volume "b"	Length "c"	Breadth "c"	Volume "c"
1	41.1 \pm 0.3 (n=30)	30.5 \pm 0.1 (n=30)	18.38 \pm 0.23 (n=30)	40.5 \pm 0.2 (n=29)	30.4 \pm 0.1 (n=29)	18.03 \pm 0.20 (n=29)	40.5 \pm 0.3 (n=28)	29.8 \pm 0.1 (n=28)	17.31 \pm 0.24 (n=28)
2	41.2 \pm 0.4 (n=21)	30.0 \pm 0.2 (n=21)	17.80 \pm 0.33 (n=21)	41.0 \pm 0.3 (n=20)	30.2 \pm 0.2 (n=20)	17.96 \pm 0.30 (n=20)	40.7 \pm 0.4 (n=16)	29.7 \pm 0.2 (n=16)	17.30 \pm 0.38 (n=16)
3	-	-	-	-	-	-	-	-	-

5.4.3.3 Clutch volume

Clutch volume did not differ significantly between the two periods in 1991 (student's t-test clutch volume by period, $t_{349}=1.54$, $P=0.13$, Table 5.29).

Table 5.29 1991 Common tern clutch volumes

Period	Clutch volume (Mean \pm s.e., c.c.)
1	51.97 \pm 0.14 (n=30)
2	48.09 \pm 0.22 (n=21)

5.4.3.4 Hatching, fledging, and breeding success

None of these measures of breeding performance varied significantly between the two periods in 1991 (Mann–Whitney U–tests, hatching success by period, $z_{\text{corrected for ties}}=-0.82$, $P=0.41$; fledging success by period, $z_{\text{corrected for ties}}=-0.62$, $P=0.54$; breeding success by period, $z_{\text{corrected for ties}}=-0.34$, Table 5.30).

Table 5.30 Hatching, fledging and breeding success by period for common terns in 1991. Medians are given with the 25% and 75% percentiles. Means and standard errors are given in italics.

Period	Hatching success $n_1=30$ $n_2=21$	Fledging success $n_1=27$ $n_2=19$	Breeding success $n_1=30$ $n_2=21$
1	1 (0.67,1) <i>0.80 ± 0.06</i>	0.33 (0,0.42) <i>0.30 ± 0.05</i>	1 (0,1) <i>0.70 ± 0.11</i>
2	1 (1,1) <i>0.85 ± 0.07</i>	0.33 (0,0.67) <i>0.35 ± 0.07</i>	1 (0,1) <i>0.81 ± 0.18</i>

5.4.4 Common tern 1992

5.4.4.1 Clutch size

Median clutch size was significantly smaller during the third period than during the first two in this year (Kruskal–Wallis one–way ANOVA $H_2=19.48$, $P=0.0001$).

5.4.4.2 Egg dimensions and volumes

Only the breadth of the second egg of a clutch varied significantly with period in 1992. Second eggs laid during the first period were broader than second eggs laid during the third period (One–way ANOVA breadth "b" by period $F_{2,27}=3.88$, $P=0.03$, followed by Bonferroni multiple comparison procedure). Although an analysis of variance showed significant differences between the volume of "b" eggs, a multiple comparison found no significant differences between the groups (One–way ANOVA volume of "b" egg by period $F_{2,27}=3.70$, $P=0.04$, followed by Bonferroni multiple comparison). There were no other differences in egg dimensions, or egg volumes between periods (One–way ANOVA length "a" by period, $F_{2,28}=0.11$, $P=0.90$; one–way ANOVA breadth "a" by period, $F_{2,27}=2.14$, $P=0.14$; one–way ANOVA volume of "a" egg by period $F_{2,28}=1.62$,

P=0.22; One-way ANOVA length "b" by period $F_{2,27}=1.19$, P=0.32; one-way ANOVA length "c" by period $F_{2,22}=0.36$, P=0.70; one-way ANOVA breadth "c" by period $F_{2,22}=0.13$, P=0.88; one-way ANOVA volume "c" egg by period $F_{2,22}=0.07$, P=0.93, Table 5.32).

Table 5.32 Common tern 1991 egg dimension and volumes by period. Means are given \pm standard error.

Sample sizes are in parentheses.

Period	Length "a"	Breadth "a"	Volume "a"	Length "b"	Breadth "b"	Volume "b"	Length "c"	Breadth "c"	Volume "c"
1	41.5 \pm 0.4 (n=16)	30.6 \pm 0.2 (n=16)	18.66 \pm 0.34 (n=16)	41.5 \pm 0.3 (n=16)	30.5 \pm 0.2 (n=16)	18.57 \pm 0.32 (n=16)	41.7 \pm 0.3 (n=16)	29.3 \pm 0.6 (n=16)	17.26 \pm 0.63 (n=16)
2	41.2 \pm 0.5 (n=9)	31.5 \pm 1.0 (n=9)	19.76 \pm 0.15 (n=9)	40.6 \pm 0.5 (n=9)	30.1 \pm 0.2 (n=9)	17.67 \pm 0.27 (n=9)	41.3 \pm 0.6 (n=8)	29.5 \pm 0.2 (n=8)	17.32 \pm 0.48 (n=8)
3	41.3 \pm 1.0 (n=6)	29.5 \pm 0.3 (n=6)	17.25 \pm 0.58 (n=6)	41.0 \pm 1.0 (n=5)	29.5 \pm 0.1 (n=5)	17.18 \pm 0.49 (n=5)			

5.4.4.3 Clutch volume

Clutch volume was significantly smaller in period three than in periods one and two, one-way ANOVA clutch volume by period $F_{2,28}=18.72$, $P<0.00001$, followed by Bonferroni multiple comparison procedure, Table 5.33).

Table 5.33 1992 Common tern clutch volumes. Means are given \pm standard error. Sample sizes are in parentheses.

Period	Clutch volume
1	54.49 \pm 0.94 (n=16)
2	52.82 \pm 0.28 (n=9)
3	34.31 \pm 0.45 (n=6)

5.4.4.4 Hatching, fledging, and breeding success

There were no significant differences between periods in any median measures of breeding performance in 1992, Hatching success, Kruskal-Wallis one-way ANOVA $H_2=3.00$, P=0.22; Fledging success, Kruskal-Wallis one-way ANOVA $\chi^2_2=0.12$, P=0.94; Breeding success, Kruskal-Wallis one-way ANOVA $\chi^2_2=5.07$, P=0.08, Table 5.34).

Table 5.34 Hatching, fledging and breeding success by period for common terns in 1992. Medians are given with the 25% and 75% percentiles. Means and standard errors are given in italics.

Period	Hatching success $n_1 = 16$ $n_2 = 9$ $n_3 = 6$	Fledging success $n_1 = 16$ $n_2 = 9$ $n_3 = 4$	Breeding success $n_1 = 16$ $n_2 = 9$ $n_3 = 6$
1	1 (0.83,1) <i>0.90 ± 0.05</i>	0.42 (0.17, 0.67) <i>0.39 ± 0.07</i>	1 (0.5,2) <i>1.06 ± 0.19</i>
2	1 (1,1) <i>0.93 ± 0.05</i>	0.33 (0.33, 0.5) <i>0.41 ± 0.09</i>	1 (1,1) <i>1.00 ± 0.17</i>
3	0.75 (0,1) <i>0.58 ± 0.20</i>	0.25 (0,0.75) <i>0.38 ± 0.24</i>	1 (0,1) <i>0.33 ± 0.21</i>

5.5 Discussion

5.5.1 Inter-year differences

5.5.1.1 Arctic tern

The significantly later, and more protracted, breeding season in 1991 may have been a consequence of poorer pre-breeding body condition, or poorer conditions of prey availability during the courtship period or a combination of both these factors in 1991. The differences in adult Arctic tern body masses between the two years given in chapter 4 suggest that breeding birds in 1991 were indeed in poorer condition.

The smaller median clutch in 1991 may also have occurred for the same reason. Birds of similar quality were known to have nested in both years, as some of the same individuals colour-ringed in 1991 also bred in 1992. The apparent non-breeding of some adults mentioned in chapter 2 is of course the earliest opportunity to modify the investment in any one breeding attempt: that of whether to breed or not. Although birds which definitely bred in 1992 apparently did "better" than birds which bred in 1991, they may have been a biased sample of birds less affected by the incurred costs of the previous year's breeding season or the costs of migration and maintenance between 1991 and 1992. The lack of any significant differences in the proportions of sandeels and non-

sandeels in courtship feeding of Arctic terns in 1991 outlined in section 5.3.1.2 suggests that any effect of courtship feeding on clutch size was due to feeding rate rather than the quality of individual prey items. Unfortunately it was not feasible to collect data on courtship feeding rate in either of the two years of this study, as it was not possible to mark birds early in the season and enable individuals to be identified.

Modifications to the reproductive investment subsequent to the decision to breed or not appear to be mediated through the modification of the clutch size and not through the investment in individual eggs, which concurs with the findings of Coulson & Horobin (1976). The significant difference in clutch volumes between the two years was due to the greater proportion of 2 egg clutches laid in that year.

The difference in the effect egg volume had on fledging success in the two years may have been due to the very different environmental conditions during the two breeding seasons. In 1991 a substantial proportion of eggs which did not hatch were abandoned by adults and/or taken by black-headed gulls. During the early weeks of the 1991 breeding season there was a prolonged period of inclement weather, with strong northerly winds and rain. As birds may have been in poorer condition, (suggested by the lower adult body mass), they may have been more likely to desert. The significant effect of egg volume on fledging success in 1992 may have been due to the improved environmental conditions during the 1992 breeding season. In the absence of the acute and drastic effects of the poor weather experienced during 1991, the advantages gained through larger egg size may have come to the fore having previously been masked by stronger environmental effects mediated through adult incubation behaviour.

The highly significant difference in breeding success was due solely to the difference in hatching success between the two years. The lack of any differences in fledging success suggests that despite inter-year differences in chick diet and adult foraging performance (see Chapter 6) provisioning of chicks was adequate in both years. However slower chick growth may affect future survival (see chapter 7 for more detail about Arctic and common tern growth patterns in 1991 and 1992).

Uttley *et al.* (1989) suggest that terns may persist in laying large clutches when faced with poor foraging conditions early in the breeding season as they have no means of knowing what food

supplies will be later in the chick rearing period. The significant differences in clutch size between years found in this study suggest the extent of this is not completely under the control of the breeding adults: Do adults choose to lay small clutches because they are in poor condition or solely because they are in poor condition do they lay smaller clutches ?

Another reasonable possibility is that breeding birds may optimise their investment on a finer than annual scale in response to different aspects of its state. A general state–dynamic model describing a general technique for finding the optimal life–history when an organism's strategy is allowed to depend on other aspects of its state is outlined in M^CNamara & Houston, (1992). One of the model's strengths is that it incorporates the realistic premise that an animal's state outwith the breeding season may have some bearing on its reproductive performance during it. This may be the case for an extreme long–distance migrant like common, and especially, Arctic terns. This modelling approach allows one to compare the initial value of a state variable, such as energy reserves at the beginning of the breeding period with their value at the end, under different behavioural strategies. The dynamic nature of the model means behaviour (modelled in this case, but potentially observed) is evaluated not as current but as future reproductive success. Although in an observationally based study such as this one the optimal clutch size is unknown other predictions of the model are borne out by the collected data for example different birds laid different clutch sizes. These may represent different optimal clutch sizes for different parents under similar environmental conditions. What influences quality, what aspects of quality have long–term effects, and the implications for clutch size remain areas where more research is required (M^CNamara & Houston, 1992).

5.5.1.2 Common tern

The data collected for common terns are unfortunately not as extensive as for Arctic terns. In 1991 no adult masses were recorded and no data on chick diet were obtained either. Consequently any hypotheses regarding the breeding performance of this species are more modest of necessity.

Although prey types fed to females during courtship did differ significantly during the years the absence of any significant differences in clutch size, or any of the individual measures of egg size suggest that the combination of courtship prey type and courtship feeding rate was adequate in both

years. The differing proportions of sandeels and non-sandeels in courtship diet suggest some flexibility on the part of male common terns in prey selection.

The lack of any significant differences between the two years suggests that the common terns were better able to cope with the inclement weather conditions of 1991 than the sympatric Arctic terns, and may have been in better condition early in the breeding season.

No common terns were double-brooded although double-brooding has been recorded in some colonies in the United States (Hays, 1984; Yuan, 1993). In neither year did any common terns raise three chicks to fledging. Courtney & Blokpoel (1980) give details of a colony where raising three chicks to fledging is apparently common. Either foraging conditions were exceptionally favourable during that study, or the experimental procedure used in this one was affecting the fledging prospects of the third chick. In a study where nest sites were not surrounded by fences, third chicks managed to fledge by wandering from the natal nest-site and being adopted by other terns (Morris, Woulfe & Wichert, 1991). The fences used in this study may have artificially inflated the mortality rate of third chicks.

5.5.2 General

Coulson & Horobin (1976) found that the oldest Arctic terns (> 8 years old) arrive at the colony first, but that there were no significant differences in the mean laying date between age classes. An important consequence of this is that older birds have the first choice of nest sites and have a longer period in the colony prior to egg laying. This would give older birds an advantage in improving body condition after their arrival at the colony post-migration.

This study did not have the considerable advantage of substantial numbers of known-aged birds that other seabird studies (Weimerskirch, 1990; Wooller *et al.*, 1990; Hamer & Furness 1991) have had. No effort was made to trap the earlier laying Arctic terns in 1991 due to the poor weather conditions and possible loss of study birds if an attempt to trap them had been made. Six of the birds trapped later in the season were of known age. These all laid after 4th June (4th, 5th, 11th, 13th, 29th June). Their ages were five, thirteen, seventeen, twenty, twenty-four, and twenty-eight year old respectively. This suggests that older birds may have achieved better condition and/or been better able to maintain their breeding attempt, although weather later in the 1991 breeding season

was better than earlier in the season (pers. obs.). The average Arctic tern may expect to have seven opportunities to breed during its lifetime (Coulson & Horobin, 1976). Five of these six birds had had more than the lifetime average breeding attempts.

The effect of egg volume on fledging success in 1992 is similar to that found in other species of birds where chicks hatching from larger eggs have a higher probability of survival to fledging, and may show better growth, than those hatching from smaller eggs (Parsons 1970; Nisbet 1973; Davis 1975; review by Williams, 1994). Nisbet (1978) found that egg size was an important determinant of chick survival during the first few days, independent of parental care. Few studies have attempted to distinguish between the effects of egg size and parental quality. In one of these, parental quality was found to be a more important determinant of chick fledging than egg size, although egg size also had an effect (Bolton, 1991). Age is a confounding variable as the relationship between age and egg size is a quadratic one, and small eggs may be produced by both inexperienced and experienced but old birds. The largest eggs may be laid by intermediately aged birds. The advantages of hatching from a larger egg may be due to more vigorous growth promoting better survival (Amundsen & Stokland, 1988). However there may be advantages in hatching from a smaller egg. Adults laying smaller eggs may be able to begin breeding earlier, or smaller chicks could require less food, both of which could be an advantage in some years (Furness 1983). Also eggs with smaller yolks and lower energy by mass may not necessarily be of lower quality as more albumen may lead to a larger hatchling (Boersma 1982). Egg size may affect fledging success by enabling larger chicks with more advanced escape behaviour to escape gape-limited predators (Quinn & Morris 1986). Quality effects may only appear during poor food years, under poor environmental conditions (Hamer & Furness 1991). However, as the main determinant of breeding success between the two years was due to differential hatching success, and as this in turn was due to environmental conditions perhaps a more reasonable conclusion and one which relies upon the minimum of assumptions is that breeding success in 1991 was primarily determined by stochastic weather events. Only a longer term study on the same individuals or an experimental study could attempt to investigate the effects of parental quality. The significantly differing proportions of one and two egg clutches between 1991 and 1992 for Arctic terns suggest some modification of reproductive investment.

5.5.3 Weather effects

Unfortunately neither weather nor prey availability data were available for this study. Temporary reductions in clutch size, egg size and breeding success of common terns in the Wadden Sea were correlated with heavy rainfalls in the days preceding egg-laying (Becker, Finck, & Anlauf, 1985). Food availability at the breeding area is an important factor influencing the time of egg-laying as well as clutch size and egg size as a consequence of variations in courtship feeding. Courtship feeding affects both clutch and egg size in terns. Food availability varies with the weather, hence foraging ability of terns varies with weather conditions (Dunn 1975, Taylor 1983,) which affect both foraging success and foraging area (Burton & Thurston, 1959; Lehtonen, 1981). Rainfall may directly affect clutch size (Lemmetynen, 1973). This may partially explain the recorded differences between the two years, with poor weather affecting the rate of courtship feeding, and the quality of courtship prey, and this in turn affecting the clutch size of female Arctic terns in 1991. As no birds were marked early in the season in 1991 no data is available on rate, but some conclusions may be drawn on courtship prey. Weather may affect chick mortality through the effects of wind and rain (Becker & Specht 1989).

In one study where prey abundance was known to differ between two colonies one in Shetland, the other on Coquet island (albeit only in terms of successful and unsuccessful colonies) no difference was found in the clutch size, egg size or hatching success between them during a period of poor prey abundance at one of the colonies. No data were presented on the weather conditions during the egg laying period in that study. The lack of any significant differences in fledging success for the two species in both years suggest that weather conditions and parental care was similar in both years.

Significant inter-year and seasonal differences in courtship feeding rate have been recorded in other studies, although these had no effect upon clutch weight (Morris, 1986). In one year courtship feeding rate by late breeding common terns were markedly lower than those of peak nesters in that year. One year later there was no difference (Morris 1986). I suggest that the courtship feeding rate and quality for Arctic terns in 1992 was of a higher quality than in 1991. The data also suggest that it may not be optimal to breed early in every year. In some year older birds

may delay laying. If prey availability was different between the two year then age may have had a more marked effect on breeding success in the year in which prey availability was poorest. Hamer and Furness (1991) report such a trend for Great skuas breeding under conditions of different prey availability.

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Chapter 6 Prey selection and foraging performance of Arctic and common terns

6.1 Introduction

Variations in the type and size of prey fed to chicks have been reported in both terrestrial and marine birds. Both availability and chick age are important determinants of this variation. For example Moreno (1987) reported a decrease in the proportion of spiders in the diet of nestling wheatears *Oenanthe oenanthe* with chick age but not with season, although the degree of correlation between the covariates chick age and date was not reported and may have confounded his multiple regression analysis. Increases in the proportions of chitinous prey in the diet of passerines may be due to improved digestive capabilities of chicks with age. Alternatively chicks may be able to handle prey better as they grow older. Grundel (1990) reported both age and seasonal effects in chick provisioning in the mountain chickadee *Parus gambeli*. Similar age related trends in chick diet have been found amongst the Alcidae (Harris & Hislop 1978) and amongst the Sternidae (Langham 1968, Lemmetyinen 1973). Often it is uncertain whether availability or shifts of preference is the more important factor in determining prey choice.

Fagerstrom, Moreno & Carlson (1983) developed a theoretical model to examine the effects chick age might have on prey selection by parents. They suggested that the "receptive and digestive capacity of the nestlings during the early phases of development would impose a constraint on the foraging capacity of the parents by forcing them to collect and deliver loads of smaller size than would be energetically optimal." They predicted an increase in the mean load size during chick rearing as a consequence of this constraint. Load number in terns is on the whole fixed as it is unusual for a bird to bring more than one fish back to the colony in its bill, although load mass varies with the size of prey caught. Central to all energy optimisation models is the assumption that given equal availability and distribution of prey all foragers should select food in a consistent, repeatable, though perhaps stochastic manner (Grundel 1990). If prey type and size available varies seasonally interpretation of data collected in the field to test hypotheses related to this and other prey selection

models will be complicated. In this study, variation in the chick diet provisioning patterns were examined in relation to both chick age and time of season in Arctic and common terns.

However the effects of chick age and prey availability have rarely been partitioned unequivocally in studies into their relative importance in explaining variation in chick provisioning. This makes interpretation of which is the more important determinant of chick provisioning, chick age or the seasonal availability of prey, difficult. This part of the study aimed to examine the relative importance of these two factors in determining provisioning of chicks in common terns. Since terns breed synchronously an experimental approach was used to do this. In order to test the null hypothesis that chick age had no effect on the range of prey types and sizes fed to chicks of different ages, an egg storage experiment was performed to separate the chick age and seasonal effects by delaying the hatching of an experimental group. This fulfilled the requirement of having differently aged chicks being fed at the same time, under what were assumed to have been similar conditions of prey availability for the two groups.

6.2 Methods

6.2.1 General methods

The numbers of nests observed in both years are given in chapter 2. During the 1991 breeding season no observations of common terns were made during the chick rearing period. In 1992 observational watches of Arctic and common terns were contemporaneous. This enabled a comparison of the types of prey fed to the two sympatric species of tern.

Data collected for known nest sites only were used. Sample sizes (number of nests from which prey information were collected) were 50 and 21 for Arctic terns in 1991 and 1992 respectively, and 35 for common terns in 1992.

Data from experimental and non-experimental nests are analysed separately as appropriate.

6.2.2 Prey size

Where subsequent statistical analyses using the size categories given in chapter two led to expected frequencies of less than one and/or the proportion of categories with expected frequencies

of less than 5 were > 20% of the total, these four size categories were collapsed into two categories (less than 8 cm and greater than 8 cm).

6.2.3 Prey energy content

Energy values for sandeels and sprats were calculated using the values given by Hislop, Harris & Smith (1991) (June figure Sandeel $E = 0.0024 \text{ Length}^{3.806}$; Sprat $E = 0.0096 \text{ Length}^{3.845}$. Calorific value determined by calorimetry. N.B. these are energy contents for fish collected from seabirds). No equivalent equations are available for rockling (Uttley, 1991). Consequently the energy content of rockling are those used by Uttley 1991 and are a fixed value of 2.051 kJ fish⁻¹. Details of energy values of different sizes of sandeels and sprats are given in Table 6.1.

Table 6.1 Calculated energy values of sandeels *Ammodytes sp.* and Sprats *Sprattus sprattus* (kJ fish⁻¹ of each size).

Prey size (cm)	Sandeel energy content (kJ)	Sprat energy content (kJ)
1 (0-<4)	0.034 (2 cm)	0.138
2 (>4-<8)	2.197 (6 cm)	9.425
3 (>8-<12)	15.354 (10 cm)	67.185
4 (>12-<16)	55.255 (14 cm)	244.982

Data were collected on prey brought to the nest by breeding adults between the dates shown below (Table 6.2).

Table 6.2 Species/year combinations for dates of data collection

Species/year	Period of data collection
Arctic tern 1991	18th June–29th July
Arctic tern 1992	13th June–17th July
Common tern 1992	28th June–28th July

Nest sites where neither the laying date of the first egg nor its hatch date were known were excluded for both species for both years. Where hatching date was unknown it was estimated as laying date plus twenty-two days (the mean incubation period for both species in both years).

Chick age was calculated by subtracting hatching date from the day of observation. Both of these temporal measures were expressed as days after the 30th April. Chicks were grouped into three categories according to age: 0–6 days old; 7–13 days old; and 14–20 days old.

Only prey fed to chicks aged between 0 and 20 days old were included in analyses of prey type and prey size brought to the colony to feed chicks in both years. In analyses examining prey size, only prey of a known type and of a known size were included.

Prey were identified to species level whenever possible. However, if a prey item was unidentified but was obviously not a sandeel, and not a sprat or a rockling, it was categorised as 'other non-sandeel'. All previous records of sandeels from Druridge bay bar one have been of *Ammodytes marinus* (Walker, 1984). Terns may have been feeding elsewhere. However without telemetric data, that was outwith the logistic and budgetary means of this study, it was not possible to establish with any certainty where both species were feeding.

Where necessary prey were grouped into two categories, sandeels and non-sandeels, to satisfy statistical criteria necessary for the valid application of the Chi-square test. Non-sandeels were classified as all known prey types which weren't sandeels and included the category 'other non-sandeels'.

The day was split into four periods (Period 1: 4 a.m. – 8.29 am.; Period 2 : 8.30 a.m. – 12.59 p.m.; Period 3: 1.00 p.m. – 5.29 p.m.; Period 4: 5.30 p.m. – 9.59 p.m.).

No distinction was made in 1991 between sprats and rockling less than 8 cm in length but these were separated in 1992. However all sprats greater than 8 cm in length were correctly identified. No rockling greater than 6 cm long was brought back to the colony by either species in either year. Analyses of prey size effects are limited to sandeels in 1991 and to sandeels and sprats in 1992 as a consequence of this.

6.2.4 Foraging rate/Profitability analyses.

Foraging rate was calculated on a per nest basis. Only first visits to the nest with a prey item were included. Only visits to the nest site by known individuals were recorded. If a known bird was seen to pass a prey item to the chick, leave the nest site, and return with another prey item, this was counted as a visit. This removed complications due to repeat visits to the nest with the same prey item. The number of visits to a nest within a watch period on a particular watch date was recorded for each nest. This figure was divided by the number of hours within that watch to give a prey delivery rate of number of feeds per hour. This figure was divided by the current brood size to give a value for the number of feeds per chick per hour. Analyses were possible for Arctic tern in 1991 and 1992 and for common terns in 1992. Profitability was calculated using the energy values given above. Profitability was measured as energy delivered to the nest per minute's absence. Analyses of profitability are limited to 1992 data due to the possible confusion of small sprats with rockling in 1991. However as sandeels were consistently correctly identified in both years a between years comparison of the energy and profitability of this prey type was possible. Analyses were restricted to sandeels, sprats, and rockling as these accounted for greater than 98 % of all prey brought to the nest in both years. Analyses of diet were limited to exclude fish fed to chicks from the experimental group.

6.2.5 Resistance of eggs to chilling

Eggs from birds of a range of species and genera have been found to be pre-adapted to chilling (Webb 1987). This property has been studied for its inherent interest and as part of other studies. It is also used commercially in the storage of eggs of the domestic fowl (Mather and Laughlin 1976). Not all of these studies have used newly laid eggs. Some have been primarily concerned with the effects of chilling upon embryos of different ages. The age of the embryo can strongly affect the survivorship of embryos and their subsequent hatchability. This is especially the case at low temperatures and for storage durations of more than several hours (Webb, 1987). Species may also differ in their age-specific resistance to chilling (Gaston and Powell, 1989).

No specific studies on the resistance of tern eggs to chilling have been undertaken. However there is some evidence that common tern eggs and embryos can withstand chilling throughout

incubation. In a study of common terns subject to predation by Great Horned owls *Bubo virginianus*, adult terns deserted the colony for 6.5–8 hours each night throughout incubation (Nisbet and Walton, 1984). No information on night-time ambient temperatures was given but presumably these were some way below incubation temperatures. In Nisbet and Walton's study the laying period was split into four sub-periods. Hatching success varied between 36% and 89%, with late layers showing the lowest hatching success. The incubation period increased from the usual 21–23 days to 27–31 days presumably as a consequence of nocturnal desertion (Nisbet and Walton, 1984). A similar phenomenon occurs where short-eared owls *Asio flammeus* prey upon common terns at a colony in Northern Germany (Becker pers comm.). No studies of Arctic tern egg resistance to cooling have been done, but their close relation to common terns suggested that their eggs may also be tolerant of chilling.

Eggs of several species of Laridae have been stored with varying degrees of success. In a study of glaucous-winged gulls *Larus glaucescens*, shelf life of first laid eggs was determined by placing the eggs in an unincubated and unshaded nest for 0–8 days. Storage temperature and humidity were not controlled in this study since its aim was to investigate the need to begin incubation immediately. Ambient temperatures varied between 4 and 26 degrees Celsius. This is significant to the outcome of this experiment (see below for a fuller discussion of the implications of storage temperature and humidity upon subsequent hatchability). No detailed chronology of ambient temperatures during the experiment was given. Hatching success was found not to vary significantly between the five groups that had been stored for 0, 2, 4, 6, and, 8 days (Reid, 1987).

6.2.6 Egg storage

The majority of research into the effects of storage upon subsequent egg viability has been done on the domestic fowl. The following summarises the most recent review of Butler, 1991; an earlier review by Lundy (1969); and other relevant research papers.

Lundy (1969) defined a zone of suspended development within which : "incubated eggs retain the potential to develop over periods determined by the temperature level and the age of the embryo. Egg storage temperatures are within this zone." Egg storage affects hatchability and delays the hatch in chickens (Mather and Loughlin 1976). These effects are dependent upon storage

conditions and may be exaggerated by sub-optimal conditions (Mather and Loughlin, 1976). Reviewing previous studies upon the interaction between holding time and storage temperature Butler (1991) suggested the following table of recommendations for various periods of egg storage in the domestic fowl.

Table 6.3 Recommended temperature and relative humidity for various holding periods for domestic fowls
(after Butler 1991)

Holding time (days)	Temperature (degrees Celsius)	Relative humidity
<4	18-28	75-80
4-7	15-16	75-85
7-14	11-12	80-85
>14	11-12	80-90

The state of development of the blastoderm at the time of collection is likely to have an important bearing upon subsequent hatchability (Coleman and Siegel 1966; Arora and Kosin 1966). This effect may be further complicated by genetic effects. In chickens high hatchability genotypes were more advanced in gastrulation at oviposition and may have had an enhanced ability to withstand pre-incubation egg holding. However pre-heating artificially in an incubator improved the hatchability of eggs stored at 10 degrees Celsius over those placed immediately at this temperature (Becker and Bearse 1958, in Butler 1991). The planned storage period in this study, of 7 days, fell upon the boundary of the period for which pre-heating has been found to have an effect upon hatchability in chickens. Chicken eggs stored for less than 7 days may not require pre-storage heat treatment, provided that the storage temperature is within the range of 15-28 degrees Celsius (Butler 1991). However eggs which are to be stored for periods of more than 7 days will benefit from pre-heating. This ensures that the embryo is sufficiently well developed across all eggs.

In the field it is difficult to ascertain the precise age of all eggs or their degree of embryonic development. In consultation with C.Mather from the AFRC poultry research station (*pers. comm.*) I

concluded that natural incubation by the adult tern could mimic artificial pre-heating, and that the embryo may consequently have been sufficiently well developed to withstand chilling but not to the extent that the partially developed embryo would suffer any lethal effects.

Proudfoot (1969) and Reinhart and Hurnik (1982) specify 75–90% as the optimal relative humidity level during egg holding. C. Mather (*pers. comm.*) advised me that holding tern eggs in sealed polythene bags would ensure a sufficiently humid storage environment.

6.2.7 The advantages of egg storage as a field technique.

Egg storage is a potentially useful field technique for a variety of studies including for example dietary and age variation (as in this study) and the costs of reproduction. There is evidence to suggest that egg production is expensive for some species of birds (Hiom *et al.*1991). Few studies have involved clutch manipulation to investigate the proximate costs of egg production (Winkler,1985; Bolton,1991). In clutch removal experiments, aimed at delaying hatching date, (e.g. Parsons, 1976), the costs of producing a replacement clutch may alter the body condition of the laying female and thus have an ultimate effect upon reproductive success/fitness. Egg storage, if successful, removes this cost from any such experiment. There may of course be costs of an increased incubation period which may need to be quantified.

6.2.8 Experimental protocol

Within a colony common terns may lay synchronously and as a consequence there will be a close correlation between date and chick age. Thus in order to differentiate between seasonal prey availability effects and chick age effects in provisioning, an experimental approach is required. Furthermore late laying birds may be of different quality to early laying birds. This confounding factor necessarily prevents the use of natural laying variation to create additional control groups. Novel use was made of egg storage techniques to disrupt this close correlation. The first fifteen nests in the study plot where eggs were laid were marked with numbered bamboo canes. The clutches from thirteen subsequent nests were removed for storage. The aim was to create a discrete late cohort of chicks of the same age for comparison with control chicks hatched earlier. As eggs within this group were not laid on exactly the same day they were stored for varying periods in order

to reduce variability in hatching date. Eggs were removed (under licence from English Nature) and stored under controlled conditions for periods of 1–7 days (7 days $n_{\text{clutches}}=5$; 5 days $n_{\text{clutches}}=2$; 4 days $n_{\text{clutches}}=2$; 3 days $n_{\text{clutches}}=2$; 1 day $n_{\text{clutches}}=1$). Dummy eggs were placed in the nests during this period. No pairs deserted during the storage period. Eggs were marked with indelible ink: 'a', 'b', 'or 'c' according to their position in the laying sequence. They were then placed in sealable polythene bags and placed on egg trays within a refrigerator. The polythene bags ensured a continuously high humidity during the storage period.

6.2.9 Chicks/Adults

Chicken wire nest surrounds were placed around nests from both experimental and control groups after eighteen days of incubation. This gave adults time to become habituated to their presence and ensured that after hatching chicks could be relocated. A shelter was placed in each nest surround to give chicks a refuge.

A sample of nests from each of the two groups was watched for periods of 1.75–8 hours daily. 189 hours of watches were done during the chick rearing period of 35 days. Watches were randomised in an attempt to control for any diurnal effects in provisioning. No observed nests were more than ten metres from the hide. Where necessary vegetation was cut using garden shears to improve visibility.

Analytical categories were combined for all nests, as samples for each nest were often too small for adequate statistical analysis due to differing provisioning rates between nests, watches, and days.

6.3 Arctic and common tern chick diet

6.3.1 Arctic tern chick diet

6.3.1.1 Chick age effects

In total 20.3 % ($n=187$) of prey were unidentified in 1991 and 28.3 % ($n=608$) in 1992. The proportions of sandeels and non-sandeels fed to chicks of all ages differed significantly between 1991 and 1992, with a greater non-sandeel component in 1992 than in 1991 (χ^2_1 corrected for continuity = 210.55, $P < 0.0001$, Table 6.3a). There was also a significant difference between years in

the proportions fed to chicks within the two eldest chick age classes. However, chicks aged up to 6 days were not fed significantly different proportions of sandeels and non-sandeels in their diet in 1991 compared to 1992 (χ^2_1 corrected for continuity = 0.10, $P < 0.75$, Table 6.3a). The difference in the proportion of sandeels and non-sandeels was more evident for the intermediate group aged 7–13 days old (χ^2_1 corrected for continuity = 190.70, $P < 0.0001$, Table 6.3a). The main difference between the two years was in the high proportion of small non-sandeels in the diet of chicks of this age in 1992. Although no distinction was made in 1991 between small sprats and rockling, Figure 6.3 shows how marked a difference between the two years. Rockling formed the majority of the small non-sandeels fed to Arctic tern chicks in 1992. Table 6.3a also shows the prey fed to Arctic tern chicks 14–20 days old in 1991 and 1992. Chicks in this age group were also fed highly significantly different proportions of sandeels and non-sandeels in the two years (χ^2_1 corrected for continuity = 139.25, $P < 0.0001$).

Table 6.3a Proportions of sandeels and non-sandeels in the diet of Arctic tern chicks in 1991 and 1992

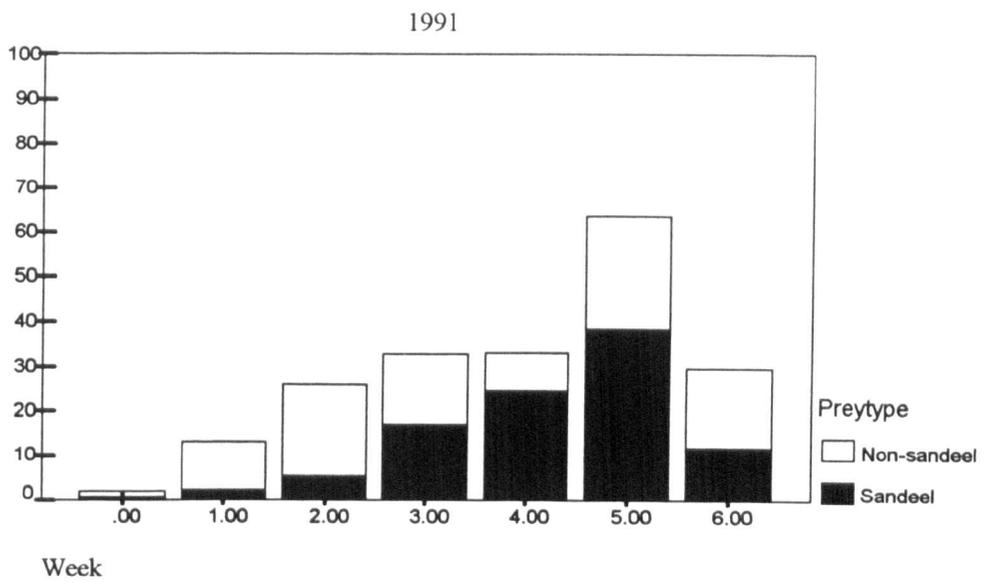
	All ages n ₁₉₉₁ = 734 n ₁₉₉₂ = 1541		0–6 days old n ₁₉₉₁ = 193 n ₁₉₉₂ = 472		7–13 days old n ₁₉₉₁ = 269 n ₁₉₉₂ = 521		14–20 days old n ₁₉₉₁ = 272 n ₁₉₉₂ = 548	
	Sandeel	Non-sandeel	Sandeel	Non-sandeel	Sandeel	Non-sandeel	Sandeel	Non-sandeel
Year								
1991	59.8	40.2	48.7	51.3	68.0	32.0	59.6	40.4
1992	28.2	71.8	50.4	49.6	18.2	81.8	18.4	81.6

6.3.1.2 Arctic tern chick diet (Seasonal prey effect)

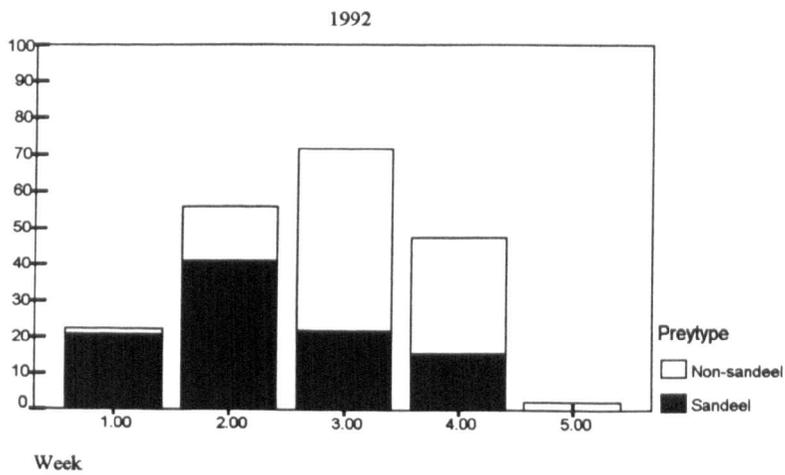
The proportions of sandeels and non-sandeels fed to Arctic tern chicks also varied with season in 1991 and 1992. In 1991 due to the protracted breeding season data were available for 6 weeks. In 1992 data were collected over 4 weeks. (1991 $\chi^2_6 = 94.63$, $P < 0.0001$, $n = 734$; 1992 $\chi^2_4 = 370.80$, $P < 0.0001$, $n = 1541$, Figure 6.1).

Figure 6.1 Proportions of sandeels and non-sandeels in the diet of Arctic tern chicks of all pre-fledging ages by week of observation in 1991 and 1992. (n1991=734; n1992=1541)

Percentage



Percentage



6.3.2 Common tern chick diet

6.3.2.1 Chick age effects and comparison with Arctic tern diet in 1992

Table 6.3b shows that in comparison to the diet of Arctic tern chicks in 1992 common tern chicks of all pre-fledging ages were fed a greater proportion of sandeels, and sprats, and a smaller proportion of rockling than Arctic tern chicks ($\chi^2_2=465.70$, $P<0.0001$) (compare with Table 6.3a). This trend was apparent for all three age groups. The following chi-squared values are calculated on the numbers of sandeels, sprats, and rockling, which accounted for more than 98 % of prey fed to all three chick age groups. shows the diet of 0–6 day old common tern chicks in 1992 (compare with Table 6.3a) ($\chi^2_2=157.85$, $P<0.0001$; $n_{\text{Arctic}}=464$, $n_{\text{common}}=460$). shows the diet of 7–13 day old common tern chicks in 1992 (compare with Table 6.3a) ($\chi^2_2=99.81$, $P<0.0001$; $n_{\text{Arctic}}=514$, $n_{\text{common}}=681$). The diet of 14–20 day old common tern chicks in 1992 is shown in ($\chi^2_2=305.10$, $P<0.0001$) (compare with Table 6.3a).

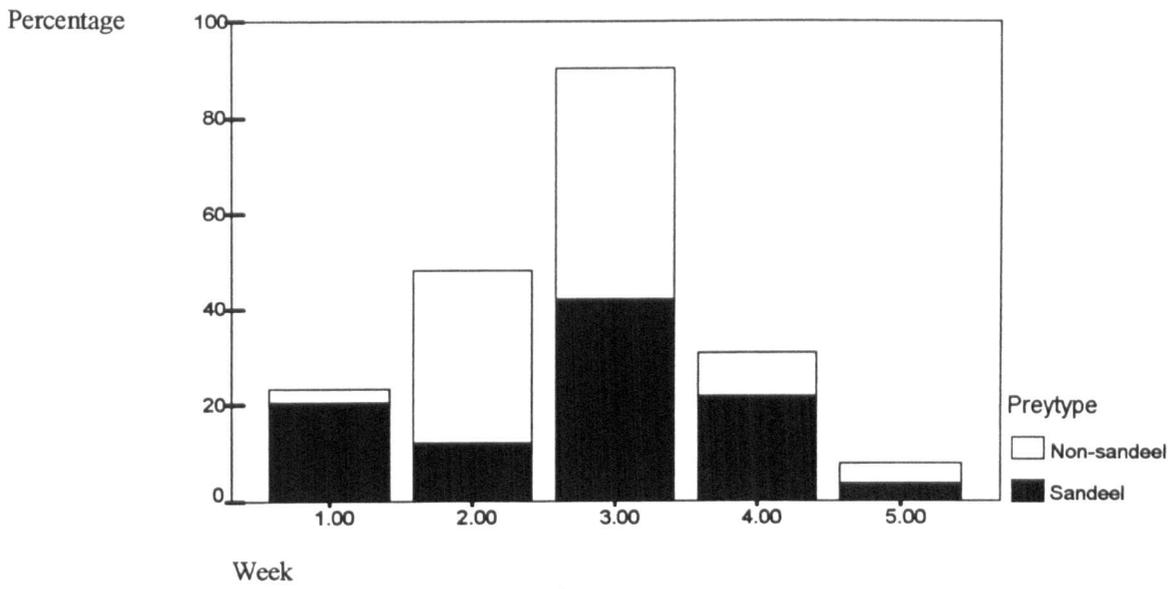
Table 6.3b Proportions of sandeels and non-sandeels in the diet of common tern chicks in 1992

	All ages $n_{1992}=1776$		0–6 days old $n_{1992}=460$		7–13 days old $n_{1992}=681$		14–20 days old $n_{1992}=635$	
	Sandeel	Non-sandeel (% Sprat Upper figure; % rockling lower figure)	Sandeel	Non-sandeel (% Sprat Upper figure; % rockling lower figure)	Sandeel	Non-sandeel (% Sprat Upper figure; % rockling lower figure)	Sandeel	Non-sandeel (% Sprat Upper figure; % rockling lower figure)
Year								
1992	46.7	31.0 22.3	61.7	29.8 8.5	22.0	48.9 29.1	62.4	12.6 25.0

6.3.2.2 Seasonal effects

The proportions of sandeels and non-sandeels fed to common tern chicks also varied with time of season ($\chi^2_4=274.30$, $P<0.0001$, $n=1795$, Figure 6.2).

Figure 6.2 Proportions of sandeels and non-sandeels in the diet of common tern chicks of all pre-fledging ages by week of observation in 1992. (n1992=1795)



6.3.3 Variations in the size of prey fed to chicks

6.3.3.1 Arctic tern 1991

Table 6.3c shows the size of prey of all types fed to Arctic tern chicks in 1991. There was a significant difference in the size of prey of all types fed to chicks of different ages ($\chi^2_6=49.01$, $P<0.0001$). The trend in 1991 was for older chicks to be fed larger prey. The size of sandeels in 1991 is shown in table 6.3c. This also varied significantly with chick age ($\chi^2_2=12.32$, $P=0.0021$). (Size categories were collapsed into ≤ 8 cm and ≥ 8 cm to account for correct assumptions for the validity of the chi-squared statistic). There was a trend for chicks older than 7 days old to be fed a greater proportion of fish within the 8–12 cm size category. The proportions of non-sandeels in different size categories fed to chicks also varied with age ($\chi^2_2=13.28$, $P=0.0013$, table 6.3c) The proportion of non-sandeels in the smallest size category fed to chicks declined with increasing chick age.

Table 6.3c Proportions of differently sized prey in the diet of Arctic tern chicks in 1991 and 1992

	Chick age											
	0-6 days old				7-13 days old				14-20 days old			
Prey size	Size 1	Size 2	Size 3	Size 4	Size 1	Size 2	Size 3	Size 4	Size 1	Size 2	Size 3	Size 4
1991												
Prey type												
All	11.9	36.8	47.7	3.6	4.1	23.6	70.0	2.2	3.0	42.1	54.6	0.4
0-6 n = 193												
7-13 n = 267												
14-20 n = 271												
Sandeel	4.3	13.8	75.5	6.4	0	4.9	92.9	2.2	0	12.3	87.0	0.6
0-6 n = 94												
7-13 n = 182												
14-20 n = 162												

Non- sandeel 0-6 n = 99 7-13 n = 85 14-20 n = 109	19.2	58.6	21.2	1.0	12.9	63.5	21.2	2.4	7.3	86.2	6.4	0
1992												
Prey type												
All 0-6 n = 468 7-13 n = 516 14-20 n = 548	51.5	38.5	10.0	0	58.3	32.2	9.1	0.4	75.4	20.8	3.8	0
Sandeel 0-6 n = 235 7-13 n = 95 14-20 n = 101	22.6	60.0	17.4	0	21.1	69.5	8.4	1.1	20.8	69.3	9.9	0
Sprats 0-6 n = 37 7-13 n = 124 14-20 n = 32	5.3	73.5	20.6	0.7	10.0	51.0	37.6	1.3	12.5	60.9	23.6	3.0

6.3.3.2 Arctic tern 1992

The proportions of differently sized prey of all types again varied significantly with chick age ($\chi^2_2 = 17.62$, $P=0.00015$, table 6.3c). Unlike 1991 prey less than 8 cm in length predominated in the diet of chicks of all pre-fledging ages. The increase in the proportion of prey larger than 8 cm in the diet of chicks as they aged was not repeated in 1991. There was no significant difference in the size of sandeels fed to young and old Arctic tern chicks in 1992 ($\chi^2_2 = 5.37$, $P=0.068$, table 6.3c), nor was there any difference in the size of sprats fed to Arctic tern chicks with age ($\chi^2_2 = 3.96$, $P=0.14$, table 6.3c). As previously stated, all rockling fed to chicks were less than 8 cm. There were no chick age related trends in the size of fish fed to Arctic tern chicks in 1992.

6.3.3.3 Common tern 1992

There was a significant difference in the proportions of prey of different sizes fed to the three age classes of common tern chicks in 1992 ($\chi^2_6=82.02$, $P<0.0001$). Table 6.3d shows the percentages of differently sized sandeels fed to common tern chicks within the three age groups in 1992. There was no significant difference in the proportion of sandeels of different sizes fed to the chick with increasing age of the chick ($\chi^2_2=1.71$, $P=0.43$, table 6.3d). However chicks were fed a greater proportion of sprats in the largest two size categories with increasing age ($\chi^2_2=93.72$, $P<0.0001$, table 6.3d).

Table 6.3d Proportions of differently sized prey in the diet of common tern chicks in 1992

		Chick age											
		0-6 days old				7-13 days old				14-20 days old			
Prey size		Size 1	Size 2	Size 3	Size 4	Size 1	Size 2	Size 3	Size 4	Size 1	Size 2	Size 3	Size 4
1992													
Prey type													
All 0-6 n = 457 7-13 n = 670 14-20 n = 631		5.3	73.5	20.6	0.7	10.0	51.0	37.6	1.3	12.5	60.9	23.6	3.0
Sandeel 0-6 n = 201 7-13 n = 349 14-20 n = 393		1.8	78.3	18.9	1.1	4.7	72.5	17.4	5.4	3.6	72.3	19.8	4.3
Sprat 0-6 n = 132 7-13 n = 321 14-20 n = 79		0	69.7	30.3	0	0.3	29.0	70.4	0.3	0	10.1	87.3	2.5

6.4 Kleptoparasitism

In the two years of this study only common terns were appreciably kleptoparasitised at the nest by their conspecifics. Figures 6.3-6.5 show the levels of kleptoparasitism experienced by Arctic terns in 1991 and 1992, and common terns in 1992 (note different scales on the three graphs). For both species the overwhelming majority of kleptoparasitism at the nest was by conspecifics.

Figure 6.3 1991 Arctic tern fate of prey brought to the nest (n=2143)

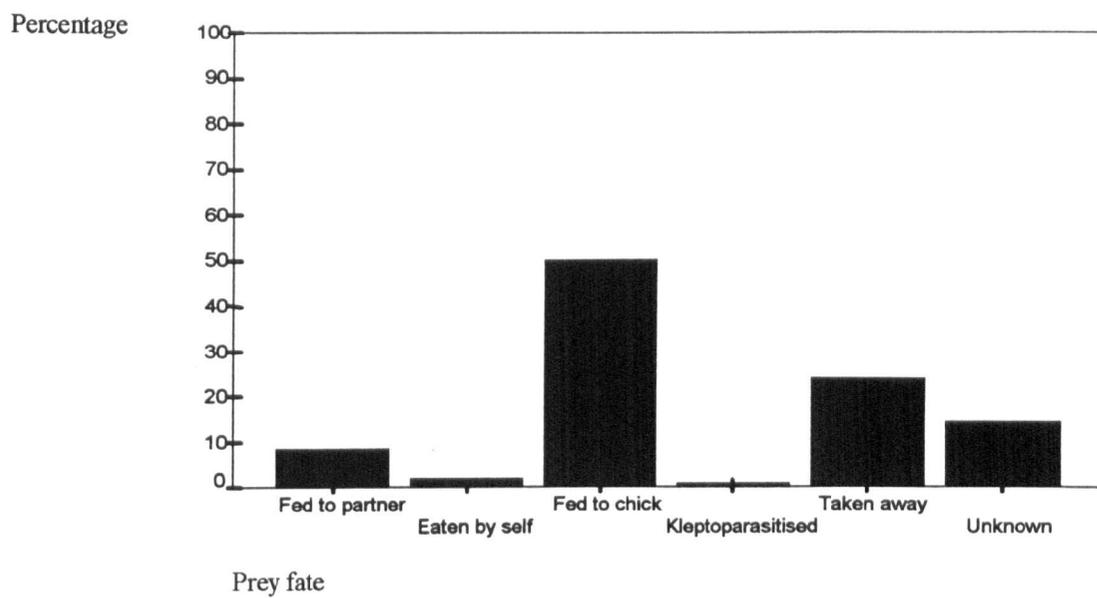


Figure 6.4 1992 Arctic tern fate of prey brought to the nest (n=2796)

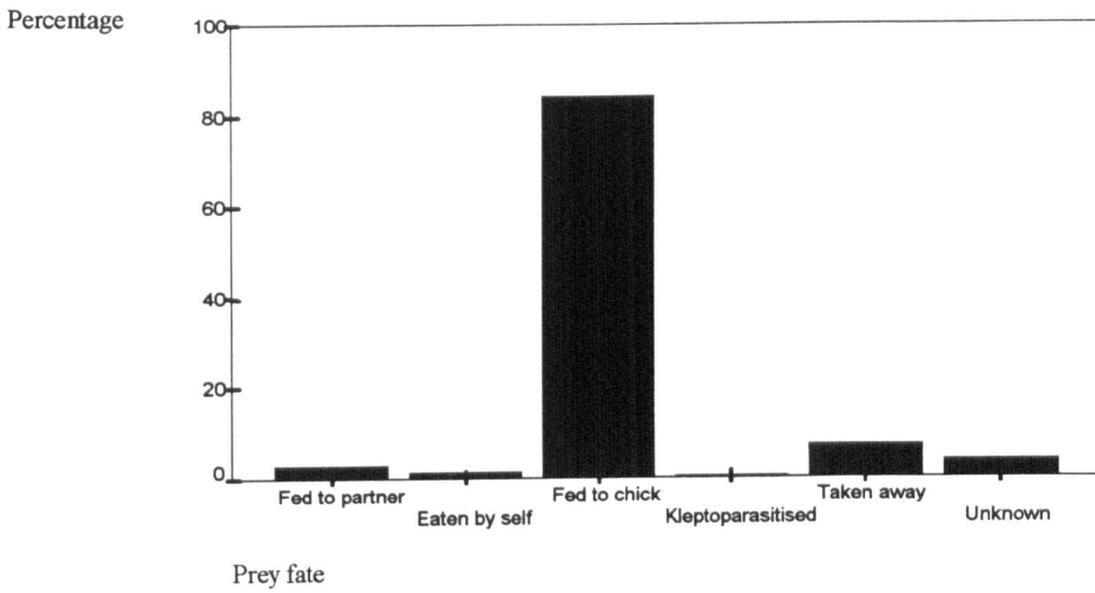
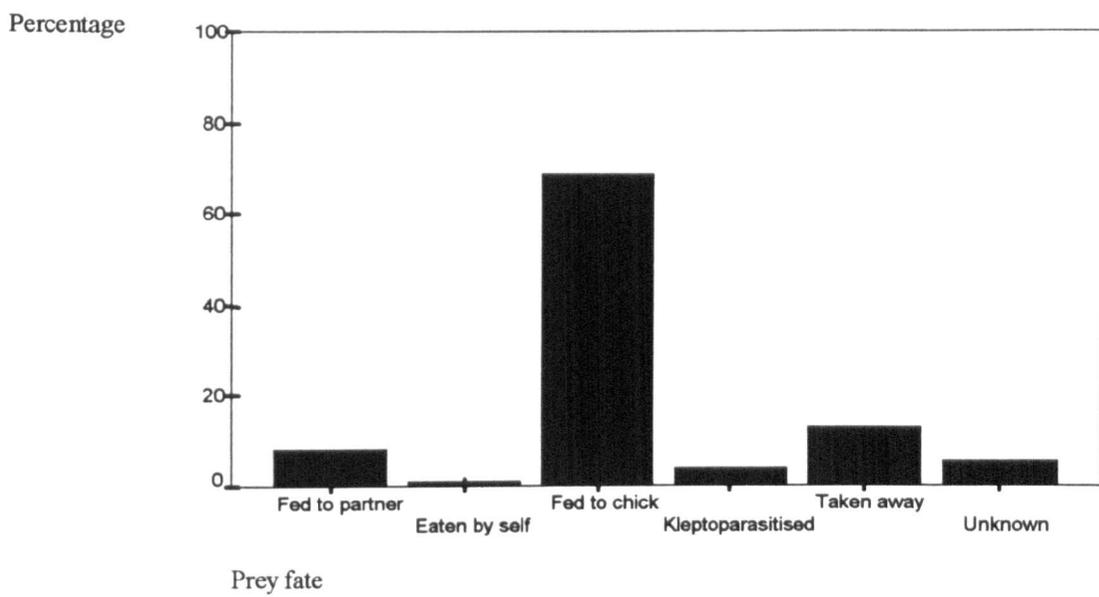


Figure 6.5 1992 common tern fate of prey brought to the nest (n=4620)



6.5 Experimental examination of adult prey choice

6.5.1 Introduction

As mentioned above, egg storage was used in order to delay the hatching of a group of common tern chicks to enable chicks to enable the comparison of the diet of chicks of different ages being fed simultaneously, thereby differentiating between seasonal prey availability effects and chick age effects.

6.5.2 Results

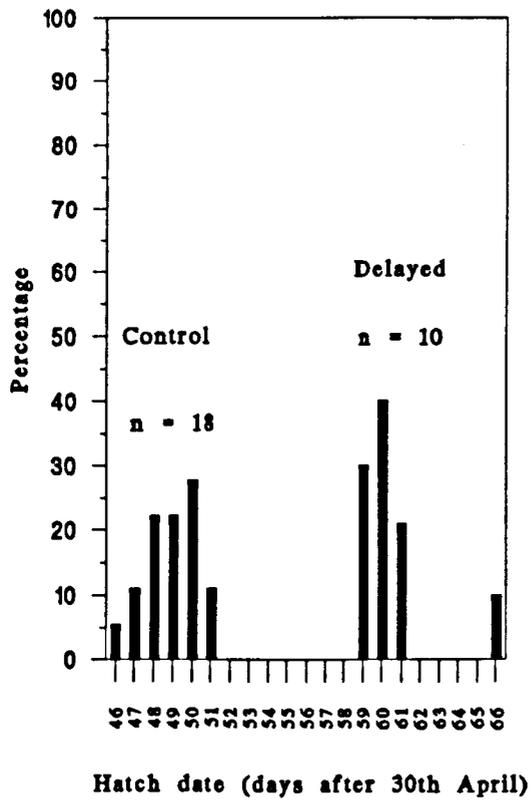
6.5.2.1 The effect of egg storage on hatching success.

There was a significant difference between the experimental and control groups in the hatching success of the eggs suggesting that storing eggs had a harmful effect on egg viability (Table 6.4, $\chi^2_1=7.74$, $P<0.05$). Despite this however, 20 of the stored eggs hatched and 6 of the experimental nest fledged chicks, enabling the necessary comparison of diet to be made. Figure 6.6 shows the hatch dates of the two groups. Chicks from the stored egg group, the 'young' group were always at least eight days younger than control, 'intermediate', chicks.

Table 6.4 Hatching success of experimental and control groups of common terns in 1992

Experimental group	Original laying date range	Number of eggs hatched (%)	Number of eggs not hatched	Number of eggs laid
Stored eggs (delayed hatching) $n_{\text{nests}} = 13$	30th May – 5th June	20 (59)	14	34
Control $n_{\text{nests}} = 27$	24th May – 17th June	61(83)	12	73

Figure 6.6 Hatching dates of common terns eggs from the experimentally manipulated and control groups in 1992 (Ncontrol=18; Nexperimental=10)



6.5.2.2 Chick age effects on the provisioning of common tern chicks

6.5.2.2.1 Prey selection by experimental and control groups of common terns (Same week)

The percentages of prey fed to chicks in two different age classes during the same week were compared. Six nests from the 'young' group, and fifteen from the 'intermediate' group were watched during this week. Sandeels, sprats, and rockling accounted for 97.6 % of all prey fed to the chicks. There was a highly significant difference between the proportions of prey fed to the two groups, $\chi^2_1 = 54.49$, $P < 0.0001$, Figure 6.7). There was a highly significant difference in the proportions of prey of different size fed to chicks from the two groups. Highly significant differences were also observed in the proportions of sandeels, ($\chi^2_{1\text{corrected for continuity}} = 18.24$, $P < 0.001$, Figure 6.8), and sprats ($\chi^2_{1\text{corrected for ties}} = 17.40$, $P < 0.001$, Figure 6.9) fed to chicks in the two groups within the same week. All rockling fed to chicks within the two groups were similarly sized (Figure 6.10). Chicks from the experimental group were fed sandeels and rockling mainly. Of these the majority of sandeels and all the rockling were less than eight cm in length, and thus of a size that these small chicks could readily handle and ingest. Sprats were a very minor constituent of the diet of the experimental group. The very few that were fed to young chicks were all less than eight cm in length. In contrast intermediately aged chicks were fed a greater proportion of sandeels and sprats and fewer rockling than were chicks from the experimental group. Intermediately aged chicks were fed a greater proportion of sandeels and sprats greater than 8 cm in length than were the experimental group. As both sets of parents were foraging under similar conditions it seems likely that parents provisioning the younger chicks in the experimental group were selecting prey of an appropriate size and type from the available prey.

Figure 6.7 Proportions of sandeels, sprats, and rockling fed to common tern chicks from the experimentally manipulated and control groups in 1992

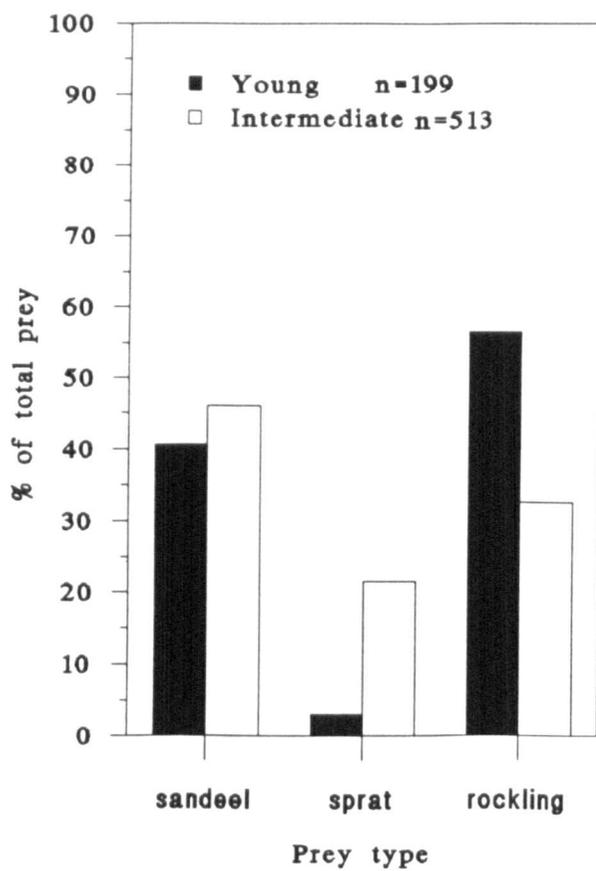


Figure 6.8 Proportions of sandeels of different sizes fed to common tern chicks from the experimentally manipulated and control groups in 1992

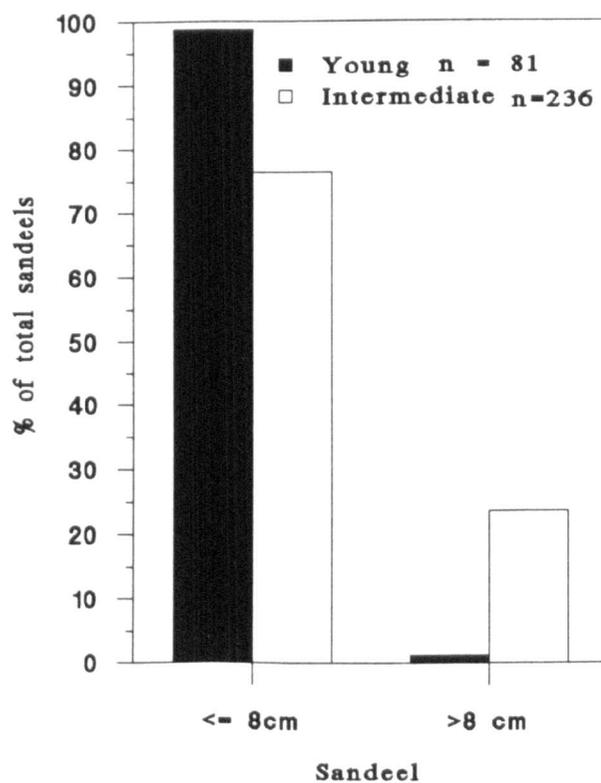


Figure 6.9 Proportions of sprats of different sizes fed to common terns from the experimentally manipulated and control groups in 1992

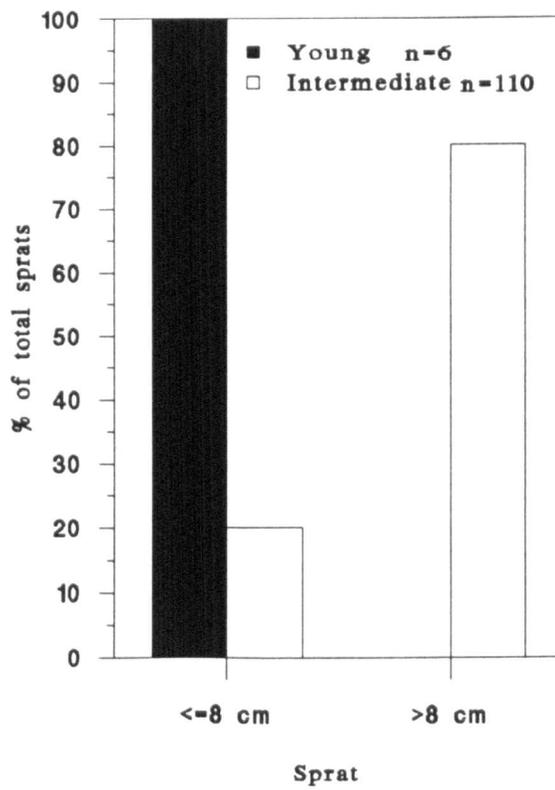
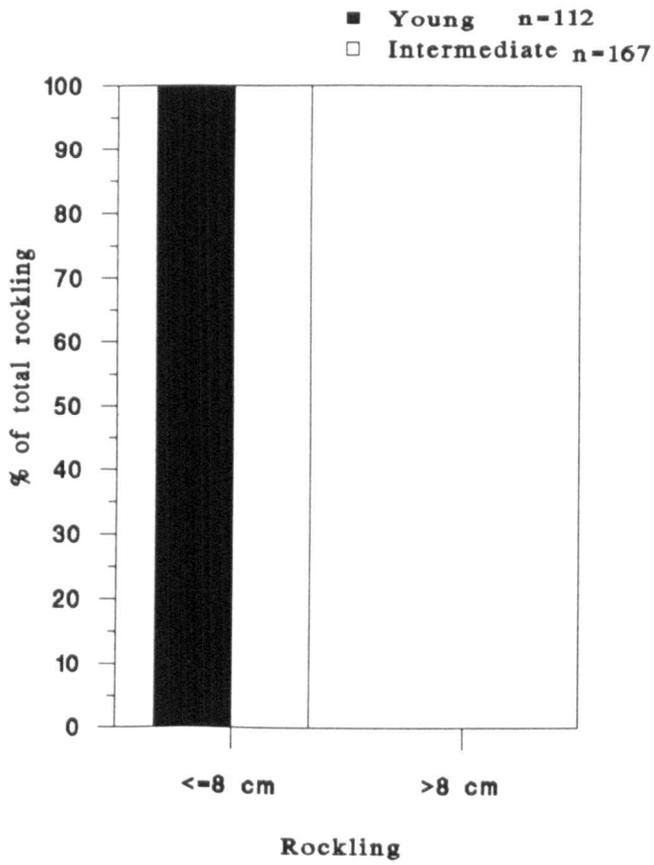


Figure 6.10 Proportions of rockling of the same size fed to common tern chicks from the experimentally manipulated and control groups in 1992



6.5.2.2.2 Prey selection by experimental and control groups of common terns (All weeks)

To further examine differences between the control and experimental groups data from all weeks that these two groups were observed were compared. There was a highly significant difference in the proportions of prey fed to chicks from the two groups, ($\chi^2_2 = 199.51, P < 0.0001, n_{\text{control}} = 1409; n_{\text{delayed}} = 523$, Figure 6.11). There were highly significant differences in the proportions of all types of prey fed to chicks of different ages from different groups 0–6 days old: $\chi^2_2 = 262.78, P < 0.0001, n_{\text{control}} = 355; n_{\text{delayed}} = 218$; Figure 6.12; 7–13 days old: $\chi^2_2 = 154.55, P < 0.0001, n_{\text{control}} = 546; n_{\text{delayed}} = 107$, Figure 6.13; 14–20 days old $\chi^2_2 = 13.53, P < 0.0001, n_{\text{control}} = 508; n_{\text{delayed}} = 198$, Figure 6.14. Chicks from the experimental group were fed more sandeels and rockling and fewer sprats than chicks from the control group over the whole of the pre-fledging period. Chicks aged 0–6 days old from the experimental group were fed a greater proportion of rockling, but fewer sprats and sandeels than chicks of this age from the control group. Chicks aged 7–13 days old from the experimental group were fed a greater proportion of sandeels, and fewer sprats and rockling than were chicks of this age from the control group. Finally chicks aged 14–20 days old were fed roughly similar proportions of sandeels, but fewer sprats and more rockling than were chicks from the control group. As birds within both groups were of similar age it seems likely that prey availability changed during the observation period.

The broad picture that emerges from the experiment is of a change in prey availability week by week, with adult selection of prey appropriate for young chicks within this context.

6.5.2.3 Fate of prey not fed to chicks.

A total of two thousand six hundred and fifty eight prey items of known size were brought to the nests by the experimental and control groups during the 1992 breeding season. Of these 60.4 % ($n=1605$) were less than 8 cm long. The remaining prey were greater than 8 cm in length (39.6 %, $n=1053$). Figure 6.15 shows the fate of prey brought to the nest but not fed to chicks.

Under the null hypothesis of no difference in the proportions of prey brought to the colony and those stolen by other common terns significantly ($\chi^2_1=74.032, P < 0.001$) more prey greater than 8 cm in length were kleptoparasitised by conspecifics. Similarly significantly more prey were taken away by the adult if they were greater than 8 cm in length.

Figure 6.11 Proportions of different types of prey fed to common tern chicks from the experimentally manipulated and control groups in different weeks in 1992 (N_{control}=1409; N_{manipulated}=523)

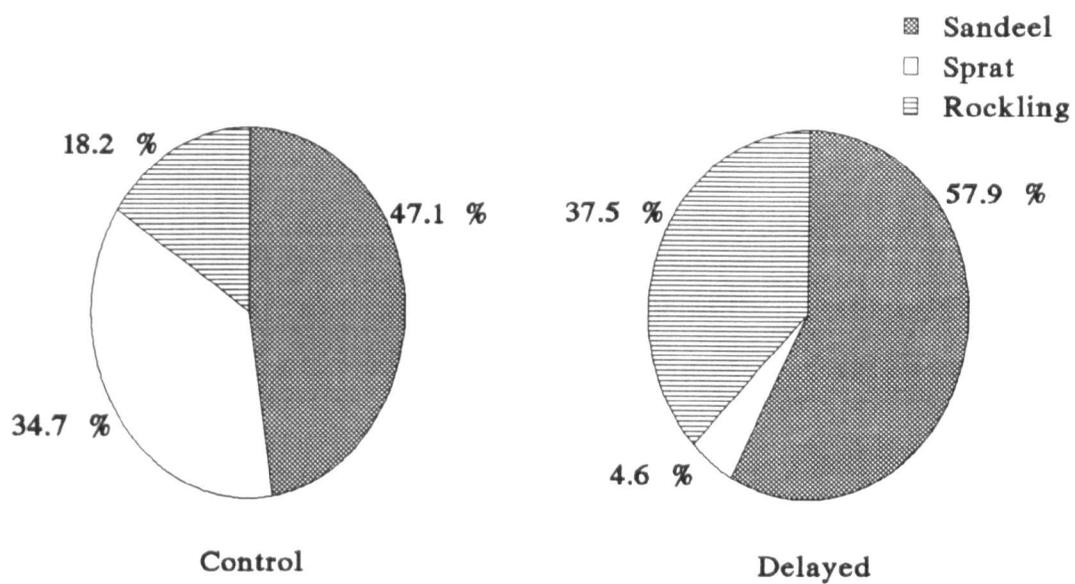


Figure 6.12 Proportions of different types of prey fed to common tern chicks 0-6 days old from the experimentally manipulated and control groups in different weeks in 1992 (Ncontrol=355; Nmanipulated=218)

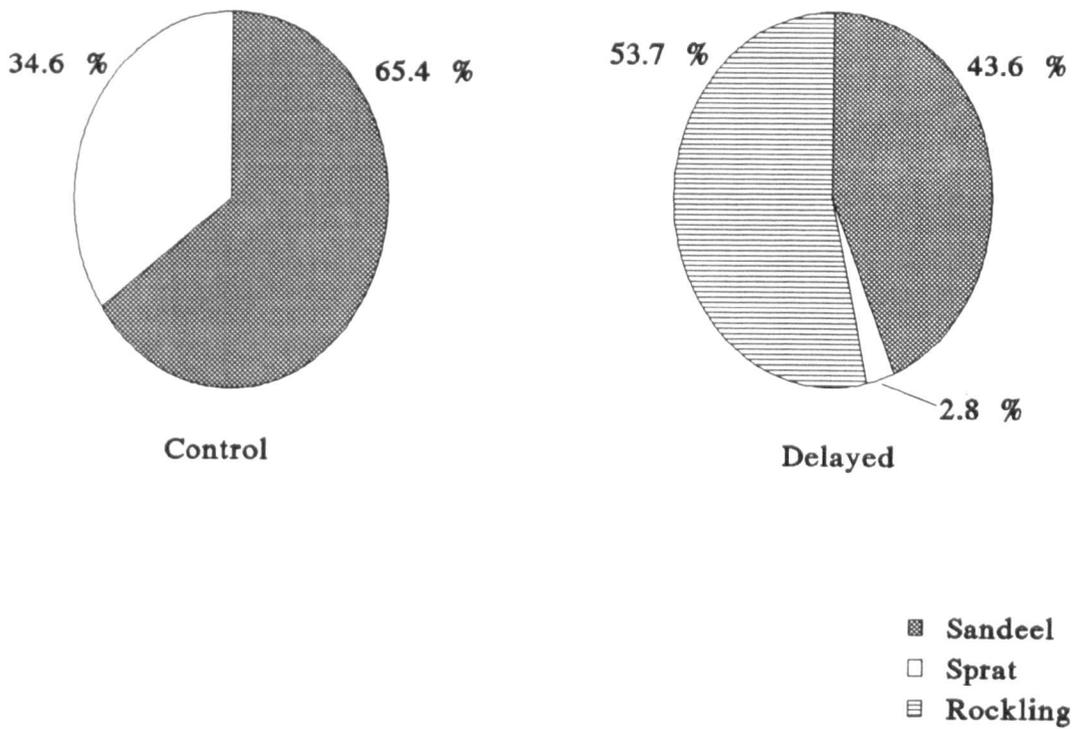


Figure 6.13 Proportions of different types of prey fed to common tern chicks 7-13 days old from the experimentally manipulated and control groups in different weeks in 1992 (N_{control}=546; N_{manipulated}=107)

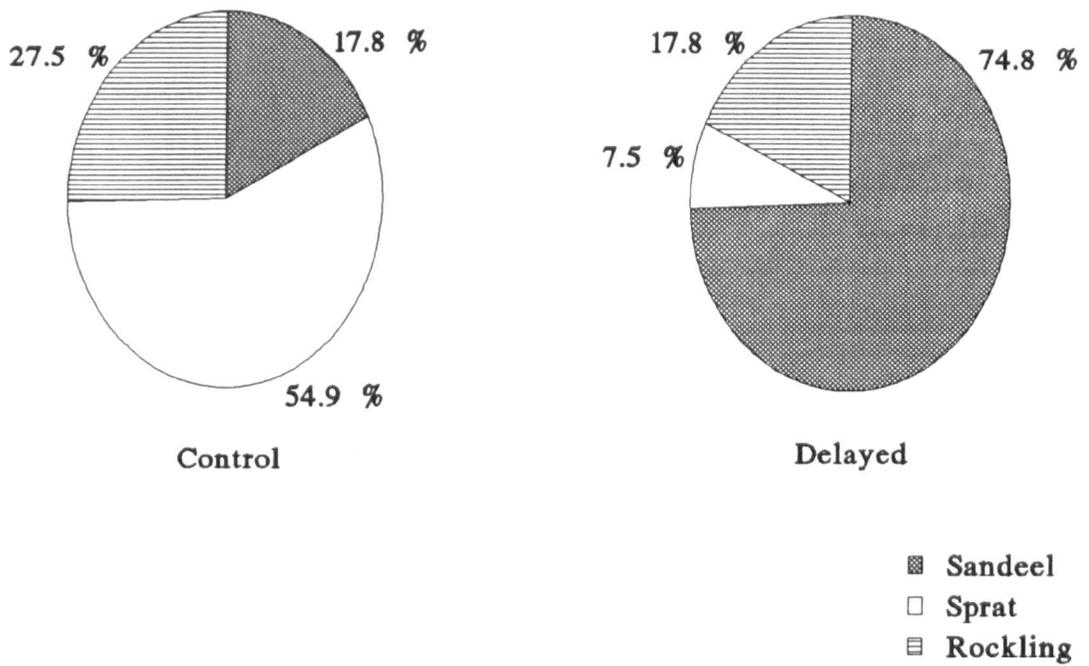


Figure 6.14 Proportions of different types of prey fed to common tern chicks 14-20 days old from the experimentally manipulated and control groups in different weeks in 1992 (Ncontrol=508; Nmanipulated=198)

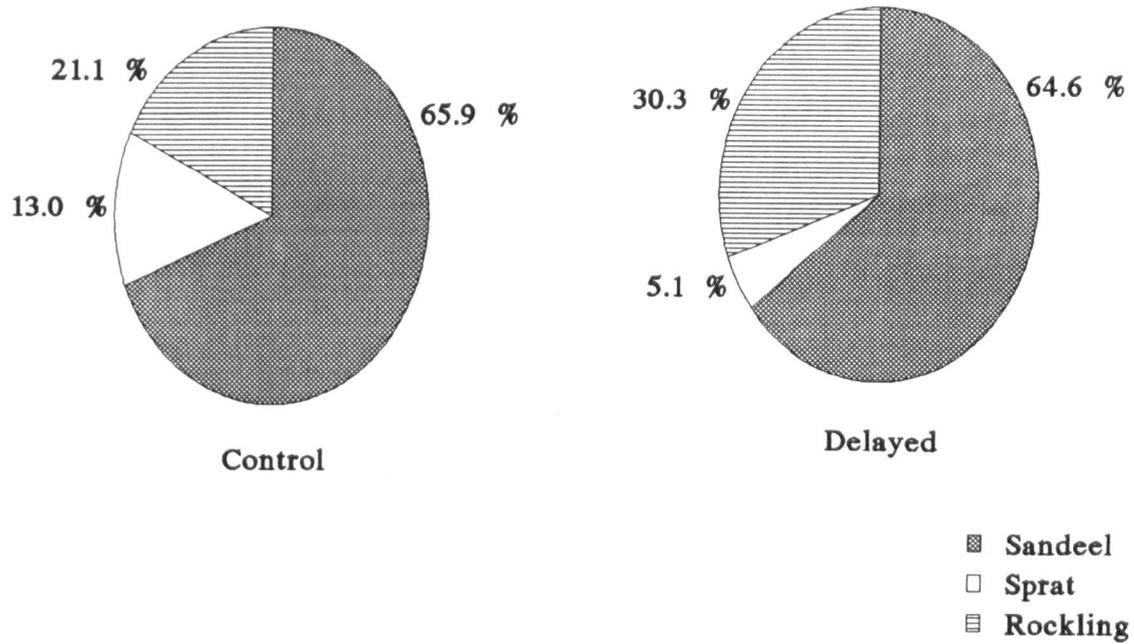
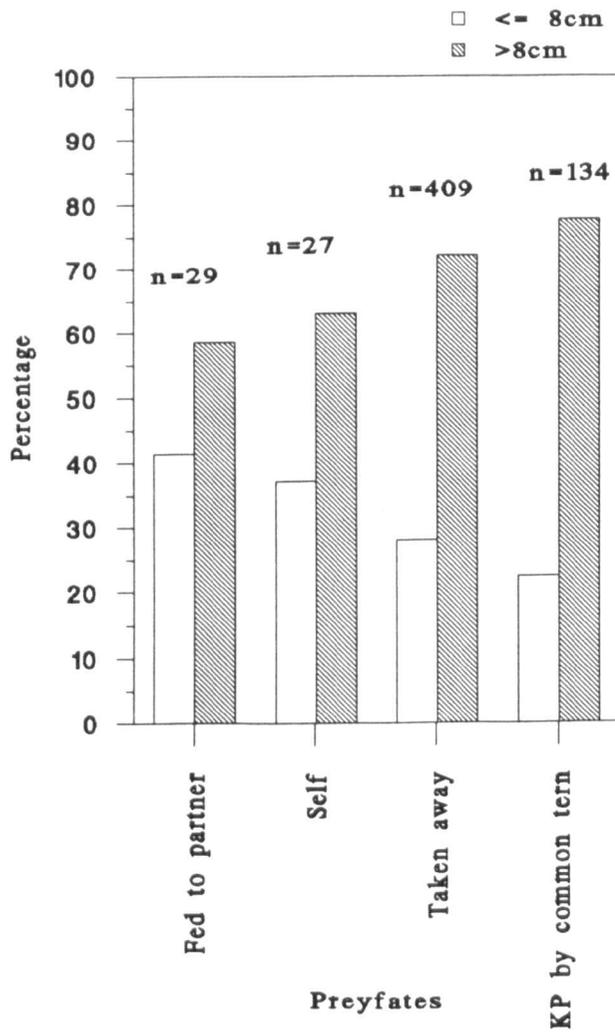


Figure 6.15 Fate of prey not fed to common tern chicks



6.6 Intra-specific effects of prey type, brood size, chick age, parental sex, seasonal availability, and time of day upon the foraging performance of Arctic and common terns.

6.6.1 Arctic tern (Intra-year analysis)

6.6.1.1 Effects of brood size, chick age, parental sex, and season upon foraging trip duration

Median foraging trip times for all prey types were not significantly different between broods of two and broods of one in 1991 (median _{one chick} = 18 minutes, IQR = 43 minutes; median _{two chicks} = 14 minutes, IQR = 33 minutes; Mann-Whitney U-test, $z_{\text{corrected for ties}} = -1.52$, $P=0.13$, Figure 6.16), and in 1992 (median _{one chick} = 11 minutes, IQR = 23 minutes; median _{two chicks} = 12 minutes, IQR = 22 minutes; Mann-Whitney U-test, $z_{\text{corrected for ties}} = -0.78$, $P=0.44$, Figure 6.17).

Trip time did not vary significantly with sex of the parent in either year (1991 Mann-Whitney U-test, $z_{\text{corrected for ties}} = -0.79$ $P=0.43$; 1992 Mann-Whitney U-test, $z_{\text{corrected for ties}} = -1.26$, $P=0.21$, Figures 6.18 & 6.19). See figure legend for details of foraging trip durations.

To examine any potential effects of seasonal availability on foraging trip length a two-way ANOVA was performed using transformed trip times with brood size and week. Samples of trip durations were grouped into weekly categories. These are given for 1991 (Table 6.5) and 1992 (Table 6.6).

Figure 6.16 Arctic tern median foraging trip durations for all prey types for current brood sizes of one and two in 1991.

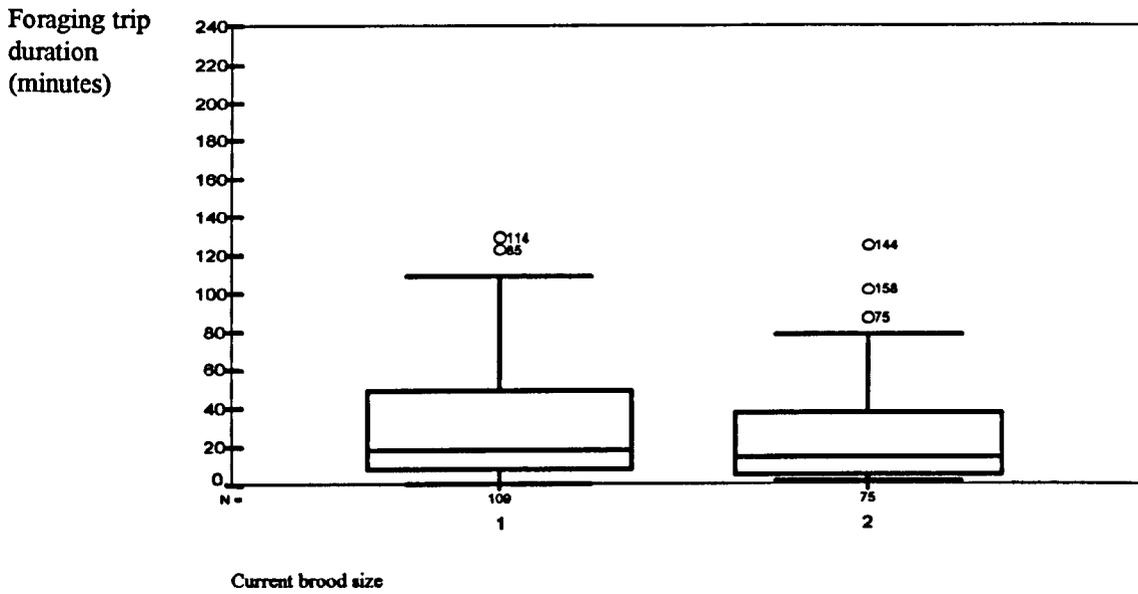


Figure 6.18 Arctic tern median foraging trip durations for all prey types for adult males and females in 1991

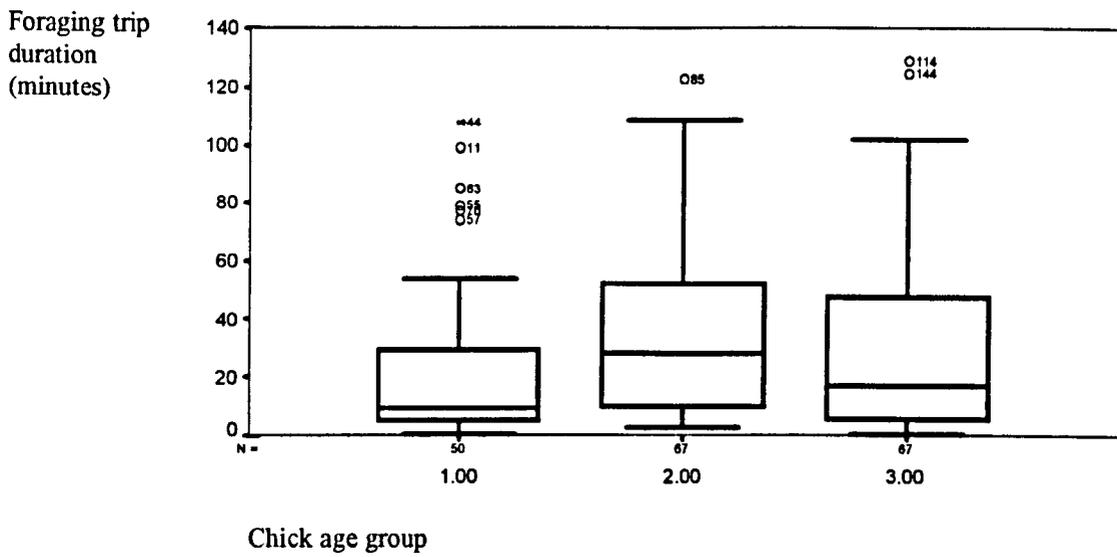


Figure 6.19 Arctic tern median foraging trip durations for all prey types for adult males and females in 1992.

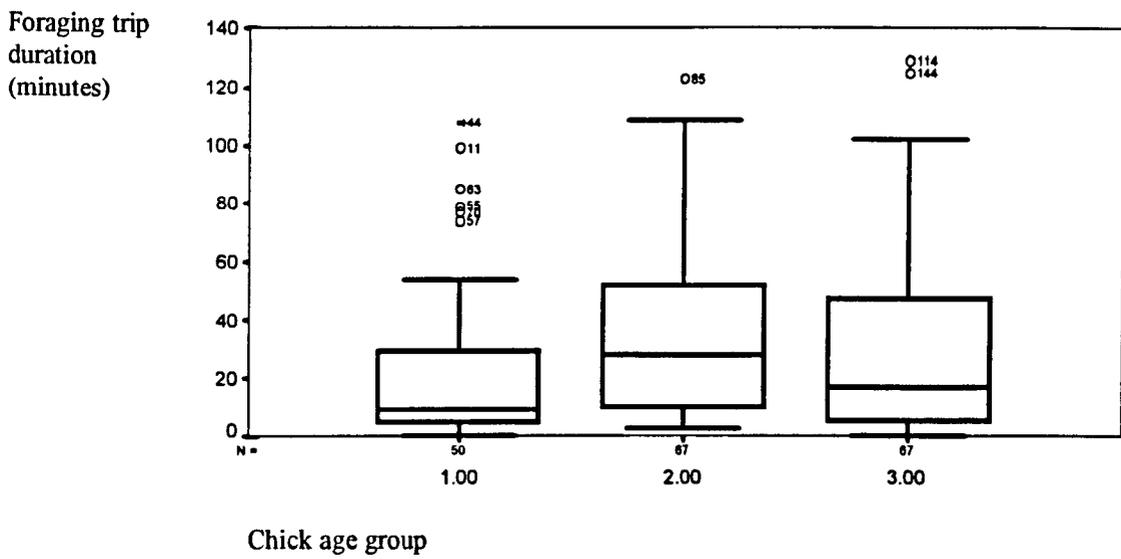


Table 6.5 Two-way ANOVA of the effects of brood size and season upon Arctic tern foraging trip duration in 1991.

	Sum of squares	Degrees of freedom	Mean Square	F	Significance of F
Main effects	121.44	6	20.24	3.15	0.006
Brood size	8.17	1	8.17	1.27	0.26
Week (season)	111.97	5	22.39	3.48	0.005
Brood size by week	85.48	5	17.10	2.66	0.024
Explained	201.99	11	18.36	2.86	0.002
Residual	1099.24	171	6.43		
Total	1301.23	182	7.15		

Table 6.6 Two-way ANOVA of the effects of brood size and season upon Arctic tern foraging trip duration in 1992.

	Sum of squares	Degrees of freedom	Mean Square	F	Significance of F
Main effects	117.44	5	23.49	4.39	0.001
Brood size	3.13	1	3.13	0.58	0.44
Week (season)	113.77	4	28.44	5.31	0.000
Brood size by week	46.64	3	15.54	2.90	0.034
Explained	152.85	8	19.11	3.57	0.000
Residual	4439.32	829	5.36		
Total	4592.17	837	5.49		

In both 1991 and 1992 there was no significant linear relationship between foraging trip duration and chick age for either one or two chick broods (1991 one chick: $r=0.1448$, $P=0.1243$, $n=108$; 1991 two chicks: $r=-0.0116$, $P=0.9237$, $n=71$; 1992 One chick: $r=-0.094$, $P=0.0839$, $n=340$; 1992 two chicks: $r=-0.038$, $P=0.5127$, $n=300$ Figure 6.20). To examine other potential relationships between foraging trip duration and chick age a Kruskal–Wallis one–way ANOVA was performed on data for both years. Median foraging trip length between the three chick age groups were significantly different in 1991, but not in 1992 (Figure 6.21 and 6.22). Parents provisioning chicks less than 6 days old made significantly shorter trips than parents provisioning 7–13 day old chicks in 1991. No other differences were significant (1991 $H_{\text{corrected for ties}} = 8.69$, $P=0.013$, followed by multiple comparison between groups; 1992 $H=0.89$, $P=0.64$, Siegel and Castellan 1988). This increased trip length in the second week of chick rearing presumably reflects the switch in diet to sandeels from small non–sandeels which occurred in 1991. In 1992 non–sandeels (predominantly rockling) remained a major constituent of chick diet with increasing chick age. Foraging trip durations for non–sandeels, including rockling, were significantly shorter than those for sandeels in both years (see later section in this chapter).

6.6.1.2 Diurnal effects

A Kruskal–Wallis one–way ANOVA was performed on data for both years to ascertain whether there were any diurnal differences in foraging trip duration. Diurnal effects upon foraging trip duration were apparent in both 1991 & 1992 (1991: $H_{\text{corrected for ties}}=7.97$, $P=0.047$, $n=184$; 1992: $H_{\text{corrected for ties}}=13.96$, $P=0.003$, $n=855$, Figures 6.23 & 6.24). Mid–morning foraging trips were significantly different from afternoon trips. A multiple range comparison (Siegel and Castellan 1988) was performed to determine where the diurnal differences in foraging trip duration lay (Table 6.7) .

Figure 6.20 Arctic tern linear regressions of foraging trip duration with chick age for current brood sizes of one and two in 1991 and 1992.

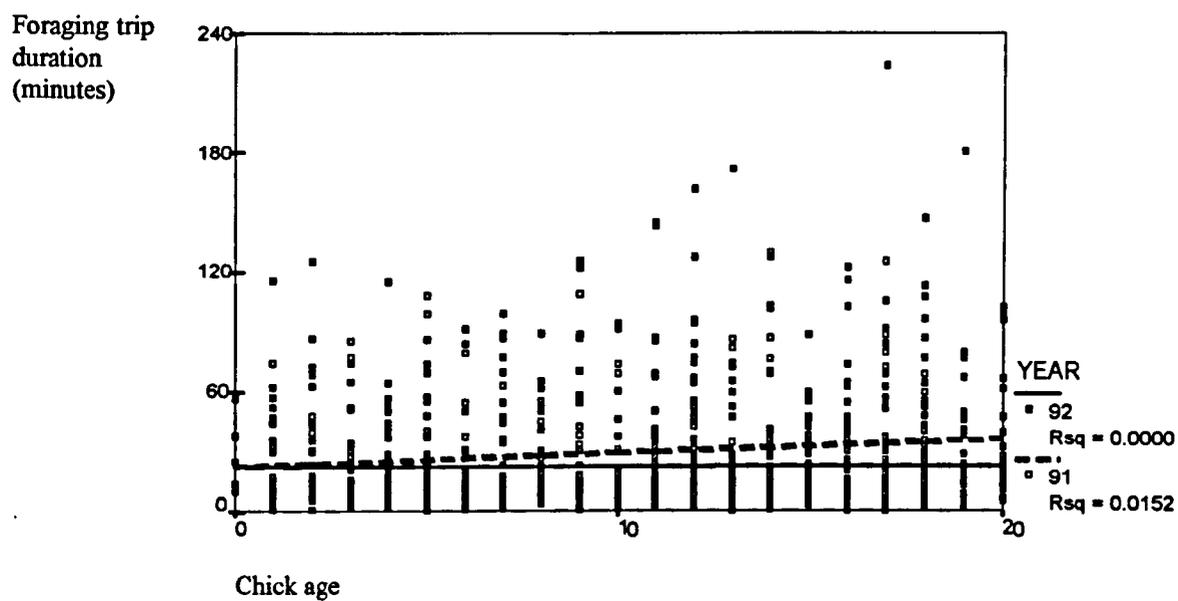


Figure 6.21 Arctic tern foraging trip durations for all prey types for chick age groups 0-6, 7-13, and 14-20 days old in 1991

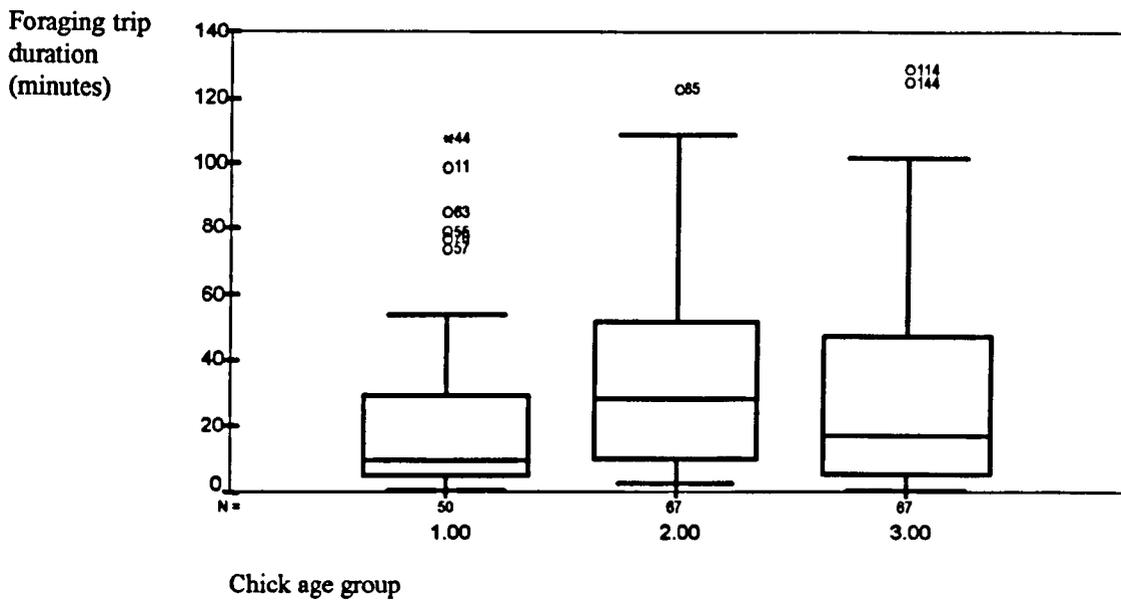


Figure 6.22 Arctic tern foraging trip durations for all prey types for chick age groups 0-6, 7-13, and 14-20 days old in 1992

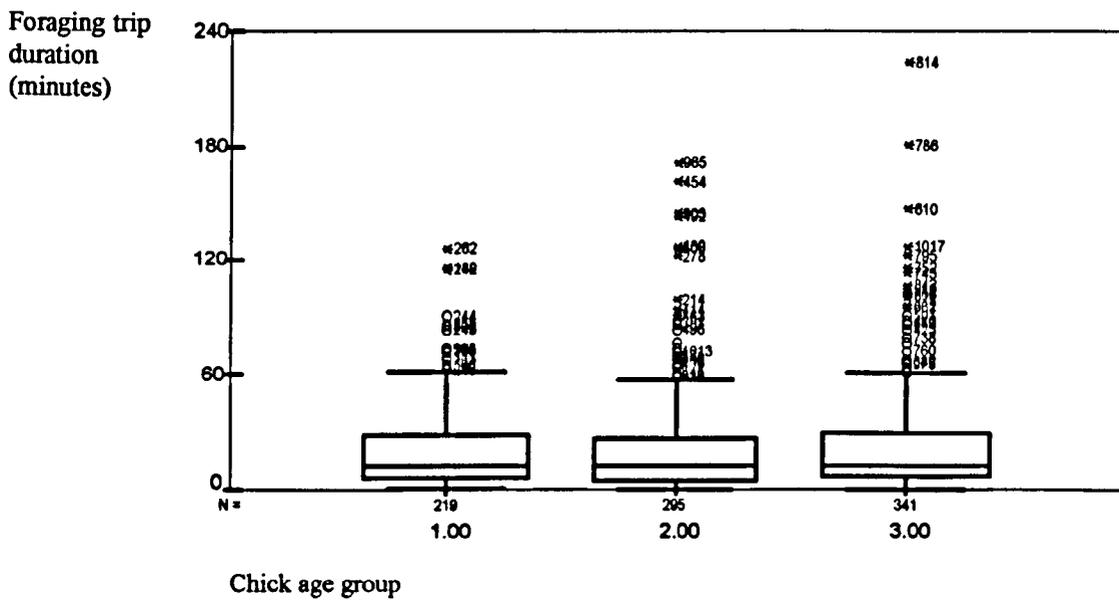


Figure 6.23 Arctic tern foraging trip durations for all prey types at different times of day in 1991

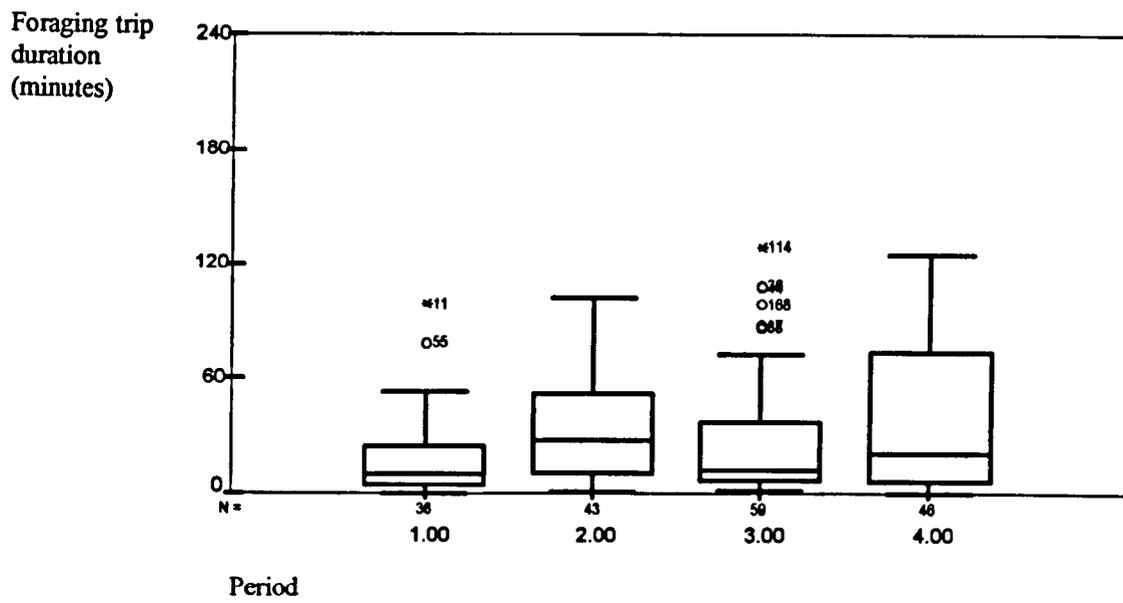


Table 6.7 Multiple comparison test comparing Arctic tern foraging trip durations for all prey types during different times of the day. Multiple significance level is constrained to $\alpha=0.05$. Significant differences are shown by inequalities.

Period	4	3	2	1
1	1=4	1=3	2=1	
2	2=4	2>3		
3	4=3			
4				

6.6.2 Prey specific analyses

6.6.2.1 Prey type

In 1991 and 1992 the median foraging trip duration for sandeels was significantly longer than that for non-sandeels (1991 Mann-Whitney U-test, $z_{\text{corrected for ties}} = -6.65$, $P < 0.0001$, 1992 Mann-Whitney U-test, $z_{\text{corrected for ties}} = -5.57$, $P < 0.0001$, Figures 6.25 and 6.26). In 1992 non-sandeel prey were identified in more detail. Foraging trips for rockling were significantly shorter than those for sandeels and sprats (Kruskal-Wallis one-way ANOVA $H_{2\text{corrected for ties}} = 86.96$, $P < 0.0001$ Figure 6.27). This was followed by a multiple comparison test to determine where between prey species differences in foraging trip durations lay. The median foraging trip length for sprats (37 minutes) was significantly longer than those for sandeels (17 minutes) and rockling (10 minutes). Median foraging trip duration for sandeels was also significantly greater than that for rockling.

6.6.2.2 Prey size effects

There was no significant relationship between square root transformed trip time and sandeel size in 1991 (one-way ANOVA $F_{1,77} = 0.28$, $P = 0.0.59$). A two-way ANOVA showed no significant effect of prey type (sandeels or sprat) or prey size (<8 cm or >8 cm) on trip duration in 1992. There

Figure 6.25 Arctic tern foraging trip durations for chicks of all ages for sandeels and non-sandeels in 1991

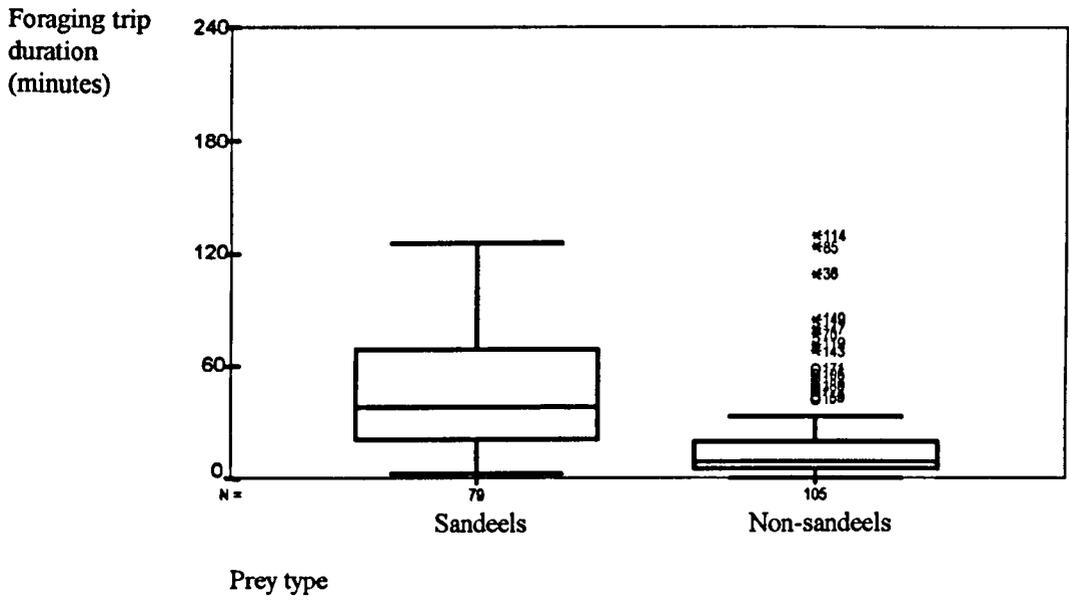


Figure 6.26 Arctic tern foraging trip durations for chicks of all ages for sandeels and non-sandeels in 1992

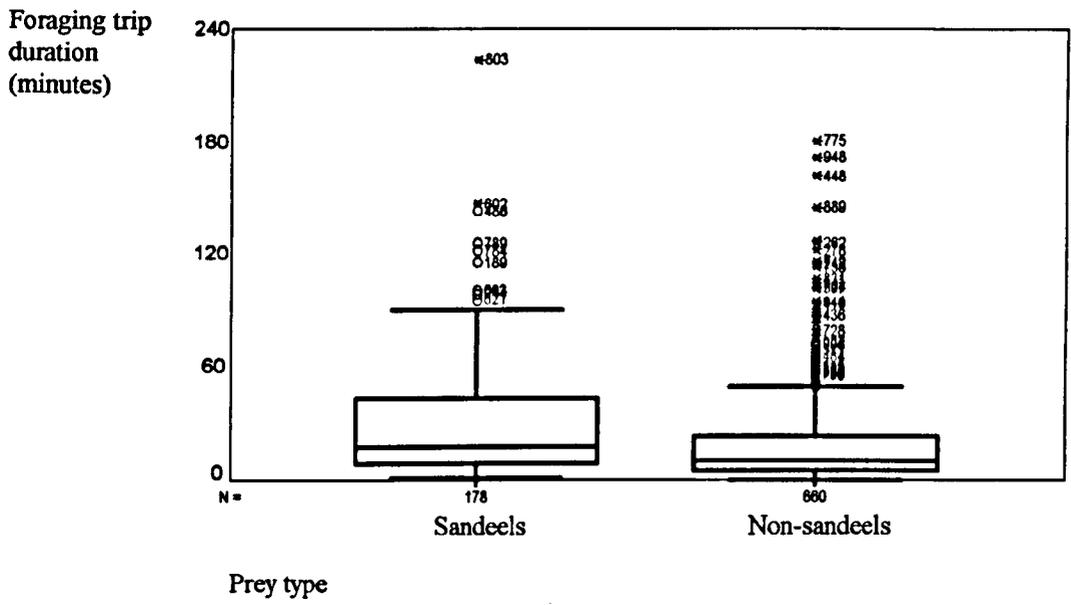
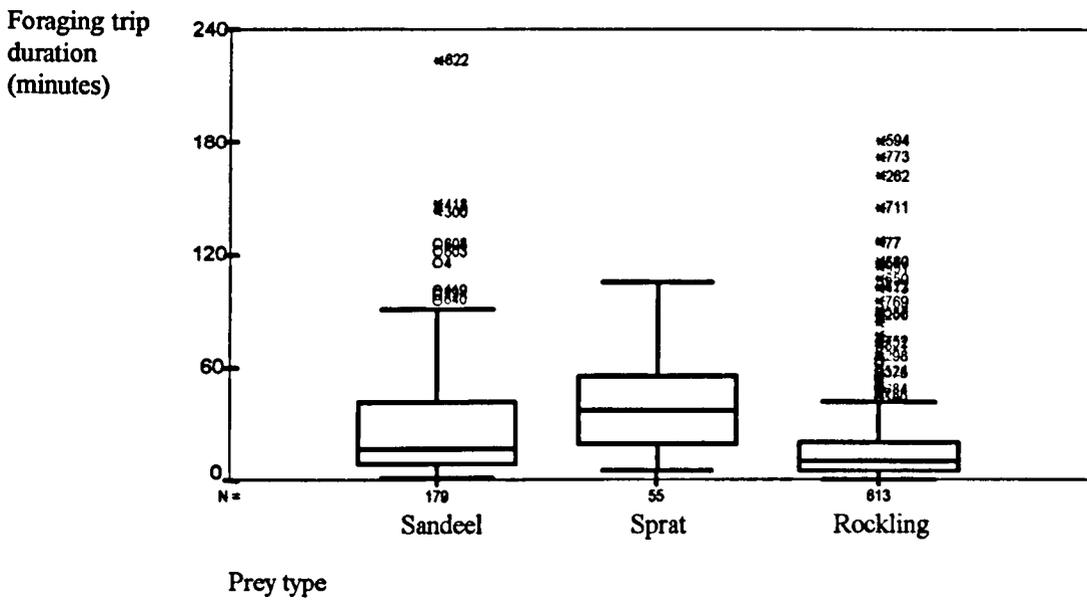


Figure 6.27 Arctic tern foraging trip durations for chicks of all ages for sandeels, sprats, and rockling in 1992



was a significant interaction of prey type and prey size, suggesting that prey of a particular type were liable to be of a certain size (Table 6.8).

Table 6.8 Two way analysis of variance of the effect of prey type and prey size on Arctic tern foraging trip duration in 1992.

Source of Variance	Sum of squares	Degrees of freedom	Mean square	F	Significance of F
Main effects	41.18	2	20.59	3.50	0.032
Prey type	7.81	1	7.81	1.33	0.25
Prey size	25.95	1	25.95	4.41	0.04
Interaction	3.45	1	3.45	0.585	0.45
Explained	74.78	3	24.93	4.23	0.006
Residual	1342.80	228	5.89		
Total	1417.58	231	6.14		

Table 6.9 Two way analysis of variance of the effect of prey type and chick age group on Arctic tern foraging trip duration in 1992.

Source of Variance	Sum of squares	Degrees of freedom	Mean square	F	Significance of F
Main effects	387.94	4	96.99	19.63	<0.0001
Prey type	356.29	2	178.15	36.06	<0.0001
Chick age group	17.92	4	2.22	0.45	0.64
Interaction	17.92	4	4.48	0.91	0.46
Explained	440.30	8	55.04	11.14	<0.0001
Residual	4140.37	838	4.94		
Total	4580	846	5.42		

The only significant effect was of prey type showing that prey of a particular type tended to require similar lengths of foraging trip.

6.6.2.3 Arctic tern between year differences

Median foraging trip duration for all prey types was significantly greater in 1991 than in 1992 (Mann-Whitney U-test, $z_{\text{corrected for ties}} = -2.88$, $P=0.04$, Figure 6.28). Foraging trip durations for non-sandeels did not differ significantly between 1991 and 1992 (Mann-Whitney U-test, $z_{\text{corrected for ties}} = -1.29$, $P=0.20$ Figure 6.29), but those for sandeels did (Mann-Whitney U-test, $z_{\text{corrected for ties}} = -4.00$, $P=0.0001$, Figure 6.30). The energetic consequences of this difference in reference to parental foraging effort are discussed later in this chapter.

6.7 Common tern

6.7.1 Effects of brood size, parental sex, chick age, and watch date on foraging trip durations

There was no significant difference in overall foraging trip duration in relation to brood size (Kruskal-Wallis one-way ANOVA H_2 corrected for ties = 3.90, $P=0.14$, $n=913$, Figure 6.31). Female common terns did not make significantly shorter foraging trips than males when provisioning chicks (Mann-Whitney U-test, $z_{\text{corrected for ties}} = -1.96$, $P=0.05$, $n=772$ Figure 6.32). There was no linear correlation between foraging trip duration and season ($r=-0.049$, $P=0.14$, $n=923$). Foraging trip duration was not significantly correlated with chick age ($r=0.0316$, $P=0.34$, $n=923$). Nor were there any significant differences in foraging trip duration between the three chick age groups (Kruskal-Wallis one-way ANOVA H_2 corrected for ties = 2.38, $P=0.31$, $n=923$). There was no significant effect upon foraging trip duration (Kruskal-Wallis one-way ANOVA, H_3 corrected for ties = 6.45, $P=0.42$, Figure 6.33).

6.7.2 Prey specific analyses

Analyses were limited to sandeels, sprats and rockling as these accounted for 98 % of foraging trips for which a trip duration was recorded. A highly significant difference was found between foraging trip duration for the three prey types (Kruskal-Wallis one-way ANOVA, H_2

Figure 6.29 Arctic tern inter-year comparison of foraging trip durations for chicks of all ages for non-sandeels

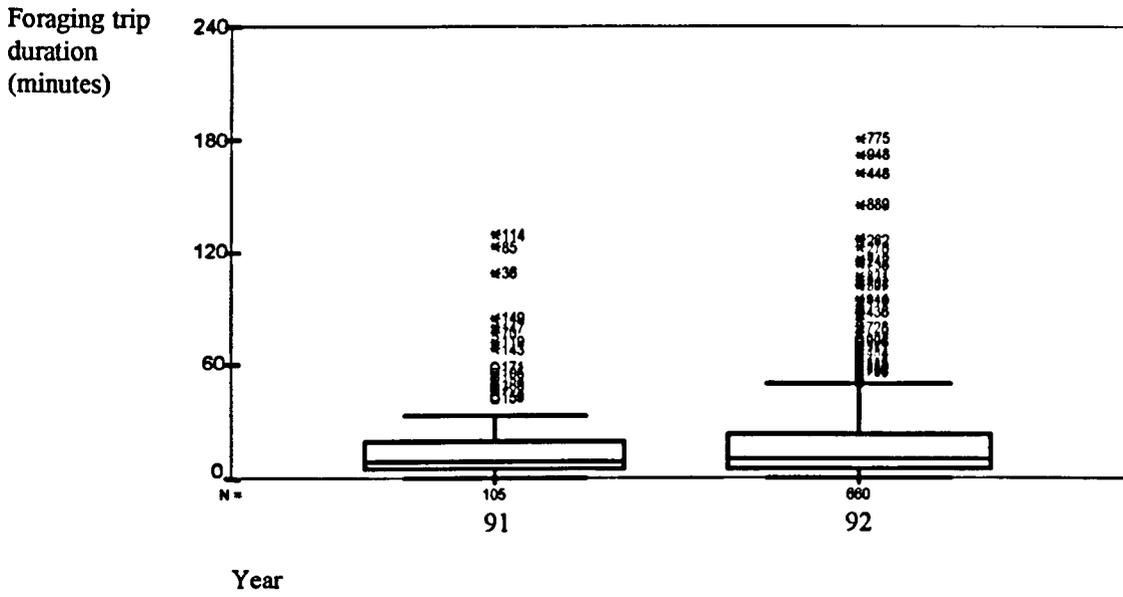


Figure 6.30 Arctic tern inter-year comparison of foraging trip durations for chicks of all ages for sandeels

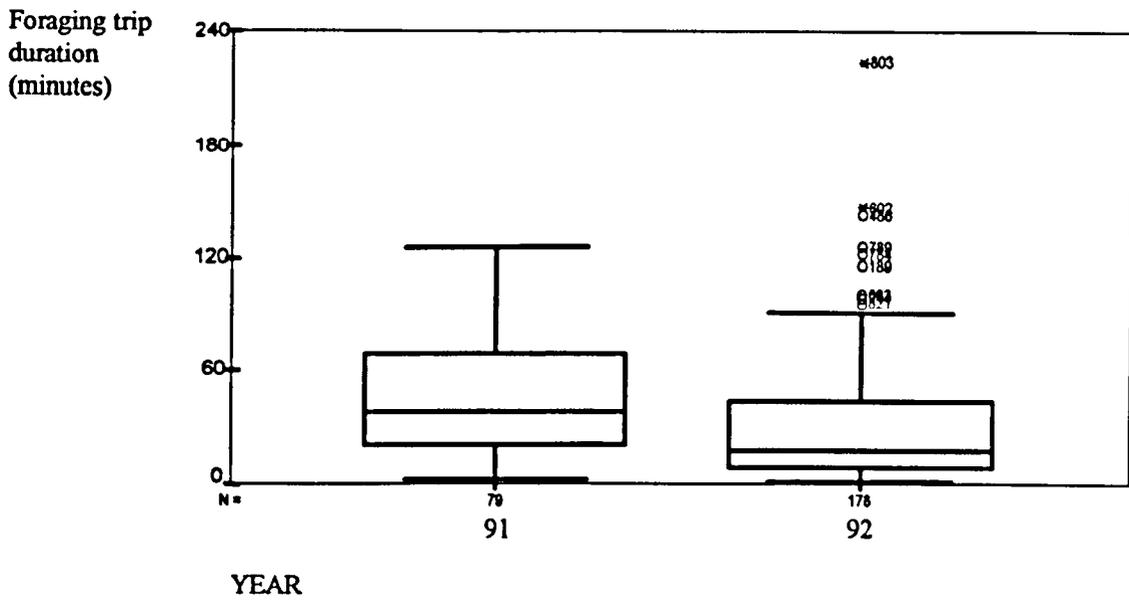


Figure 6.32 Common tern male and female foraging trip durations for all prey types in 1992

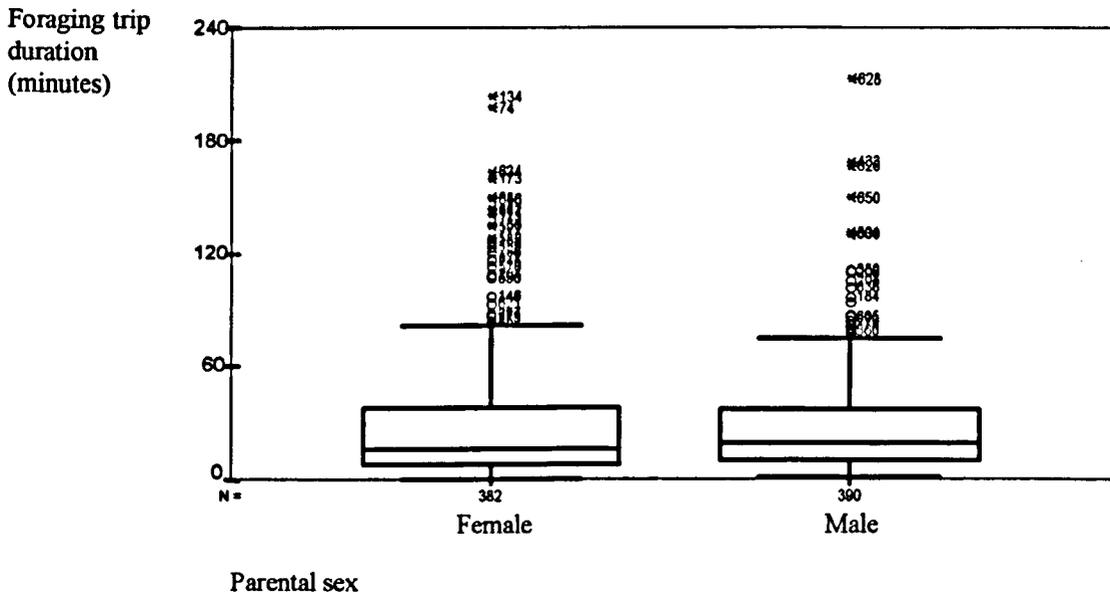
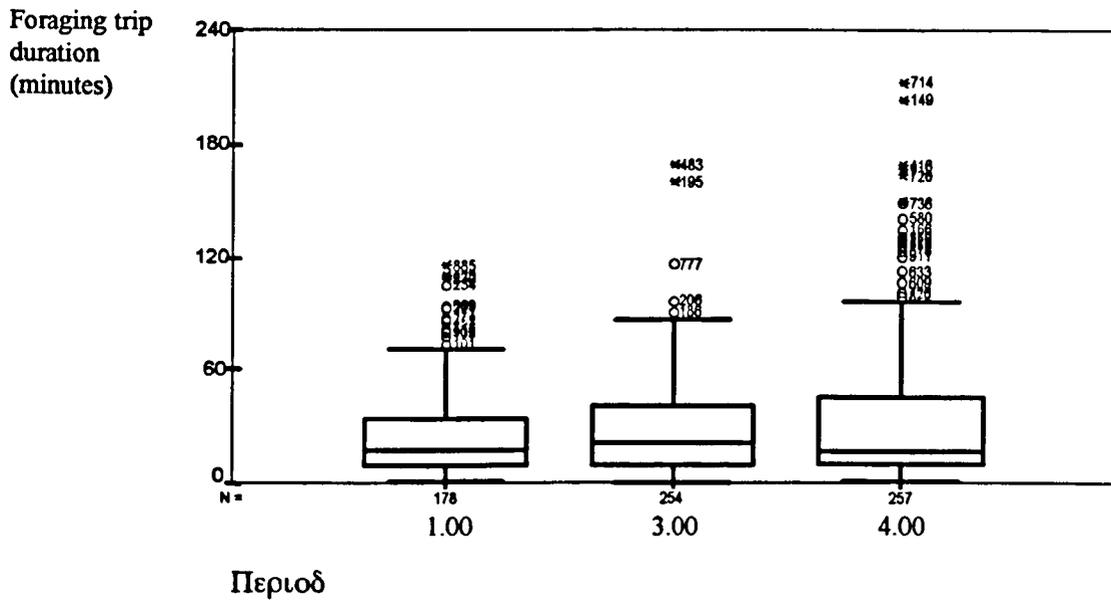


Figure 6.33 Common tern foraging trip durations for current brood sizes of one, two and three in 1992



corrected for ties=53.46, n=907, $P<0.0001$). Sandeel (median trip duration= 21 minutes, IQR = 30.5) and sprat (median trip duration= 23 minutes, IQR = 30.5) trips did not differ from each other in duration but both were significantly longer than trips where rockling (median trip duration= 11 minutes, IQR = 15.25 minutes) were retrieved.

Median foraging trip durations and inter-quartile ranges for the three prey types are shown in Figure 6.34.

6.7.3 Multivariate analyses

To further investigate the relationship of prey type and size upon foraging trip duration a two-way ANOVA was performed on square root transformed foraging trip times with prey type (sandeel or sprat) and prey size (combined size categories <8 cm and >8 cm). Rockling were not included in this analysis as these varied little in size with no rockling larger than 8 cm fed to chicks during the observational period. No statistically significant main effects of prey type on transformed foraging trip duration was found. Nor was there any statistically significant interaction between these variables (Table 6.10). However prey size did have a significant effect on foraging trip duration.

Figure 6.34 Common tern foraging trip durations for sandeels, sprats, and rockling in 1992

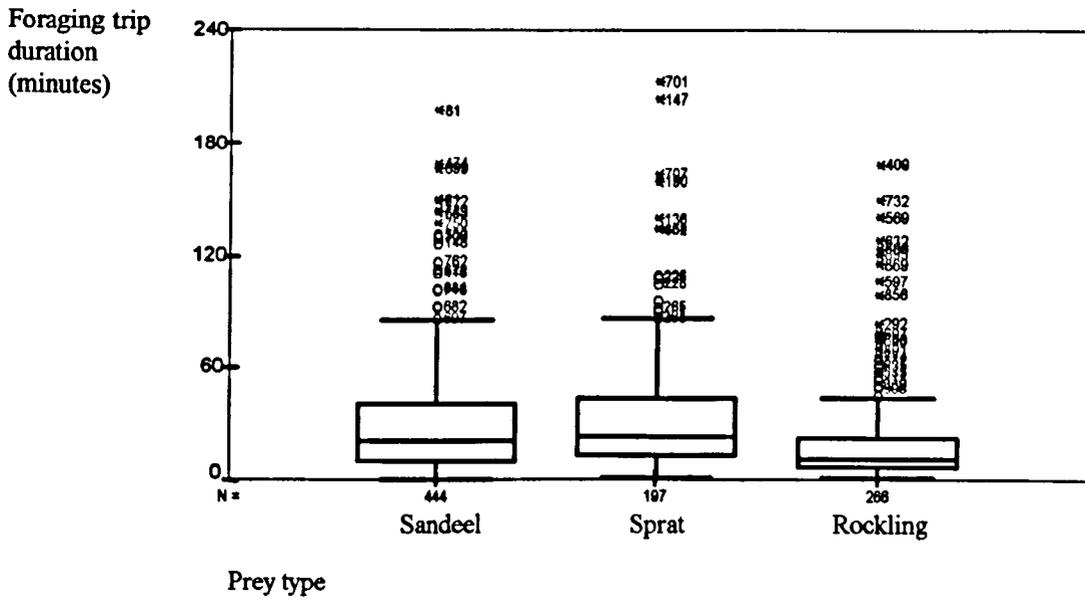


Table 6.10 Two-way ANOVA of the effect of prey type and prey size on square root-transformed foraging trip duration by common terns

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	Significance of F
Main effects	82.54	2	41.27	7.26	0.001
Prey type	1.91	1	1.91	0.33	0.56
Prey size	66.29	1	66.29	11.66	0.001
Prey type * Prey size	0.37	1	0.37	0.06	0.80
Explained	87.82	3	29.27	5.15	0.002
Residual	3571.77	628	5.688		
Total	3571.77	628	5.69		

However previous experimental work highlighted the importance of small prey to young chicks, and also showed that the types of prey fed to chicks changes with season and with chick age. To test the null hypothesis of no difference in foraging trip duration with prey type and chick age a two-way ANOVA was performed. There were significant effects on transformed foraging trip duration of both prey type and chick age. The interaction between prey type and chick age group was also significant (Table 6.11).

Table 6.11 Two-way ANOVA of the effects of prey type and chick age group upon common tern foraging trip

duration

Source of variation	Sum of squares	Degrees of freedom	Mean Square	F	Significance of F
Main effects	302.57	4	75.64	13.95	0.000
Prey type	265.90	2	132.95	24.51	0.000
Chick age group	89.94	2	44.97	8.29	0.000
Prey type * chick age group	76.30	4	19.08	3.52	0.007
Explained	329.34	8	41.17	7.59	0.000
Residual	4870.19	898	5.423		
Total	5199.53	906	5.739		

6.8 Foraging rate and foraging economics

6.8.1 Foraging rate

6.8.1.1 Arctic tern 1991

In 1991 foraging rate did not vary significantly with chick age (Kruskal-Wallis one-way ANOVA

H_{20} corrected for ties = 21.40, $P=0.37$, Table 6.12, Figure 6.35). The following table is only included for

comparison with 1992 Arctic tern foraging rate analysis.

Table 6.12 Arctic tern 1991 foraging rate (Medians are given with 25% and 75 % percentiles).

Chick age group (days old)	Foraging rate (trips/chick/hour ⁻¹)
0-6 (n=17)	0.51 (0.45, 0.85)
7-13 (n=14)	0.76 (0.43, 1.09)
14-20 (n=14)	0.76 (0.53, 1.04)

6.8.1.2 Arctic tern 1992

In 1992 the foraging rate corrected for brood size increased with increasing chick age (Table 6.13, Figure 6.36). (Kruskal-Wallis one-way ANOVA H_{20} corrected for ties=92.15, $P<0.0001$). As a significant difference was found between parental foraging rates for Arctic terns feeding chicks of different ages a multiple comparison was done to establish where the differences lay. However as the number of comparisons is $\#c = k(k-1)/2$ (Siegel & Castellan, 1988), 180 comparisons between ages would have had to be done ! Because of this data were aggregated into chick age groups before the multiple comparison procedure (Table 6.13).

Table 6.13 Arctic tern 1992 foraging rate (Medians are given with 25% and 75 % percentiles).

Chick age group (days old)	Foraging rate (trips/chick/hour ⁻¹)
0-6 (n=15)	0.71 (0.57, 0.86)
7-13 (n=13)	1.08 (0.96, 1.43)
14-20 (n=12)	1.74 (1.47, 2.54)

The only significant difference found between foraging rates was between age groups 1 and 3.

6.8.1.3 Common tern 1992

Prey delivery rate at different chick ages was significantly different in 1992 (Kruskal-Wallis one-way ANOVA H_{20} corrected for ties= 37.25, $P=0.01$).

Figure 6.36 Arctic tern foraging rate for all prey types in 1992

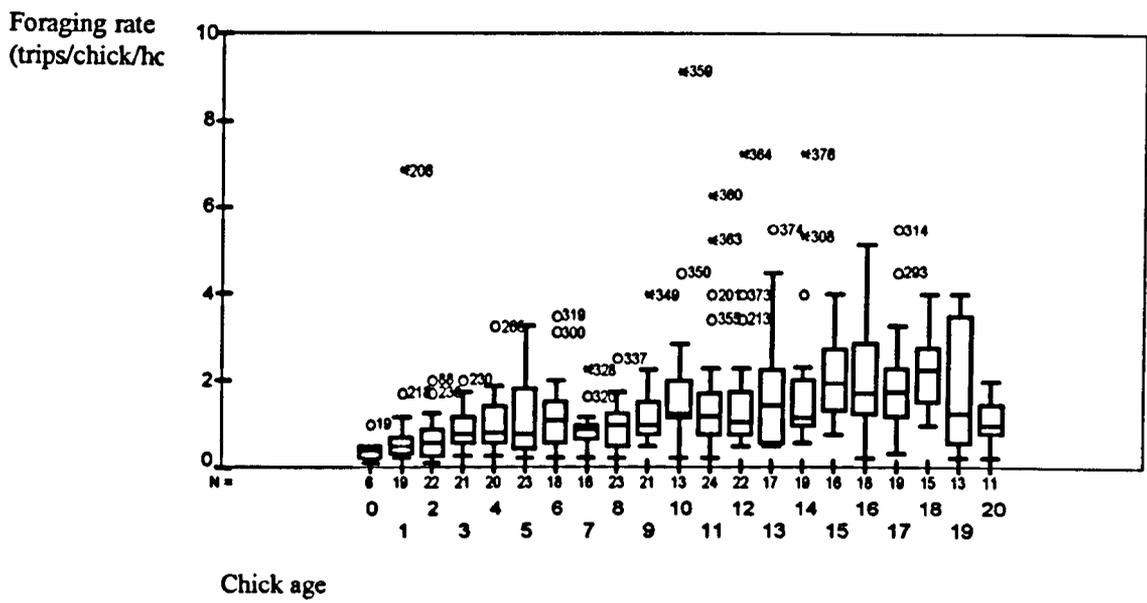


Table 6.14 Common tern 1992 foraging rate (Medians are given with 25% and 75 % percentiles).

Chick age group (days old)	Foraging rate (trips/chick/hour ⁻¹)
0-6 (n=24)	0.26 (0.21, 0.34)
7-13 (n=13)	0.38 (0.28, 0.64)
14-20 (n=12)	0.55 (0.33, 0.80)

As for Arctic terns the data were aggregated to give means of means for each chick age group. Once again the only significant difference in foraging rate was found between age groups 1 and 3.

6.8.2 Foraging profitability

6.8.2.1 Arctic tern foraging profitability

6.8.2.1.1 Profitability by prey type

The profitability (defined as energy in kilo-joules brought to the nest per minutes absence) of all prey types irrespective of chick age were significantly different (Kruskal-Wallis one-way ANOVA H_2 corrected for ties=117.68, $P<0.0001$). A subsequent multiple comparison found significant differences between the profitabilities of the three major prey types. Sprats were more profitable than rockling which were in turn more profitable than sandeels.

6.8.2.1.2 Energy/Profitability by chick age group

As an initial examination of whether any simple linear trends existed in energy delivery or profitability of all prey types and different prey types Spearman's rank correlations were performed on the data (Table 6.15). The level of significance used was $\alpha = 0.01$. As energy level for rockling was a fixed amount only profitability was compared for this prey type.

There was a small but significant decline in the profitability of rockling with increasing chick age. No other significant linear trends in either energy delivered nor profitability for sprats or sandeels.

Table 6.15 Spearman rank correlations energy and profitability by chick age for Arctic terns. Probabilities are given in brackets.

Prey type	Energy by chick age	Profitability by chick age
All	-0.05 (0.18)	-0.002 (0.96)
Sandeel	-0.06 (0.40)	0.15 (0.05)
Sprat	0.19 (0.16)	0.17 (0.21)
Rockling	-	-0.11 (0.008)

6.8.2.1.3 Profitability by age group

There was no significant difference in the profitability of sandeels or sprats with age groups (Sandeels: Kruskal-Wallis one-way ANOVA H_2 corrected for ties=2.21, $P=0.33$, $n=177$; Sprats: Kruskal-Wallis one-way ANOVA H_2 corrected for ties=2.29, $P=0.32$, $n=55$). Rockling became significantly less profitable with increasing chick age (Kruskal-Wallis one-way ANOVA H_2 corrected for ties=8.84, $P=0.01$, $n=613$). A multiple comparison found significant differences, with the profitability for age group one greater than for age group three and the profitability for age group two greater than for age group three. No significant difference was found between the profitability of rockling for age groups one and two.

6.8.2.1.4 Within each age group: Profitability by prey type.

There were significant differences between the profitabilities of each prey item within each chick age group (0-6 days old: Kruskal-Wallis one-way ANOVA H_2 corrected for ties=43.67, $P<0.0001$, $n=214$; 7-13 days old: Kruskal-Wallis one-way ANOVA H_2 corrected for ties=43.98, $P<0.0001$, $n=290$; 14-20 days old Kruskal-Wallis one-way ANOVA H_2 corrected for ties=23.80, $P<0.0001$, $n=341$). For age group one sprats were significantly more profitable than sandeels, and rockling were more profitable than sandeels. There was no significant difference in the profitabilities of sprats and rockling.

For age group two sprats were more profitable than rockling which were more profitable than sandeels. This was also the case for age group three.

6.8.2.1.5 Inter -year comparison.

The profitability of sandeels was significantly different between years. (Mann-Whitney U-test, $Z_{\text{corrected for ties}} = -8.02, P < 0.0001, n_{1991} = 79; n_{1992} = 177$).

6.8.2.2 Common tern foraging profitability

6.8.2.2.1 Profitability by prey type (irrespective of age group)

The profitabilities of sandeels, sprats, and rockling were significantly different (Kruskal-Wallis one-way ANOVA H_2 corrected for ties = 268.38, $P < 0.0001, n = 898$). Irrespective of chick age sprats were more profitable than sandeels, and sprats were more profitable than rockling. Sandeel and rockling profitabilities did not vary significantly. There was no significant linear relationship between energy brought to the nest ($r_s = 0.0495, P = 0.14$), nor its profitability ($r_s = -0.008, P = 0.80$) when all prey types were included.

6.8.2.2.2 Energy/Profitability by chick age group

For both sandeels and sprats the energy delivered to the nest and the profitability of each prey item increased with increasing chick age (Table 6.16)

Table 6.16 Spearman rank correlations energy and profitability by chick age for common terns. Probabilities are given in brackets.

Prey type	Energy by chick age	Profitability by chick age
All	0.05 (0.14)	-0.008 (0.803)
Sandeel	0.13 (0.005)	0.15 (0.001)
Sprat	0.44 (<0.0001)	0.33 (<0.0001)

Rockling	-	-0.016 (0.008)
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For each prey type there were significant differences in profitability between age groups (Sandeels: Kruskal-Wallis one-way ANOVA H_2 corrected for ties=13.79, $P<0.0001$, $n=442$; Sprats: Kruskal-Wallis one-way ANOVA H_2 corrected for ties=18.27, $P<0.0001$, $n=190$; Rockling: Kruskal-Wallis one-way ANOVA H_2 corrected for ties=8.31, $P=0.0157$, $n=266$). Sandeels were significantly more profitable for age groups three than one, and for age groups three than two. There was no significant difference in the profitability of sandeels for age groups one and two. Sprats were significantly more profitable for age groups three than one and for age groups two than one. There was no significant difference between age groups two and three. The only significant difference in the profitability of rockling was between age groups one and three, where for age group three rockling were less profitable than for age group one.

6.8.2.2.3 Profitability by age group

Within each age group the profitabilities of different prey types were significantly different. (0-6 days old: Kruskal-Wallis one-way ANOVA H_2 corrected for ties=61.60, $P<0.0001$, $n=250$; 7-13 days old: Kruskal-Wallis one-way ANOVA H_2 corrected for ties=157.83, $P<0.0001$, $n=318$; 14-20 days old: Kruskal-Wallis one-way ANOVA H_2 corrected for ties=57.20, $P<0.0001$, $n=330$).

For age group one sprats were significantly more profitable than rockling, which were more profitable than sandeels. For age group two sprats were significantly more profitable than both sandeels and rockling. There was no significant difference in the profitability of sandeels and rockling. Within age group three sprats were more profitable than sandeels which were more profitable than rockling.

6.9 Discussion

6.9.1 Arctic and common tern chick diet

The non-sandeels component of Arctic tern chick diet in 1992 was much larger in 1992 than in 1991. These were predominantly rockling. In both years similar proportions of sandeels and non-

sandeels were fed to chicks less than 6 days old. The majority of these were smaller than 8 cm in length and were a size which Arctic tern chicks could easily handle and ingest. In 1991 needle sandeels (< 4cms) found to have been an important part of the diet of young Arctic tern chicks elsewhere were apparently scarce and were replaced by small rockling. Needle sandeels were more prevalent in 1992 but rockling remained the most important part of the diet of chicks less than 6 days old in 1992. The major difference between the two years in the diet of Arctic terns was the persistence of a large proportion of small rockling in the diet of chicks aged from 7–20 days old. In 1991 the proportion of prey over 8 cm in length fed to chicks increased with increasing age for sandeels but less so for non-sandeels. However, in 1992 chicks of all pre-fledging ages were fed both sandeels and sprats of similar size, and the majority of these were less than 8 cm in length. As the major part of pre-fledging age chick diet was rockling in 1992 this meant that the bulk of chick diet was composed of small prey less than 8 cm in length in 1992.

As watches of common and Arctic terns were contemporaneous any differences in prey fed to their chicks must have been due to active selection by the foraging adults and consequent niche partitioning of the available prey. Common terns fed their chicks more sandeels and sprats and fewer rockling than Arctic terns. This trend was consistent across all chick ages. As for the Arctic terns the numbers of larger sandeels (≥ 8 cm) fed to chicks did not increase with increasing chick age. However for sprats the proportion of larger fish fed to chicks did increase with increasing chick age.

Do the differing profitabilities of prey captured by both species give any insights into prey selection? For the 0–6 day old age groups sprat and rockling profitabilities were not significantly different, and both were more profitable than sandeels. For rockling the shorter median foraging trip duration was the primary determinant of higher profitability, for sprats it was the higher energy content of the fish. For the remaining two older age groups of Arctic tern chicks in 1992 sprats were more profitable than rockling which were more profitable than sandeels. Why then did Arctic terns not feed older chicks on an increasing number of larger sprats than common terns? However the measure of profitability used in the preceding analyses are relatively crude and do not take account of the energetic costs of catching a fish and transporting it back to the nest. It is possible that sprat and rockling are differently distributed in the water column and require different foraging techniques

to capture them. Of course the spatial distribution of prey species may also differ. Sprats may have been available further offshore necessitating longer foraging flights by the common terns.

Terns do use different foraging techniques (e.g. Kirkham & Nisbet, 1987) although data on the prey captured using them is scant. Another possibility is that sprats vary in quality at this time of year due to their allocation of body resources into reproduction. It may be a more effective foraging 'policy' to capture a less profitable, but one with a consistent energy level, than a more profitable one which varies in quality. Other data included in this chapter demonstrate that the larger a fish is the more likely a bird is to depart immediately from the nest upon return from a foraging trip. This is an index of disturbance at the nest site. Birds returning with large fish were often harassed by conspecifics attempting to kleptoparasitise them. This forced these adults to leave with their prey. The fates of these fish were unknown. Unlike previous studies of kleptoparasitism in terns (e.g. Uttley, 1991) breeding adults stole fish from their neighbours. Later in the season failed breeders and juveniles also stole fish. Another possibility is that the longer foraging trip durations for sprats may have been at least partly attributable to the increased risk of having a sprat stolen by another tern. The experiment with common terns in 1992 showed that adults will select prey of a size that young chicks can easily handle and ingest. The relative speed with which a rockling can be transferred from adult to chick and swallowed may count in their favour if there is a risk of kleptoparasitism. Lastly the marked difference in the size, shape, and mass of rockling and sprats may mean that there is a larger energetic cost of transport back to the nest with a sprat than with a rockling.

For common terns all age groups were fed a significantly smaller proportion of small prey than Arctic terns. This trend was reflected across all age groups for sandeels and for sprats. Consequently the range of sizes of sandeels and sprats taken by common terns were on the whole larger than those taken by Arctic terns. This explains the differences in profitabilities of prey found between Arctic and common terns. As for Arctic terns it is the interaction of prey size, energy content, and foraging trip duration that may explain some of the variation in chick diet witnessed. It may be that energy costs of capturing and transporting larger prey are less for common terns than for Arctic terns. Alternatively they may be more efficient foragers for sprats than Arctic terns.

The results of the egg storage experiment separating chick age and time of season may be summarised as follows (a) Prey selection varies with date where date is analogous to seasonal availability of prey. (b) Chick age has a marked effect on prey selection. (c) This selection is primarily determined by the physical limitations of the smallest chicks which are unable to ingest fish larger than 4cm long. They are similarly limited by the keel depth of fish. The smallest chicks have difficulty in handling fish where the keel depth is greater than their gape size. Both these factors increase the risk of kleptoparasitism by other terns. (d) Prey selection by size operates within a framework of changing seasonal availability of prey. (e) The persistence of smaller prey in older chicks' diets when it would appear that larger prey would be better may be a function of several factors. By taking prey which are located first, regardless of size, the search costs of the adult may be reduced. This is an important consideration for species that rely on prey which are patchily distributed (Westoby 1978). The increased risk of having a larger fish taken by another tern even when chicks have grown sufficiently to handle them may shift the balance of which prey is optimal. When prey is patchily distributed then it may benefit the foraging adult to return to the same area, as this would enhance the chances of finding another prey item. Chicks may have nutritional requirements best satisfied by a mixed diet (Krebs and Avery 1984). However I have no information on the different nutrients present in each prey type.

Significant differences were found in the range of prey types and prey sizes fed to the two experimental groups. Chick age was a more important determinant of prey selection than inferred availability. However an analysis of prey fed to chicks of the same age on different days showed that availability changes with season also. It appears that some selection determined by the interaction of several factors operates within the constraints imposed by which prey are available. This in turn is presumably a function of interacting factors.(weather, prey behaviour, adult foraging efficiency). Previous non-experimental studies which have found a correlation between seasonal availability and prey type or size fed to the chick may be compromised by the confounding effect of chick age. Similarly those studies which report a correlation between chick age and prey type and prey size fed to the chick may be confounded by the effect of changing seasonal availability of prey. Prey selection by common terns appears to be determined through the interaction of the physical limitations of chicks less than a week old with a concurrent increased risk of kleptoparasitism, and

changes in prey availability. Small chicks less than three days old cannot handle large prey items (pers obs.) and suffer an increased risk of kleptoparasitism by other common terns as a consequence. Hulsman (1981) reports a similar physical limitation on the size of prey that bridled tern chicks can easily ingest. It would be interesting to measure the width of the gape of Arctic and common tern chicks at different pre-fledging ages to examine whether any of the variation in the size of prey the two species feed to their chicks could be explained by this factor. The conflicting constraints acting on the parent e.g. the difficulty of searching for a patchily distributed prey and the need to maximise efficiency may influence prey selection.

6.9.2 Comparison with previous studies.

This study confirmed the importance of prey of an appropriate size for young Arctic and common tern chicks previously found by other researchers (Langham, 1968; Ewins, 1985; Uttley, Monaghan & White, 1989). All of these studies stressed the importance of sandeels less than 8cm long to the diet of the youngest chicks. In Shetland during the late 1980's, during a period when sandeels of this size were only present in Shetland waters in greatly reduced numbers, breeding success of both Arctic and common terns was depressed. Alternatives to small sandeels were unavailable. In Orkney in 1989, as in this study, rockling were a major constituent of tern chick diet (Uttley, 1991). Indeed the profitability analyses in this chapter suggest that rockling may be the preferred prey of Arctic terns provisioning young on Coquet in some years. The apparent absence of small rockling as an alternative chick diet on Shetland is puzzling as adult rockling are found in Shetland waters (Nolet, Wansink, & Kruuk, 1993). Further study of the early larval stages of all these prey fish and of their distribution both on the local and the national scale is necessary to clarify such anomalies.

Lemmetyinen (1973) studying Arctic terns in the Baltic found a gradual transition from small crustaceans to larger sticklebacks with increasing chick age. In the Wadden Sea inter-colonial differences in chick diet have been recorded suggestive of different profitabilities of prey at different colonies. Clupeids, flatfish and crustaceans were the major constituents of chick diet at Wadden sea colonies while adults from more coastal colonies often brought sticklebacks back to the nest (Becker, Frank & Walter, 1987). As in this study, Massias and Becker (1990) found that chicks were not always fed the most energetically favourable clupeids, but rather shrimps and three-spined

sticklebacks *Gasterosteus aculeatus* and they suggested that these prey may be an important alternative when higher energy prey are unavailable. Rockling may have played a similar role for Arctic terns on Coquet in the absence of sandeels in the larger size classes in 1992. As other studies (Sudmann & Becker, 1992) have found the foraging rate increased in 1992 in comparison to 1991, when the type of prey fed to the chicks changed. This was probably due to the lower quality, less energetically rich prey that Arctic terns were bringing to their chicks in that year.

This study took no account of two factors which have been found to have a profound effect on foraging behaviour elsewhere, namely weather and tidal effects. Weather affects the abilities of birds that forage by plunge diving (Macher & Ydenberg, 1990). Sagar and Sagar (1989) found that for the Antarctic tern *Sterna vittata* increasing wind speed led to a decrease in capture rate and feeding success. Furthermore they found that foraging techniques used varied with the type of prey sought and sea conditions. More particularly they observed that Antarctic terns caught crustaceans mainly by contact dipping and used partial plunge diving more in moderate and rough seas. Possibly similar effects related to different weather and sea conditions in the two year of this study may help explain some of the observed difference in prey fed to chicks. Becker and Finck (1985) found that increasing amounts of rain apparently lowered the foraging success of adult terns. In this study some of the highest foraging rates were observed during a three day period of strong winds and rough seas conditions when common terns apparently specialised in capturing rockling. Such effects warrant further study.

Both Frank (1992) and Frick & Becker (1995) noted a tidal pattern to diet composition with sandeels fed to chicks more frequently after low tide and clupeids fed to chicks more around high tide. Becker, Frank and Sudmann (1993) found an obvious tidal cycle in the foraging pattern of common terns in an area of mud-flats in the Wadden Sea. They found distinct individual differences in the foraging areas used, and stressed the importance of tide in periodically producing local concentrations of prey in water conditions favourable to their capture. Perhaps most importantly of all this study demonstrated common terns ability to remember where favourable foraging areas are to be found and at what stage of the tidal cycle. Individual differences in the ability to learn where prey are likely to be under differing environmental conditions, and individual differences in the foraging ability of terns are both important to lifetime reproductive success and ultimately to fitness (Becker,

Frank and Sudmann , 1993) Other researchers have reported age related differences in seabird foraging abilities that could be related to the time required to learn where good foraging areas are and the best techniques to capture prey within them (e.g. Morrison, Slack & Shanley, 1978; Searcy, 1978; Maclean, 1986; Arnqvist, 1992). The regular return to the same areas at certain tide times could provide an alternative explanation for the apparent territorial behaviour reported by Nisbet (1983) for common terns in Massachusetts.

Similar inter-specific differences to those found in this study in 1992 in prey fed to chicks have been observed elsewhere. Lemmetyinen (1973) found that common tern fed more cyprinids to their chicks than Arctic terns which took more crustaceans and insects. Uttley, Monaghan and White (1989) recorded that common terns fed their chicks more saithe *Pollachius virens* and more large sandeels than sympatric Arctic terns during a period of apparent reduced availability of small sandeels. In other studies where the two species have been studied in sympatry common terns have been found to take larger prey than Arctic terns (Boecker, 1967; Langham, 1968; Uttley *et al.*, 1989; Frick & Becker, 1995). This may be due to difference in foraging areas between the two species of the type reported by Boecker (1967), Langham (1968), Dunn (1972), Lemmetyinen (1973) and Uttley (1991), with common terns preferring more inshore waters for foraging than Arctic terns. Only a large scale radio telemetry study of the type used by Becker and his co-workers in the German Wadden Sea could clarify this.

The results have implications for monitoring. The use of seabirds as monitors of the marine environment and particularly as monitors of small fish is increasingly advocated (Cairns 1987, Monaghan *et al.* 1989a). They have logistical and financial advantages over other sampling methods. This study has shown that prey selection can be affected by factors other than availability. Unless chick age is accounted for in ones interpretation of monitoring data, it would be easy to come to misleading conclusions. Future monitoring programmes should attempt to partition chick age and seasonal effects or at least hold chick age constant.

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Chapter 7 Variation in chick growth

7.1 Introduction

Variation in chick growth is potentially a very useful indicator of food availability for seabirds (Cairns, 1987). Various studies have found that where food supply is very poor, chick growth is depressed (e.g. Monaghan *et al.*, 1989; Massias & Becker, 1990; Mlody & Becker, 1991; Uttley *et al.*, 1994). However factors other than food availability will also influence the rate at which chicks grow. Poor parental foraging performance, due for example to inexperience, inefficiency or poor condition, may result in poor chick growth. Thus differences in chick growth between years or colonies could be mediated through, for example, differences in the age structure of the colonies, rather than food supply. Furthermore, poor quality individuals may not breed in years of poor food supply, and thus a change in the average quality of individuals breeding in a colony may effectively mask any effect on average chick growth rate (see earlier chapter for details of possible non-breeding in this study). An additional complication arises in species with brood sizes of greater than one. In such species, reductions in brood size may occur in response to poor food supplies, thereby maintaining the typical growth rates of surviving chicks, again masking an effect on chick growth. Thus in comparing chick growth between years, it is necessary to take such factors into account, though in many studies this has not been possible.

Precise information on exactly how variation in the availability of specific nutrients influences different growth parameters is very limited. The complex inter-relationships between dietary requirements, food supply, body mass, metabolic rate, and chick mortality patterns mean that considerable inter-specific differences may exist.

Most studies have concentrated on energetic considerations, though gross energy may not be the limiting factor, other nutrients may be important. (Hulsman & Smith, 1988). Ricklefs & White (1981) found that common tern chicks required about 200kJ per day for adequate growth. The variations in the prey fed to chicks and their energy content have been found to affect chick growth markedly. Massias & Becker (1990) observed depressed growth in common terns fed on three-spined sticklebacks and common shrimps *Crangon vulgaris* compared to those fed on herring *Clupea*

harengus. However these authors stressed that these lower quality foods may be an important resource at times when higher quality prey are unavailable.

Nestling metabolic rate may interact with growth rate in a complex way. Klaassen & Bech (1992) found that Arctic tern chicks which were less than 75 % of their expected body mass for their age were less able metabolically to withstand a decrease in temperature than were chicks of the same age but normal mass. These authors state that:

" Assuming a close coupling between basal or resting metabolism and working capacity, as has been suggested for both adult birds (Brody, 1945; Drent and Daan 1980; Kersten & Piersma, 1987; Daan, Masman, and Groenewold, 1990) and chicks (Drent and Klaassen, 1989; Klaassen and Drent, 1991), a decrease in basal or resting metabolism with decreasing growth rate should also be accompanied by a decrease in peak metabolism (i.e., thermogenic capacity). This might underlie some of the mortality associated with reduced growth rates in nestlings (e.g., terns: Langham 1972; Lemmetyinen, 1972; LeCroy and LeCroy, 1974; Becker and Finck 1985; Becker and Specht, 1991).

"

In the natural situation thermal challenges to the chicks occur during prolonged periods of inclement weather and may have a marked effect on chick mortality. Becker and Specht (1991) found chick mortality was mainly dependent on minimum temperature, rain and wind speed. Thus, inter-relationship of food supply, growth rate, metabolic rate, ability to withstand a thermal challenge and the timing of the thermal challenge may all affect chick mortality.

Variations in food supply may therefore not only affect growth directly but also indirectly through influencing the amount of time spent brooding by the parents.

In this chapter I examine differences in the chick growth rates of Arctic and common terns between years. Firstly, I consider colony average growth rate and follow this with more detailed comparisons taking account of adult quality (as indicated by initial clutch size) and brood size and hatching order of the chicks themselves. I also examine how the observed growth rates relate to the energetic requirements of the chicks.

7.2 Methods

Methods used to weigh and measure Arctic and common tern chicks are as described in chapter two. Chicks that failed to fledge are included in all analyses since exclusion of these chicks would bias average figures to those that survive. Chicks from relay sites or from sites where eggs were stored were excluded from the following analyses. Data from subsidiary plots were checked for significant differences from the main study plots. As no significant differences were found between these and the main study plots, data from the subsidiary plots were included in the following analyses. Individual chick ages were calculated from hatch date, and were precise. Data from the linear phase of growth from four to twenty days old only are used in regression comparisons. Due to the small numbers of common tern pairs that laid clutches of one or two eggs analyses are limited to three egg clutches for this species. There was no need to check the reliability of the only co-variate (year) as this was fixed (Tabachnick & Fidell, 1989). To account for the fact that a variable number of repeat measurements were taken on each chick, adjusted probability values are quoted for regression/co-variance statistics using degrees of freedom based on the number of individuals rather than the number of measurements.

7.3 Results

7.3.1 Arctic tern chick growth rate

7.3.1.1 Arctic tern colony average growth rate

Overall, Arctic tern chicks grew at a similar rate (as indicated by wing length) in 1991 and 1992. However, in 1991 Arctic tern chicks gained mass at a significantly faster rate than in 1992 and consequently gained mass faster in relation to their size, suggesting that they were in better condition (Figures 7.1, 7.2, & 7.3). For common terns although the rate of wing growth was similar, chicks of any given age had significantly longer wings in 1991 than in 1992 (Figure 7.4). Like Arctic terns the mass gain of common terns was faster in 1991 than in 1992 (Figure 7.5) and thus chicks gained mass faster in relation to their size, again suggesting they were in better condition (Figure 7.6).

Figure 7.1 The wing growth of Arctic tern chicks on Coquet in 1991 and 1992. Slopes of the regression lines were significantly different (ANCOVA $F_{1,833}=6.17$, $p=0.01$). 1991 $n=394$, $r=0.97$, $P<0.000$, $y=8.68x - 10.12$; 1992 $n=843$, $r=0.97$, $y=8.26x - 1.46$.

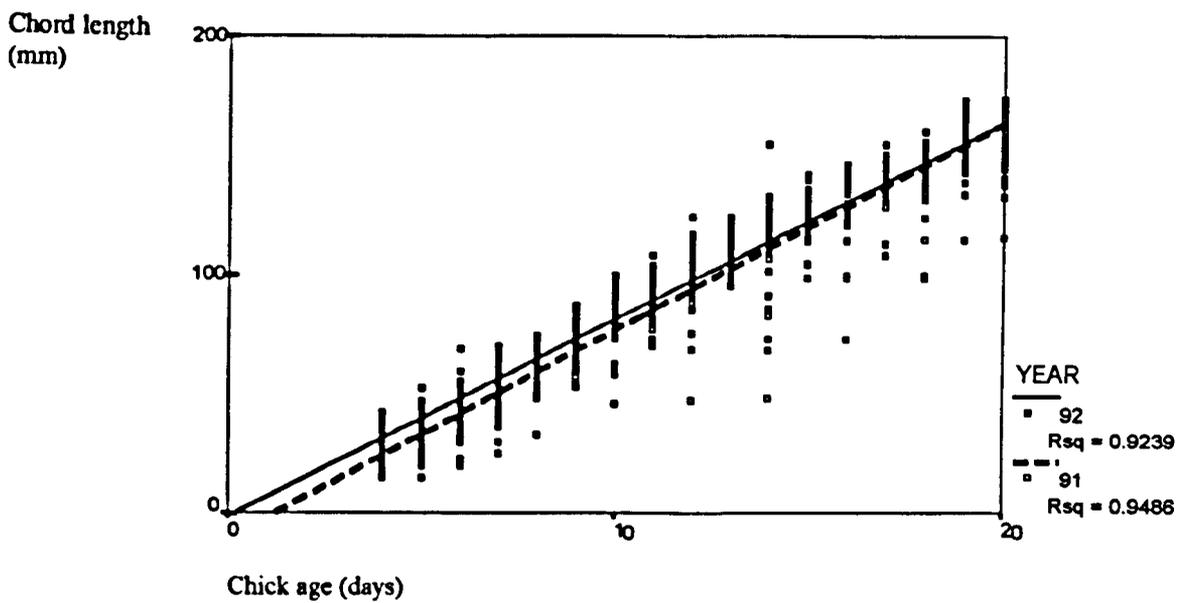


Figure 7.2 The mass growth of Arctic tern chicks on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,833}=34.99$, $p<0.0001$). 1991 $n=257$, $r=0.83$, $P<0.0001$, $y=5.38x + 13.45$; 1992 $n=580$, $r=0.75$, $y=3.92x + 26.71$.

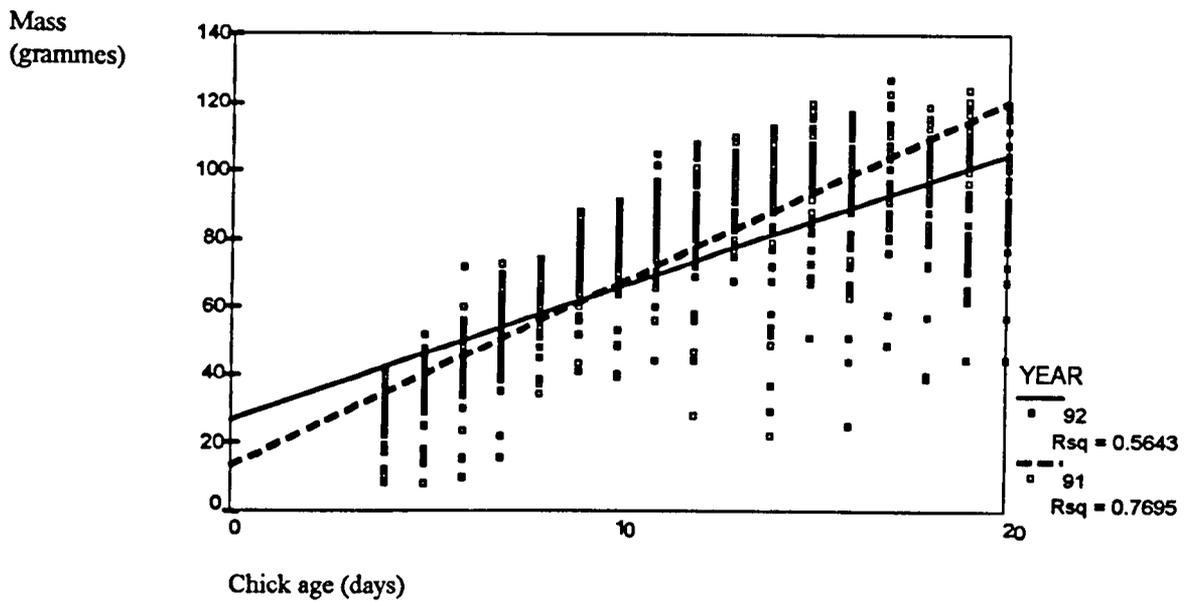


Figure 7.3 The correlation of chick mass and chord length of Arctic tern chicks on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,833}=31.24$, $p<0.0001$). 1991 $n=257$, $r=0.94$, $P<0.0001$, $y=0.64x + 17.56$; 1992 $n=580$, $r=0.86$, $y=0.52x + 22.74$

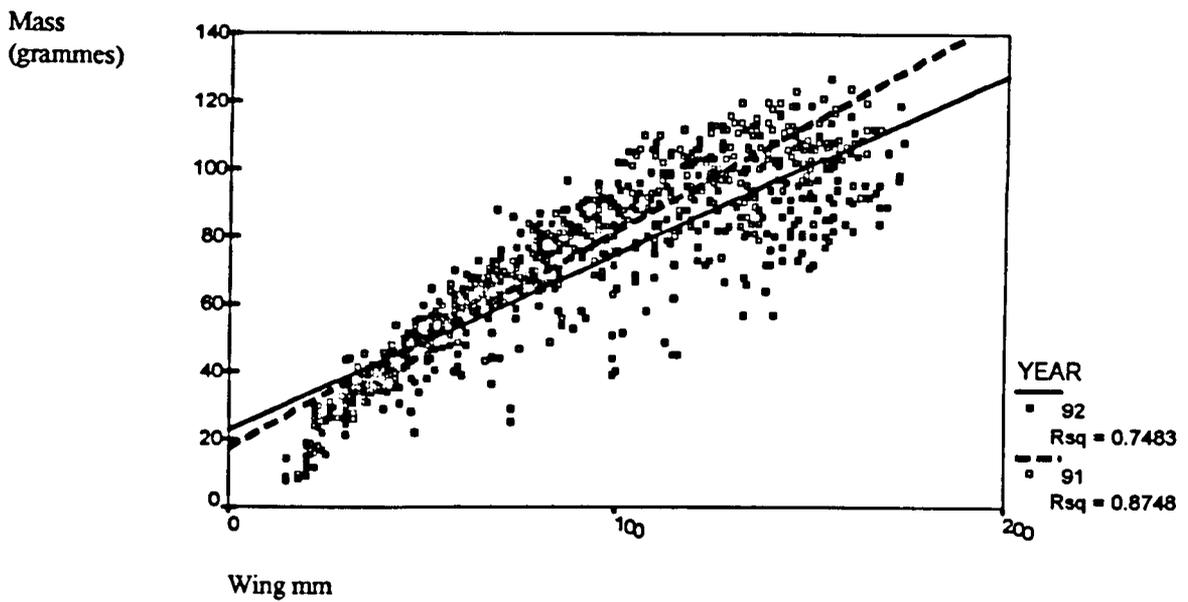


Figure 7.4 The wing growth of common tern chicks on Coquet in 1991 and 1992. Slopes of the regression lines were not significantly different (ANCOVA $F_{1,839}=0.44$, $p=0.51$). 1991 $n=404$, $r=0.94$, $P<0.0001$, $y=7.62x - 13.12$; 1992 $n=439$, $r=0.92$, $y=7.84x - 5.25$.

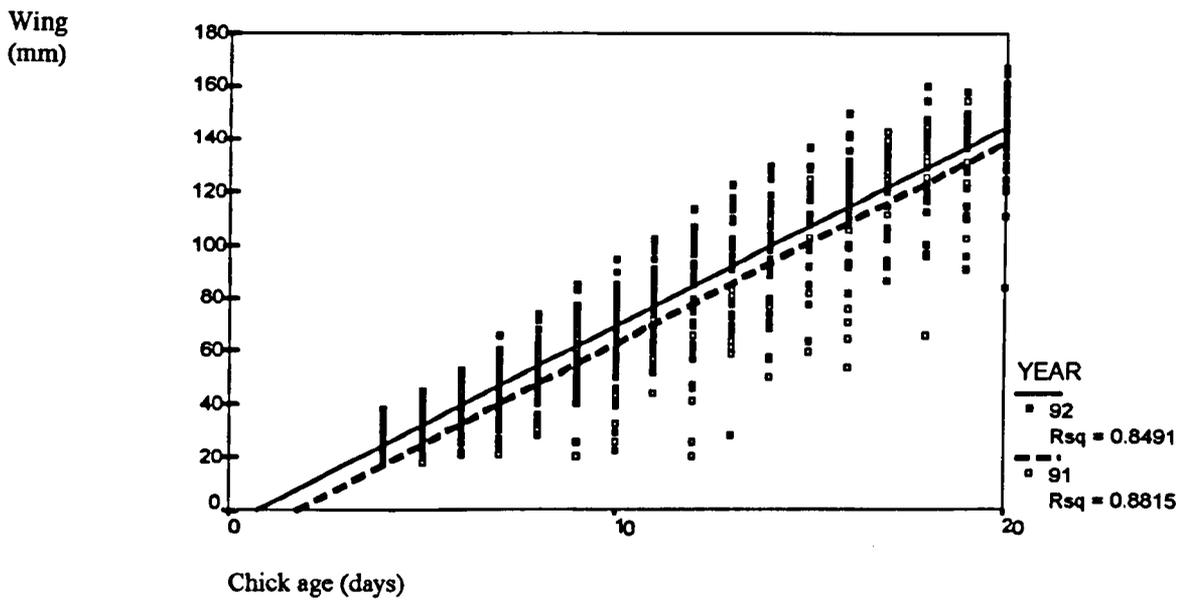


Figure 7.5 The mass growth of common tern chicks on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,839}=61.07$, $p<0.0001$). 1991 $n=404$, $r=0.86$, $P<0.0001$, $y=6.31x - 1.14$; 1992 $n=439$, $r=0.71$, $y=4.19x + 20.19$.

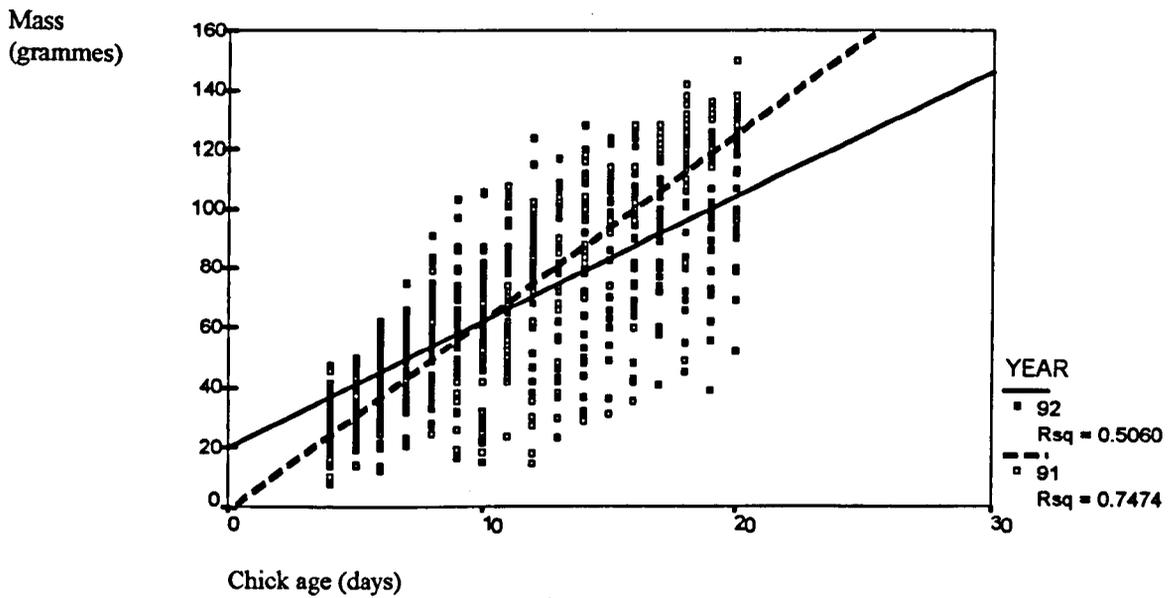
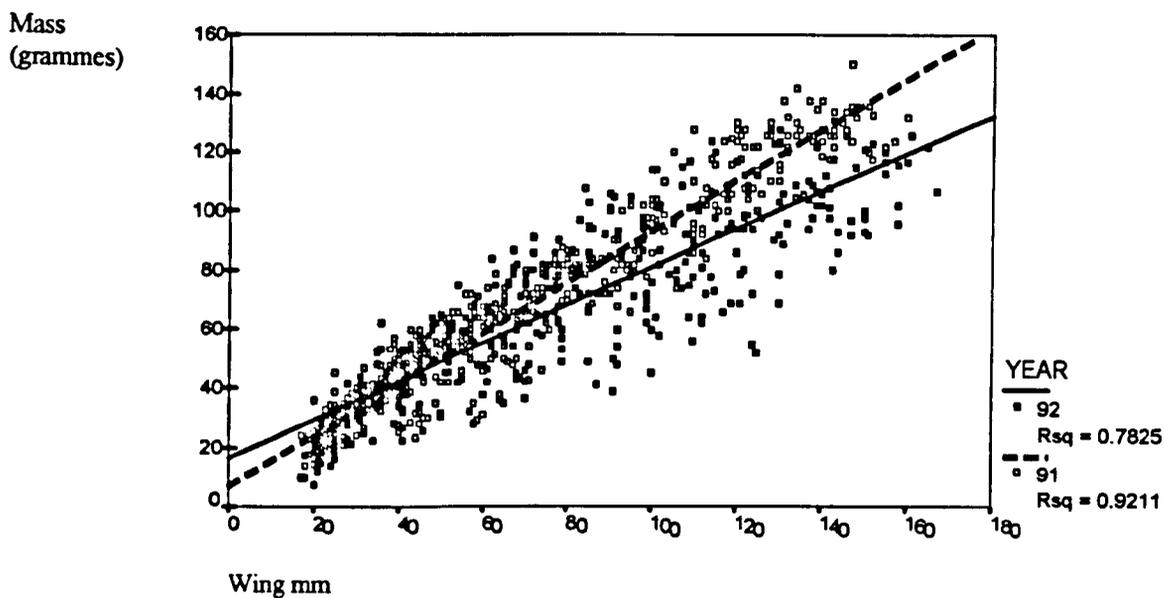


Figure 7.6 The correlation of chick mass and chord length of common tern chicks on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,839}=1805.76$, $p<0.0001$). 1991 $n=404$, $r=0.96$, $P<0.0001$, $y=0.86x + 7.19$; 1992 $n=439$, $r=0.88$, $y=0.64x + 17.04$.



7.3.1.2 Arctic tern single egg clutches

On average birds laying a single egg are likely to be of poorer quality than those laying larger clutches. In single egg clutches in Arctic terns the rate of wing growth of chicks was similar in both years, but for a given age chicks in 1992 had longer wings (Figure 7.7). Mass growth was not significantly different between the two years (Figure 7.8). For any given size, chicks attained similar masses in the two years and thus appeared to be in a similar condition. (Figure 7.9).

7.3.1.3 Arctic tern : two egg clutches: "a" chicks

Parents laying two eggs were at least of average quality. For "a" chicks, those of a given age were larger in 1992 but did not grow in size any faster than in 1991 (Figure 7.10). However their rate of mass gain was slower in 1992 than in 1991 (Figure 7.11). In relation to body size Arctic tern chicks gained mass more slowly than in 1991 suggesting that they were in poorer condition (Figure 7.12).

7.3.1.4 Arctic tern two egg clutches: "b" chicks.

The rate of wing growth was not significantly different between the two years and there was no significant difference in the growth rate of the wing (Figure 7.13). B chicks gained mass faster in 1991 than in 1992 (Figure 7.14). As was the case for the "a" chicks they also gained mass faster in relation to body size (Figure 7.15).

7.3.2 Common tern growth rate

7.3.2.1 Common tern three egg clutches: "a" chicks

Wing growth was similar in both years but for a given age chicks in 1992 were larger (Figure 7.16). However in 1991 this category of common tern chick gained mass faster in relation to chick age and size compared to 1992 and thus were apparently in better condition (Figures 7.17 & 7.18).

7.3.2.2 Common tern three egg clutches: b" chicks

For any given age chicks in this category were larger in 1992 than in 1991 (Figure 7.19) but gained mass slower in relation to age (Figure 7.20) and to body size than in 1991 (Figure 7.21).

Figure 7.7 The wing growth of Arctic tern chicks from one egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were not significantly different (ANCOVA $F_{1,84}=2.82$, $p=0.10$). There was a highly significantly difference in the elevation of the two lines (ANCOVA $F_{1,85}=31.09$, $p<0.0001$). 1991 $n=63$, $r=0.99$, $P<0.0001$, $y=8.63x - 9.52$; 1992 $n=25$, $r=0.99$, $y=9.12x - 6.95$.

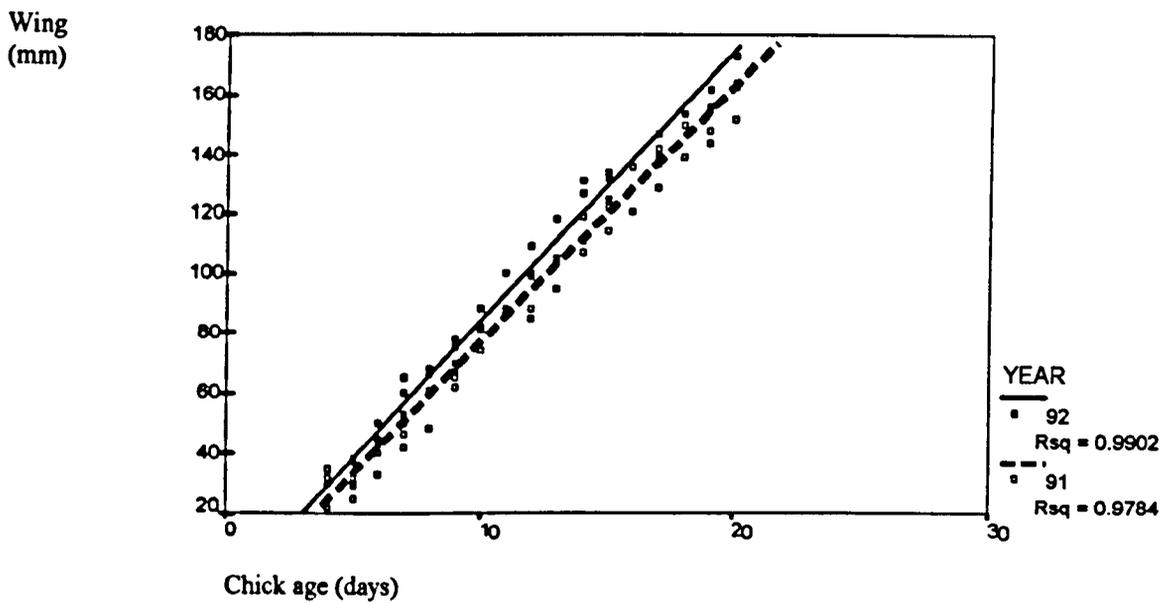


Figure 7.8 The mass growth of Arctic tern chicks from one egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were not significantly different (ANCOVA $F_{1,84}=0.80$, $p=0.37$). There was no significant difference in the elevation of the two lines (ANCOVA $F_{1,85}=1.12$, $p=0.29$). 1991 $n=63$, $r=0.93$, $P<0.0001$, $y=5.39x + 12.60$; 1992 $n=25$, $r=0.91$, $y=4.90x + 20.61$.

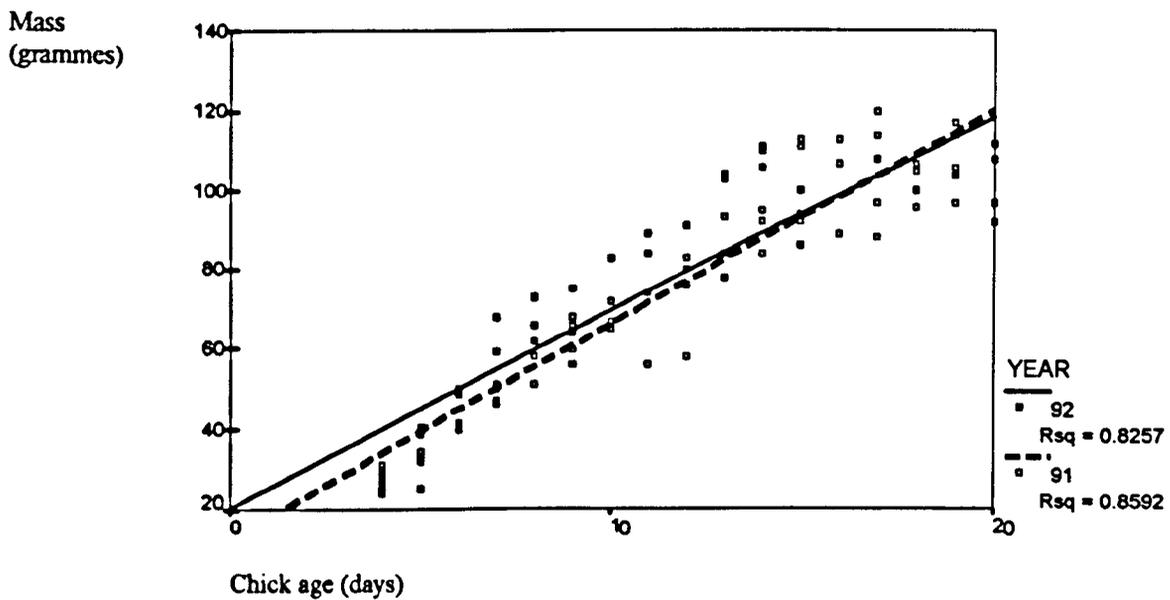


Figure 7.9 The correlation of chick mass and chord length of Arctic tern chicks from one egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were not significantly different (ANCOVA $F_{1,84}=2.18$, $p=0.14$). The elevations of the two lines were not significantly different (ANCOVA $F_{1,85}=0.76$, $p=0.39$). 1991 $n=63$, $r=0.94$, $P<0.0001$, $y=0.63x + 18.26$; 1992 $n=25$, $r=0.93$, $y=0.55x + 23.32$.

Mass
(grammes)

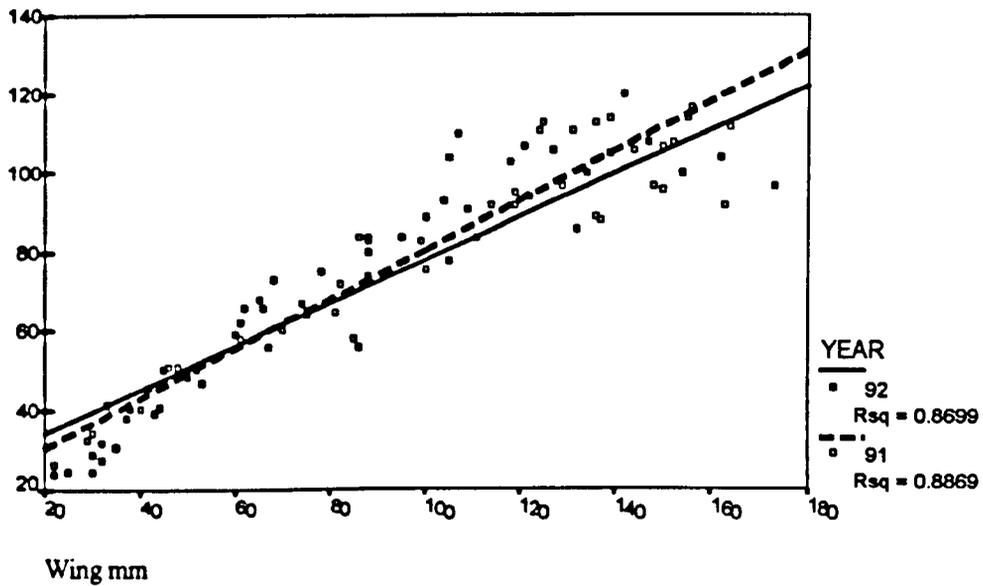


Figure 7.10 The wing growth rate of Arctic tern "a" chicks from two egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were not significantly different (ANCOVA $F_{1,429}=4.47$, $p=0.035$)

There was a highly significant difference in the elevation of the two growth curves (ANCOVA $F_{1,430}=16.64$, $P<0.0001$). 1991 $n=126$, $r=0.98$, $P<0.0001$, $y=8.69x - 7.30$; 1992 $n=307$, $r=0.97$, $y=8.24x + 2.21$.

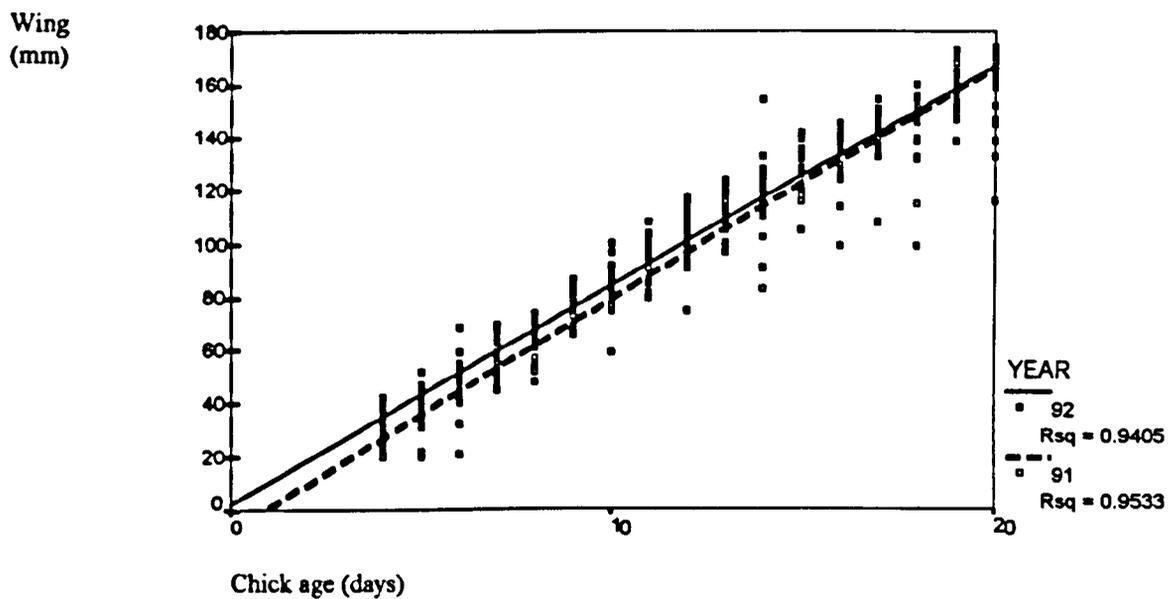


Figure 7.11 The mass growth rate of Arctic tern "a" chicks from two egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,429}=252.35$, $p<0.0001$). 1991 $n=126$, $r=0.86$, $P<0.0001$, $y=5.09x + 18.72$; 1992 $n=307$, $r=0.76$, $y=3.81x + 32.04$.

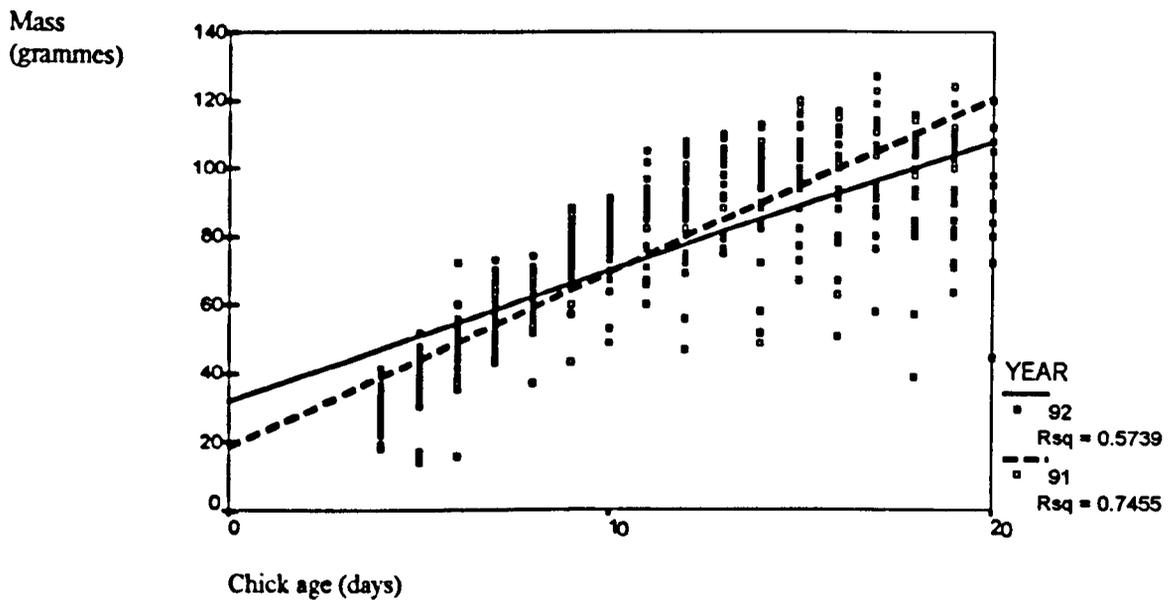


Figure 7.12 The correlation of chick mass and chord length of Arctic tern "a" chicks from two egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,429}=14.48$, $p<0.0001$). 1991 $n=126$, $r=0.93$, $P<0.0001$, $y=0.62x + 20.10$; 1992 $n=307$, $r=0.85$, $y=0.50x + 27.00$.

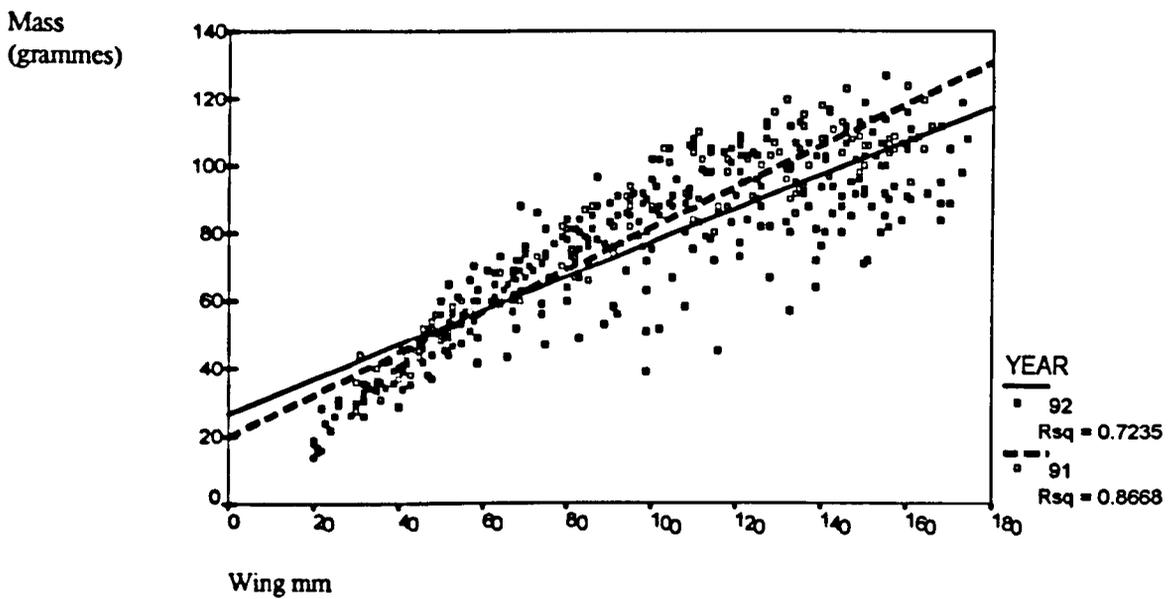


Figure 7.13 The wing growth rate of Arctic tern "b" chicks from two egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were not significantly different (ANCOVA $F_{1,280}=3.50$, $p=0.06$) There was a significant difference in the regression line elevations (ANCOVA $F_{1,281}=4.38$, $p=0.04$. 1991 $n=68$, $r=0.97$, $P<0.0001$, $y=8.70x - 15.54$; 1992 $n=216$, $r=0.96$, $y=8.06x - 4.76$).

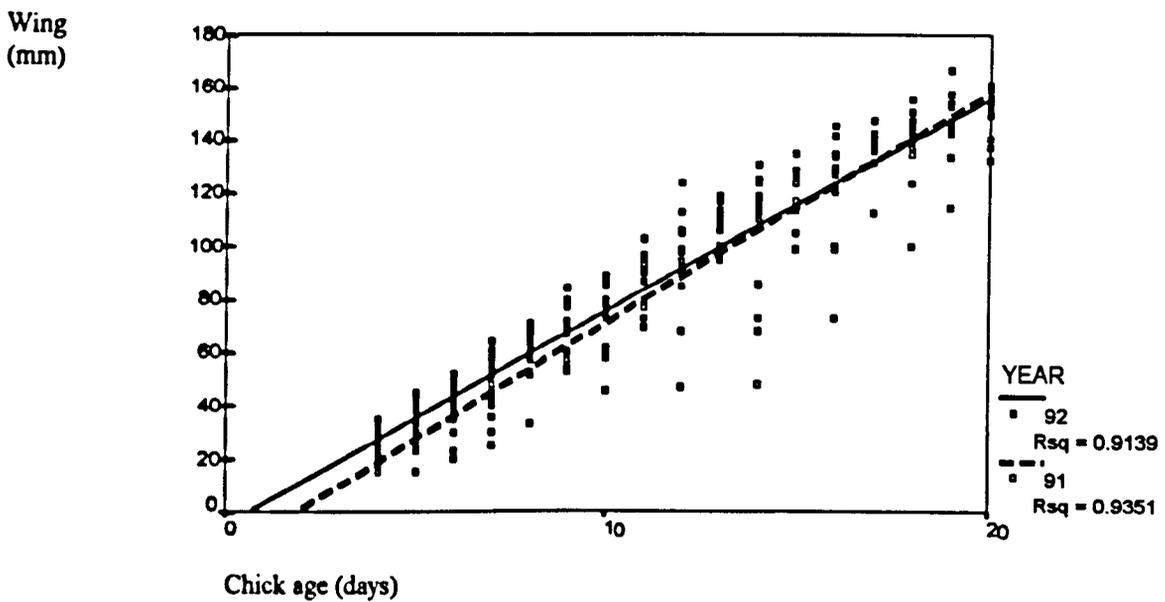


Figure 7.14 The mass growth rate of Arctic tern "b" chicks from two egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,280}=20.33$, $p<0.0001$). 1991 $n=68$, $r=0.87$, $P<0.0001$, $y=5.86x + 4.81$; 1992 $n=216$, $r=0.74$, $y=3.75x + 21.54$.

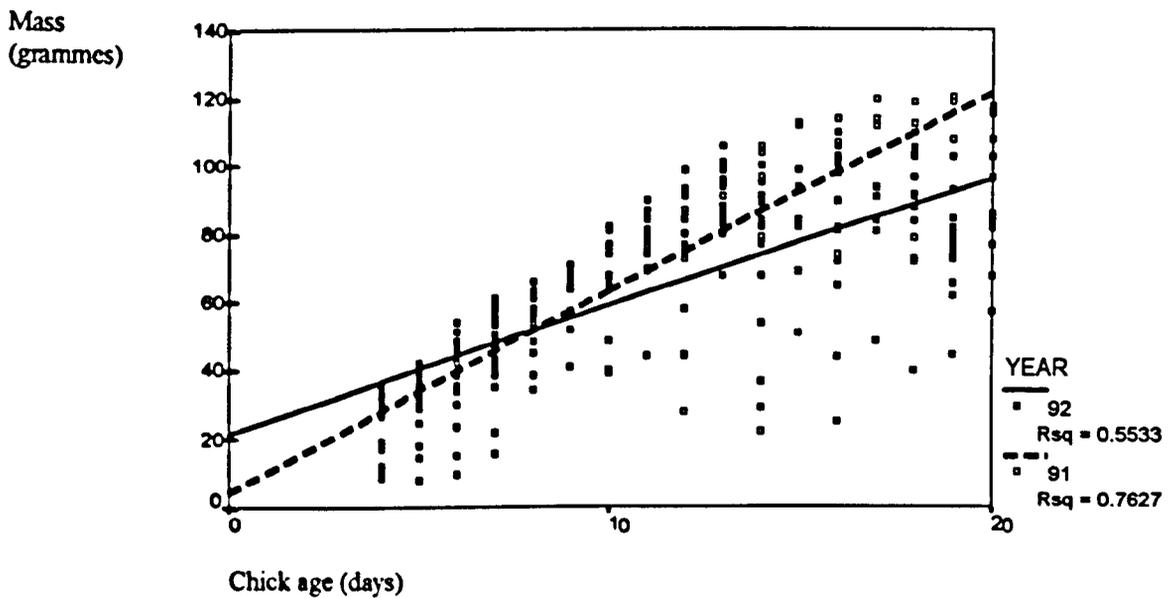


Figure 7.15 The correlation of chick mass and chord length of Arctic tern "b" chicks from two egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,280}=22.25$, $p<0.0001$). 1991 $n=68$, $r=0.94$, $P<0.0001$, $y=0.70x + 12.92$; 1992 $n=216$, $r=0.87$, $y=0.52x + 19.20$.

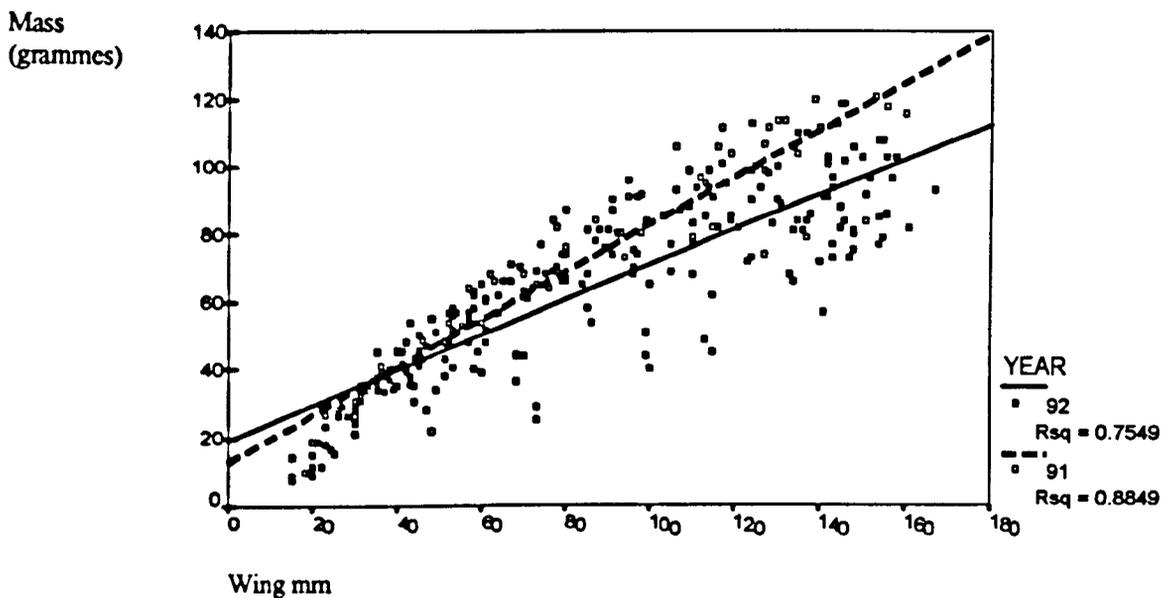


Figure 7.16 The wing growth of common tern "a" chicks from three egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were not significantly different (ANCOVA $F_{1,308}=0.18$, $p=0.67$). 1991 $n=146$, $r=0.96$, $P<0.0001$, $y=7.55x - 10.24$; 1992 $n=166$, $r=0.95$, $y=7.66x - 1.63$.

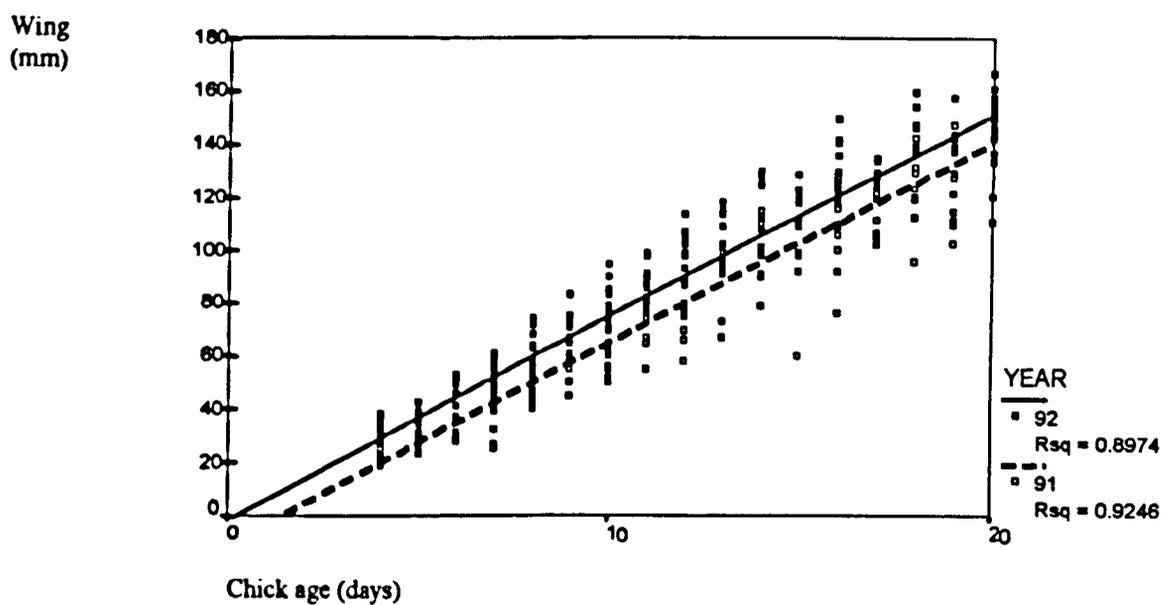


Figure 7.17 The mass growth of common tern "a" chicks from three egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,308}=25.90$, $p<0.0001$). 1991 $n=146$, $r=0.91$, $P<0.0001$, $y=6.08x + 4.51$; 1992 $n=166$, $r=0.74$, $y=4.14x + 27.61$.

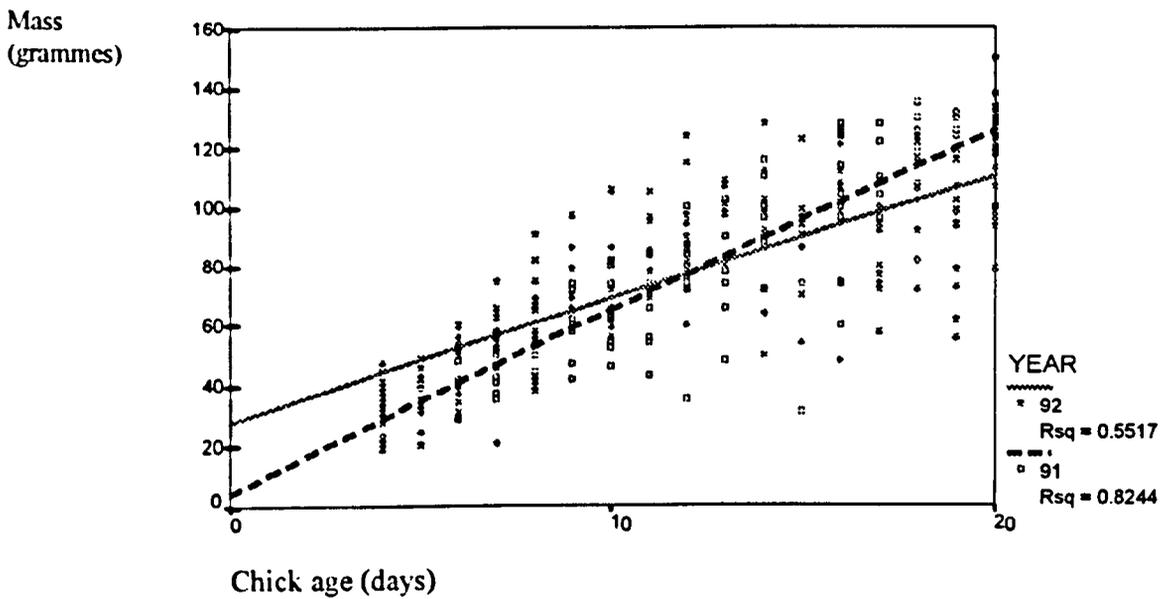


Figure 7.18 The correlation of chick mass and chord length of common tern "a" chicks from three egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,308}=38.67$, $p<0.0001$). 1991 $n=146$, $r=0.96$, $P<0.0001$, $y=0.82x + 11.89$; 1992 $n=166$, $r=0.88$, $y=0.61x + 22.75$.

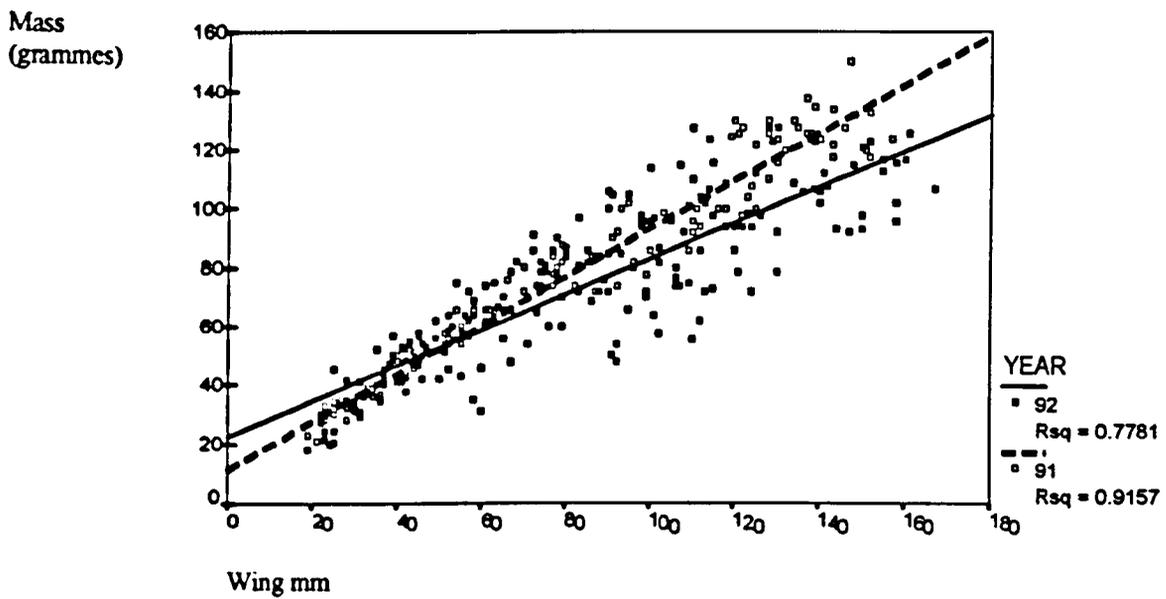


Figure 7.19 The wing growth of common tern "b" chicks from three egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were not significantly different (ANCOVA $F_{1,309}=0.37$, $p=0.554$).

There was a highly significant difference in the elevations of the two lines (ANCOVA $F_{1,310}=37.11$, $p<0.0001$). 1991 $n=149$, $r=0.91$, $y=7.23x - 10.50$; 1992 $n=164$, $r=0.93$, $y=7.44x - 2.68$.

Wing
(mm)

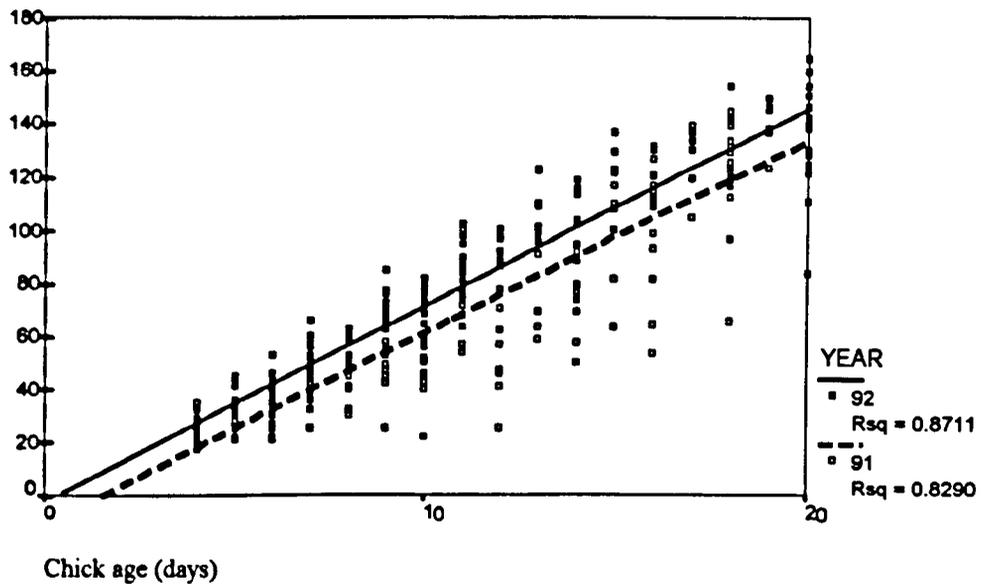


Figure 7.19 The wing growth of common tern "b" chicks from three egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were not significantly different (ANCOVA $F_{1,309}=0.37$, $p=0.554$).

There was a highly significant difference in the elevations of the two lines (ANCOVA $F_{1,310}=37.11$, $p<0.0001$). 1991 $n=149$, $r=0.91$, $y=7.23x - 10.50$; 1992 $n=164$, $r=0.93$, $y=7.44x - 2.68$.

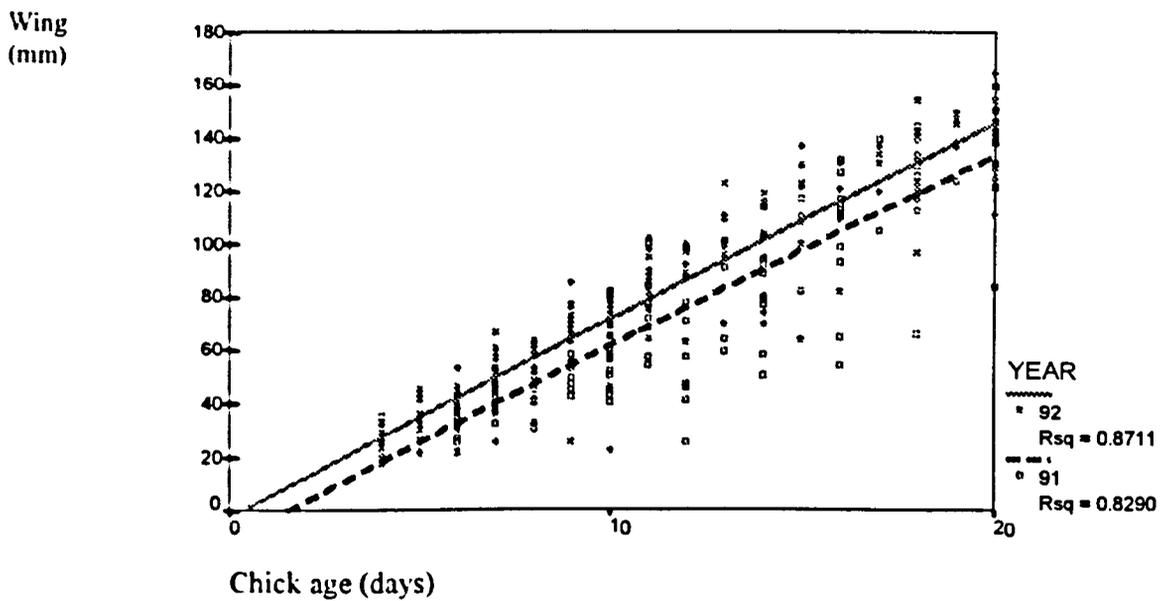


Figure 7.20 The mass growth of common tern "b" chicks from three egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were significantly different (ANCOVA $F_{1,309}=14.98$, $p<0.0001$).

1991 $n=149$, $r=0.80$, $P<0.0001$, $y=5.76x + 2.83$; 1992 $n=164$, $r=0.71$, $y=3.95x + 25.23$.

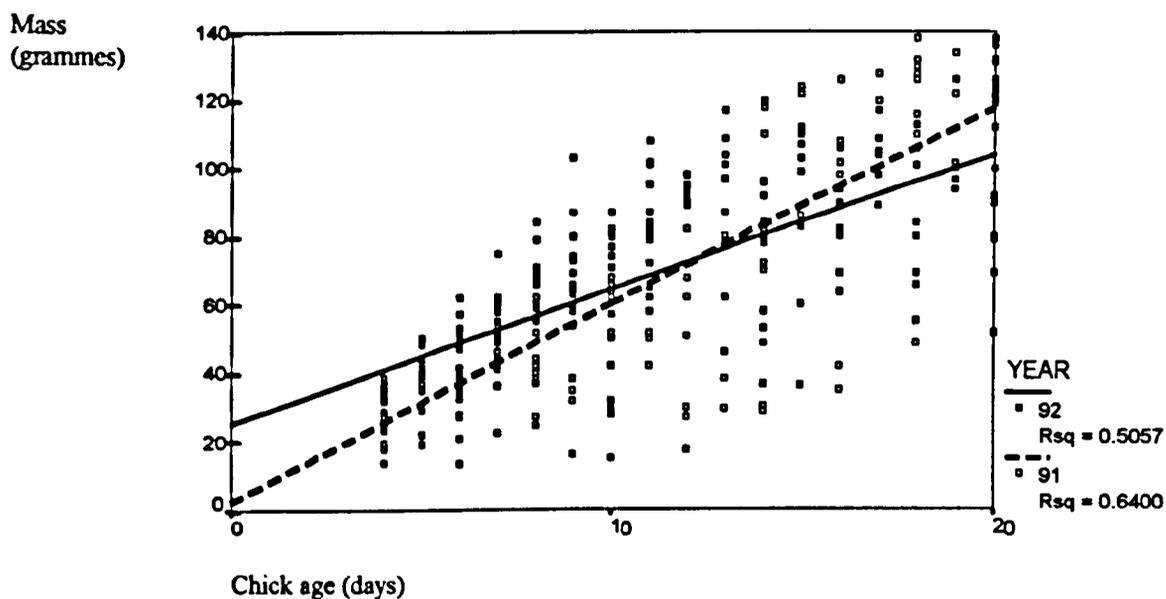
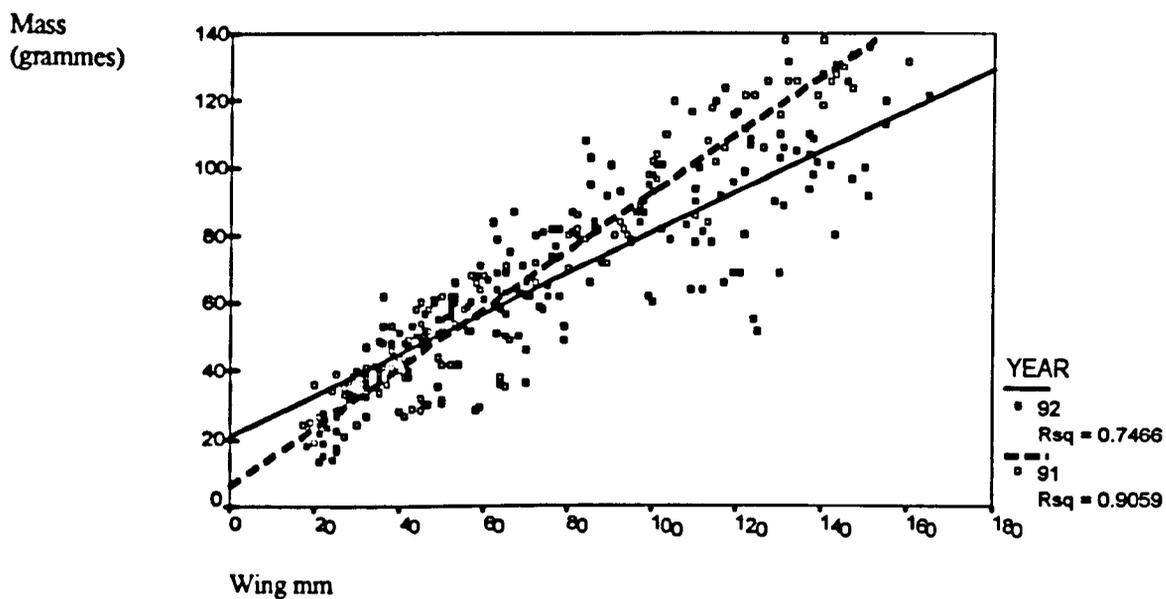


Figure 7.21 The correlation of chick mass and chord length of common tern "b" chicks from three egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,309}=52.01$, $p<0.0001$). 1991 $n=149$, $r=0.95$, $P<0.0001$, $y=0.86x + 6.57$; 1992 $n=164$, $r=0.86$, $y=0.60x + 21.12$.



7.3.2.3 Common tern three egg clutches: "c" chicks

C chicks grew slower in terms of size and mass increase in 1992 (Figure 7.22 and 7.23). They also gained mass more slowly in relation to body size in 1992 compared to 1991 Figure 7.24.

7.4 Discussion

The broad picture emerging from these comparisons is that of relatively poor growth of tern chicks in 1992 compared with 1991, despite in most cases, the chicks being larger in 1992 (egg size). However, for Arctic terns laying only a single egg, there was in fact no difference between the two years. This may have come about through some birds reducing clutch size in 1992, thereby maintaining growth in the single chick. The quality of the adults laying single egg clutches may not therefore be the same in the two years. However, the larger chicks in 1992 in the other categories suggest that food for egg production was good. This effect may therefore have come about through either poor hatching success or high mortality immediately following hatching, thus only the "best" chicks survived.

Food supply may additionally affect growth rate indirectly. Variations in food supply may influence the extent to which one or both adults is away from the nest during the period when the chick requires brooding. Klaassen, Bech, Masman, & Slagsvold (1989) using a model tern found a saving of 26 % of the energy required by the chick when brooded by an adult. If this saving were removed the energy may have to be diverted from growth to maintenance causing a decline in growth rate. This in turn would decrease the chicks ability to withstand thermal challenges caused by poor weather and would result in increased mortality.

Figure 7.22 The wing growth of common tern "c" chicks from three egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,136}=17.81$, $p<0.0001$). 1991 $n=60$, $r=0.93$, $P<0.0001$, $y=8.19x - 19.23$; 1992 $n=80$, $r=0.90$, $y=5.94x - 4.40$.

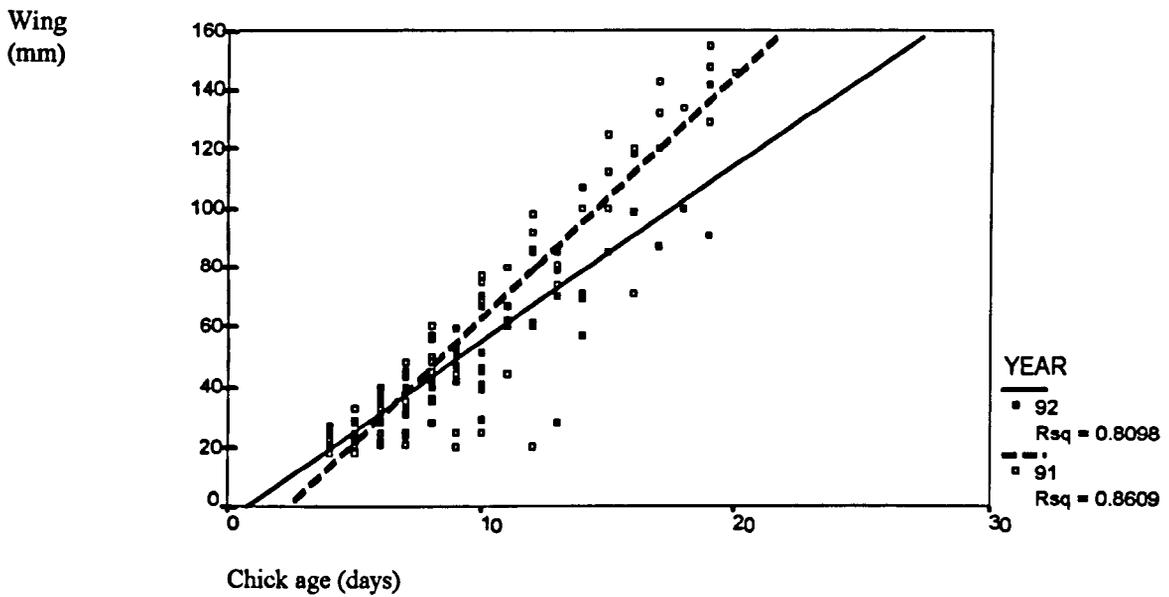


Figure 7.23 The mass growth of common tern "c" chicks from three egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,136}=33.34$, $p<0.0001$). 1991 $n=60$, $r=0.87$, $P<0.0001$, $y=7.22x - 13.29$; 1992 $n=130$, $r=0.60$, $y=3.09x + 14.74$.

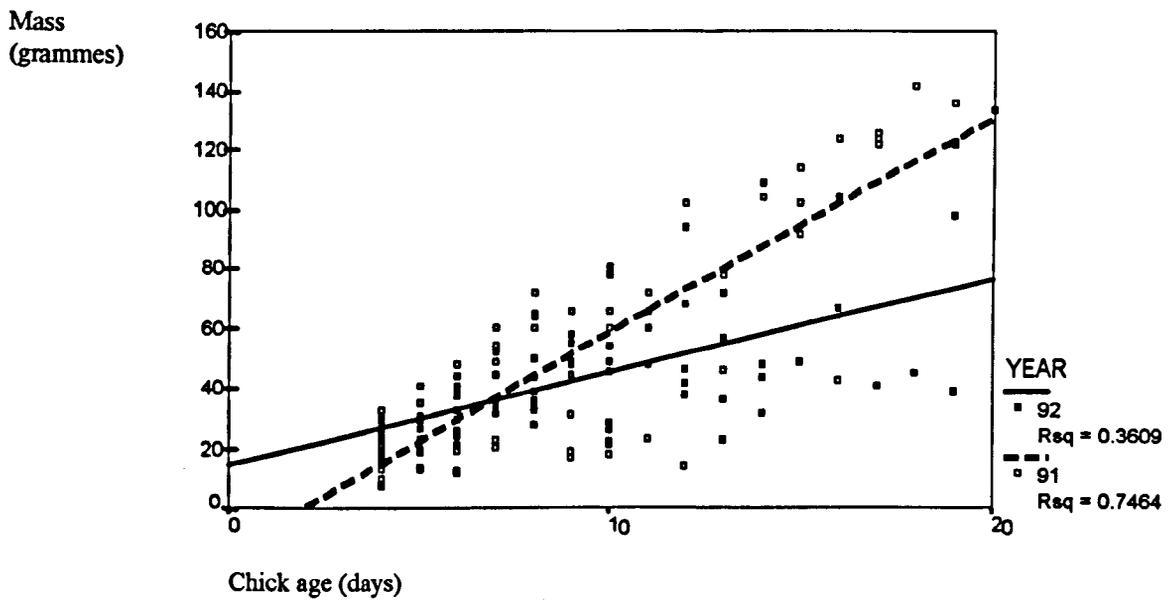
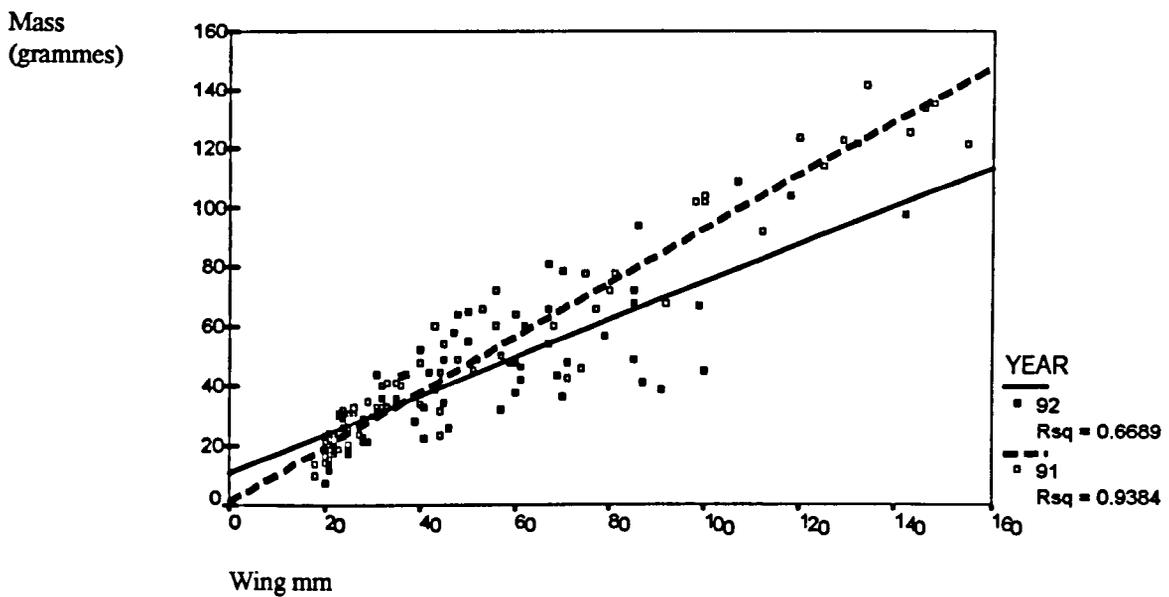


Figure 7.24 The correlation of chick mass and chord length of common tern "c" chicks from three egg clutches on Coquet in 1991 and 1992. Slopes of the regression lines were highly significantly different (ANCOVA $F_{1,136}=22.76$, $p<0.0001$). 1991 $n=60$, $r=0.97$, $P<0.0001$, $y=0.92x + 1.56$; 1992 $n=80$, $r=0.82$, $y=0.64x + 11.40$.



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Chapter 8 General Discussion

This study investigated the diet, foraging effort, breeding success, and adult condition of Arctic and common terns over two breeding seasons. Factors that influence the above parameters, such as the status of the pair bond, brood size, age of chicks and time of season were examined, the latter two being teased apart by means of an experimental manipulation. Clearly, in long-lived species such as terns, two breeding seasons are a relatively short period of time. Despite this, it is clear from the present study that inter-seasonal variation is considerable. Given this, such species need to be particularly responsive to environmental "clues" as to the likely conditions in the current breeding season if they are to adjust their effort correspondingly, thereby maximising their lifetime reproductive success. Given that their average breeding life is on average 7 years, it is clear that despite the considerable fluctuations in conditions from year to year and within a year terns do not 'overstretch' themselves in a single breeding season. Their response to such fluctuating conditions encompass dietary shifts, brood reduction, desertion and the whole colony movements for which they are well renowned.

In the present study a range of prey species were available. The two years work has highlighted the importance of sandeels, sprats, and rockling as a food resource for Arctic and common terns breeding on Coquet. Rockling has not been previously mentioned as an important constituent of chick diet for breeding terns on Coquet island (Langham, 1968; Monaghan *et al.* 1989), although they have been recorded elsewhere in the range of Arctic terns as an important constituent of chick diet. The marked intra- and inter- year variation in chick provisioning is indicative of plasticity in response to what is presumably a fluctuating food resource. The importance of these three prey types to both species of terns on Coquet cannot be overstated. In 1991 when larval sandeels were apparently scarce (only very few were brought to the colony and fed to chicks) Arctic terns fed chicks less than 6 days old predominantly on non-sandeels less than 8 cm in length. The majority of these were rockling. In 1992 rockling were the major constituent of Arctic tern diet for chicks of all pre-fledging ages. This was reflected in the very different distributions of sizes of prey fed to chicks within the three age groups during 1991 and 1992. Other

studies of Arctic terns elsewhere (Ewins 1985, Uttley 1991) have found a shift in the pattern of provisioning of chicks with increasing chick age. Older chicks are fed an increased proportion of larger prey. Apparently this is not always necessary as shown by the data collected in this study in 1992 for Arctic terns. However this study again highlighted the importance of small, easily ingested prey for tern chicks less than one week old. The pattern of provisioning of common tern chicks in 1992 confirmed the pattern observed previously elsewhere (Uttley, Monaghan, and White, 1989). The result of the experimental work showed that both chick age and seasonal factors influence prey choice in common terns. .

Both chick age and prey availability may affect adult provisioning of offspring in birds. These factors have rarely been unequivocally partitioned in studies into their relative importance in explaining chick provisioning. This makes it difficult to interpret which is the more important determinant of chick provisioning: chick age or the seasonal availability of prey. This study aimed at assessing the relative importance of these two factors in determining provisioning of chicks in common terns. An experimental approach was used to do this, thereby having differently aged chicks being fed at the same time, under similar conditions of prey availability for the two groups. Significant differences were found in the range of prey types and prey sizes fed to the two experimental groups. Chick age was a more important determinant of prey selection than availability. However an analysis of prey fed to chicks of the same age on different days showed that availability changes with season also. It appears that some selection determined by the interaction of several factors operates within the constraints imposed by which prey are available. This in turn is a function of interacting factors (e.g. weather, prey behaviour, adult foraging efficiency). Previous non-experimental studies which have found a correlation between seasonal availability and prey type or size fed to the chick may be compromised by the confounding effect of chick age. Similarly those studies which report a correlation between chick age and prey type and prey size fed to the chick may be confounded by the effect of changing seasonal availability of prey. Prey selection by common terns appears to be determined through the interaction of the physical limitations of chicks less than a week old with a concurrent increased risk of kleptoparasitism, and changes in prey availability. Small chicks less than three days old cannot handle large prey items (pers obs.) and suffer an increased risk of kleptoparasitism by other common terns as a consequence.

The conflicting constraints acting on the parent e.g. the difficulty of searching for a patchily distributed prey and not wanting to pass up the opportunity of taking such prey if they are located may explain the existence of larger prey amongst those fed to the youngest chicks.

Clearly, in the use of seabirds to monitor changes in the marine environment, potentially confounding factors such as chick age need to be taken into account. It is essential that like is compared with like. If, as occasionally occurs, the timing of breeding is delayed due to adverse weather conditions, comparison of data collected on the same calendar date could give misleading results. Such effects need to be taken into account in the design of monitoring studies.

Seabirds such as terns are presumably sensitive to changes in their own body condition arising for example from difficulties in finding food. The persistence of breeding attempts when conditions appear far from favourable (Avery *et al.*, 1992) and/or when body mass drops to a low (this study) requires an explanation. An important constituent of any explanation of these apparent inconsistencies is the concept of the reaction norm. This is defined by Stearns (1992) in the following way: "The reaction norm of a genotype is the full set of phenotypes that the genotype will express in interaction with the full set of environments in which it can survive."

For example the way in which resources are allocated for reproduction, growth, maintenance, and storage may change with environment i.e. there is a reaction norm for allocation rules. Consequently the environment can determine whether evidence for a trade-off appears at all. Although common and Arctic terns are eminently suitable for studies of the energetics of reproductive effort (see earlier) the fact that they both have such a widespread breeding distribution means they presumably have reaction norms with substantial leeway in the allocation "rules" which makes them less suitable for examining aspects of life history theory through the investigation of proposed trade-offs.

Evidence of a trade-off between reproduction and condition is mixed (Stearns, 1992). This may be because the same individuals have not been studied under different conditions i.e. only a proportion of the total variation in allocation possible within the reaction norm has been witnessed. Partridge (1990) suggests that the following factors must be controlled for in studies of reproductive costs:

1. Genotype by environment interaction
2. Phenotypic variation

3. Genetic correlations resulting from linkage disequilibriums

The first of these was unlikely to have been a confounding factor in this study as individuals studied were presumed to have encountered similar environments on average. The second is more problematic. Individuals studied may have differed in their reproductive potential due to different experiences but it is difficult to envisage how this could be controlled for in terms. The third may be ignored as all the terms within this study were from the same population. Stearns conclusion was that:

"A proper measurement of trade-off would take genetic variation among individuals and genotype by environment interactions into account. By this criterion, no trade-off has yet been well measured".

This remains a spur to further and more detailed research in this area.

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Summary

The primary aims of this project were to examine the effects of food supply upon the reproductive effort, and breeding success of terns and to assess the relative importance of seasonal availability of prey, and chick age as determinants of prey selection in Arctic and common terns. An experimental approach involving temporary storage of eggs under controlled conditions was used to disrupt the natural synchrony of hatching within the colony.

Using a sub-sample of colour-ringed birds various measures of breeding performance were examined using paired data. These birds were also used to calculate a minimum survival estimate. This was similar to other figures obtained for Arctic terns. Fledging success had no effect upon whether a bird re-appeared at the colony, nor on whether a bird bred. No effect was found of fledging success in the previous year affecting whether a bird changed partner in the subsequent year. A sizeable percentage of the sub-sample apparently did not breed in the second year of the study. Possible explanations for this are presented. Both unchanged and changed pairs showed no differences in clutch size, hatching success or fledging success. Where birds did change partner, their new partner was often a bird that had nested close to their new partner in the previous year. Growth of chicks reared by pairs with new partners in 1992 was not significantly different from that of pairs that retained the same partner.

Arctic tern adult body mass was lower in 1991 than in 1992. A distinctive pattern of adult body mass change throughout the chick rearing period was observed in 1991 when more comprehensive data were available. Both Arctic and common tern exhibited mass loss that was more consistent with mass loss due to reproductive effort rather than any adaptive mass loss to ease costs of foraging at periods of peak chick demand.

Laying was protracted and asynchronous for Arctic terns in 1991. Clutch size was significantly smaller for Arctic terns in 1991. In 1992 egg volume had a significant effect on fledging success. It is suggested that a similar effect in 1991 was masked by the acute effects of poor weather on Arctic tern breeding performance. The main difference in breeding performance of Arctic terns between the two years was in hatching success, which was lower in 1991. There were

no significant differences in clutch size of common terns between years. As for Arctic terns egg volume showed a significant effect on fledging success in 1992 but not in 1991. Intra-year differences in breeding performance are presented and discussed. Modifications of the initial reproductive investment appear to have been in clutch size rather than in egg dimensions.

An egg storage experiment was done to partition the effects of chick age and season. Prey selection of non-experimentally manipulated chicks was also presented. Chick diet of Arctic terns differed in the two years.

For two species/year combinations the size and type of prey fed to chicks varied significantly with the age of the chick. For the third species/year combination type and size of prey fed to chicks did not differ significantly with age. Factors influencing prey selection were discussed.

Marked inter-year differences were observed in the spectra of prey fed to Arctic tern chicks. The range of prey fed to Arctic and common tern chicks within the same year also differed.

The foraging behaviour of adult Arctic and common terns provisioning chicks were assessed in detail in relation to brood size, adult body weight, chick age, and weather conditions. The nutritional and energetic consequences of prey selection were discussed.