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The Comparative Breeding Ecology of Sympatric Common and Arctic Terns in N.E. England.

by

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Declaration

I declare that the material contained in this thesis has not previously been submitted for a degree in this or any other university. All the work recorded in this thesis is entirely my own, unless otherwise stated.

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by J.A.Robinson

Abstract

The life-history traits of two sympatric seabird species, the Common *Sterna hirundo* and Arctic Tern *S. paradisaea*, and the flexibility of these traits in relation to short and longer term changes in environmental conditions were measured at Coquet Island, N.E. England. The study focused primarily on inter and intraspecific differences in annual productivity and chick growth, adult time budgets and provisioning rates, and the relationships between these different aspects of reproductive performance. Of the two species, Common Terns delivered larger food items, delivered food at a higher rate to the nest and attended the nest more frequently, indicating that they made trips of shorter average duration. Daily metabolizable energy intake of chicks was about 30% higher in Common Terns than in Arctic Terns, yet the size-specific growth rates of the two species were almost identical, indicating a major difference between species in nestling energy budgets. Brooding appeared to play a less important role in the energy budgets of Common Terns, and the number of chicks that Arctic Terns could raise was probably limited not only by the rate at which parents could supply food to the nest but also by the requirements of chicks for brooding. Increased brood size, low annual food abundance and extreme weather conditions had a negative effect on chick mass development in both tern species. Flexibility of mass growth rates in Arctic and Common Terns may act as a fine-tuning mechanism to regulate provisioning in these species. By maintaining structural growth rates, final fledging mass and final fledging size of nestlings at the expense of retarded mass development rates, these species seem to be able to maximize annual reproductive output and possibly, for parents and nestlings, future survival. Predation of eggs and chicks was generally infrequent and affected mostly very young nestlings. However, Black-headed Gulls took many tern eggs in a year when inshore food supplies were particularly low.

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Chapter 1

General introduction.

> *'I believe that, in nidicolous species, the average clutch size is ultimately determined by the average number of young which the parents can successfully raise in the region and at the season in question'*
>
> Lack (1968)

An organism's life-history is its lifetime pattern of growth, differentiation, and reproduction (Stearns 1992). There is plasticity in any life-history, determined by the way in which the genotype of an organism interacts with its environment. To be able to understand the ecological significance of a life-history fully it is necessary to know which traits have been determined by evolution, how these traits interact with the environment in which an organism lives and also whether the interactions between individual traits and present environmental conditions have themselves evolved (Begon *et al.* 1986). The most telling information pertaining to evolved life-history strategies and environmental moulding of specific traits is often obtained from comparative studies either between individuals of the same species or between species themselves. This thesis deals with a comparative study of the life-history traits of two closely related sympatric seabirds which differ markedly in annual reproductive output and the flexibility of these traits in relation to changing environmental conditions.

1.1. Seabird life-histories

Seabirds are a diverse assemblage of species with an extensive world-wide breeding distribution, ranging from the tropics to both the high Arctic and Antarctica (Nelson 1980). They can be defined as those birds which depend mainly on the sea beyond the tide-line for their food. They forage using many different methods and are able to exploit most marine sources of food as well as some of those on land (Ashmole & Ashmole 1967; Becker *et al.* 1997). In comparison to other birds, seabirds share a suite of extreme life-history characteristics (Ricklefs 1990). Seabirds delay reproduction until at least the second year of life and, in highly pelagic Procellariiformes, up to 8-10 years after leaving the nest (Ashmole 1971; Harris 1977; Nelson 1978). In general, they produce between one and three offspring annually, the more pelagic species producing fewer offspring than species which forage nearer to the shore (Furness & Monaghan 1987). Seabird chicks develop very slowly in the nest, often at a rate below which maximum daily energy requirements do not decrease further (Ricklefs 1983a). They also live for a long time; the small marine terns live for over 30 years and the larger albatrosses reach well over 60 years of age (Cramp 1985; Warham 1990).

In the past the extreme life-history traits of seabirds have been explained in terms of the characteristics of the marine environment. Low annual productivity and slow nestling development suggest that the rate at which seabirds can provide food is severely limited. Ashmole (1971) suggested that seabird provisioning rates were limited because marine food supplies are patchy, sparse and are only available far away from the colony. It was also suggested that the large fat reserves accumulated by Procellariiformes indicated that they have to endure periods of reduced food supply (Lack 1968; Ricklefs 1990). Additionally, seabirds may produce a limited number of offspring annually in order to maximize future survival (Williams 1966). Seabirds show low mortality outside the breeding season and live for a long time so life-history theory predicts they should take few risks during the breeding season so that they can increase future reproductive success (Ricklefs 1983b). Indeed, some adult seabirds are able to monitor risks to their own survival and abandon breeding attempts when food supply is extremely low (Pugesek 1987; Monaghan *et al.* 1989).

In recent years many studies have shown that when seabird species are experimentally presented with additional chicks, they are able to rear them successfully and have little problem accelerating feeding rates in response to the extra requirements of the brood (see Ydenberg & Bertram 1989 for a review). In most brood enlargement studies there is little or no effect on the future survival of parents (see Stearns 1992 for a review). The evidence from this work casts doubt on the ideas proposed by Ashmole (1971) and before him Lack (1968) in that chick-feeding rates of seabirds appear to represent those which can be sustained in years of poor food supply (Ricklefs 1990). If seabirds annually produced broods of a size which could only be reared in good years the strain put on them in poor years may limit future survival, which contradicts the predictions of life-history theory (Williams 1966). However, recent work by Heaney & Monaghan (1995) has shown that brood size may also be limited by the costs incurred during egg production and incubation. Evidence from that study suggests that the results of brood-enlargement experiments which do not account for the costs of incubation and egg production must be interpreted with caution.

The thermoregulatory energy requirements of seabird chicks also limit the time that parents are able to spend foraging, and this may be important in moulding the evolution of clutch size in birds. Parent birds have to trade-off the time they spend foraging with the time chicks need brooding (Uttley 1992). Chick-feeding rates may be especially constrained during the early parts of the nestling period when thermolabile nestlings may need brooding almost continually (Busse 1983). Very little attention has focused on the relationship between chick energy requirements and the time budgets of parents but it may be very important in determining the number of chicks which can be successfully fledged from a nest.

Some seabirds raise broods of between one and three nestlings, most notably the gulls and terns *Laridae.* Life-history traits such as body size and mass at fledging, annual survival and future reproductive success may be a function of clutch size for both parents and their offspring (Roff 1992). If the rate at which these seabirds forage is constrained in some way, then parents may be able to maximize their annual reproductive output by raising large broods of slow growing nestlings without incurring risks to future survival or reproductive success. However, nestlings and parents may pay a cost of increased predation (Lack 1968) or reduced nestling or post-fledging survival (Coulson & Porter 1985; Hamer *et al.* 1991; Nisbet *et al.* 1995) if nestlings develop slowly and fledge lighter and smaller.

1.2. Environmental forces shaping seabird life-histories

Although there are trends within species, life-histories of individual organisms are essentially unique. While evolved strategies for coping with the marine environment can modify life-tables of seabirds, the past and present environment primarily shapes their general pattern. The marine environment is unpredictable with a large degree of temporal and spatial variation in food supply, weather conditions and predation events. Seabirds have to be able to respond to these changes if they are to maximize lifetime reproductive success. These responses may themselves be seen as features of the life-history.

1.2.1. *Food availability*

The food supplies of seabirds are unpredictable both spatially and temporally; the annual reproductive performance of many seabirds has been shown to be closely linked to temporal variations in marine food supply (e.g. Crawford & Shelton 1991; Anderson *et al.* 1982; Furness 1982; Ricklefs *et al.* 1984; Coulson & Thomas 1985; Hunt *et al.* 1986; Safina *et al.* 1988; Monaghan *et al.* 1989; Uttley *et al.* 1989; Hamer *et al.* 1991; Hamer *et al.* 1993). Egg production, parental provisioning rates, chick growth rates, parental attendance at the nest and annual breeding success have all been linked to food supply. Flexibility in these life-history traits may be advantageous for species which are prone to temporal variation in environmental conditions. For example, birds may lay fewer eggs and chicks may grow more slowly in years when food abundance is particularly low. Specialized surface feeders with limited foraging ranges and little extra time in their activity budgets for increased foraging are likely to be the most susceptible seabirds to such changes in food supply (Furness & Ainley 1984) and therefore may be well adapted to variable environments.

1.2.2. *The physical environment*

The weather can play an important role in determining the food available to seabirds (e.g. Dunn 1973; Birkhead 1976; Grubb 1977; Taylor 1983; Becker & Specht 1991; Frank 1992; Finney *et al.* 1999). In many cases seabirds find it more difficult to forage during periods when windspeeds and rainfall are high and sea conditions are rough. These conditions may limit the visibility of prey, alter the behaviour of the prey species or, for plunge divers, make hovering and diving difficult to achieve.

High rainfall and low temperatures may also increase the energy requirements of chicks for thermoregulation and therefore the proportion of time that adults spend brooding nestlings.

Some bird species which experience unpredictable food supplies during the breeding season are able to retard chick growth as a possible adaptation for reducing energy requirements when food supply is low over short-term periods (Lack & Lack 1951; Lack 1968; Bryant 1975; Ricklefs 1976; Emlen *et al.* 1991). Some of these species are able to resume normal growth rates when conditions improve and fledge at normal sizes and weights. It is possible that seabirds also demonstrate growth rate flexibility as an adaptation to short-term variations in food supply.

1.2.3 *Predation*

Lack (1968) suggested that for those seabirds which nest on isolated islands there is no predation pressure for selecting rapid development of nestlings. In recent years the introduction of mammalian predators to many islands has demonstrated how predation can have a large effect on the breeding success of some seabirds (Hobson *et al.* 1999; Craik 1995, 1997; Hartman *et al.* 1997). The length of time that nestlings are susceptible to ground-based predation increases with the duration of the nestling period (Lack 1968). Some seabirds may have evolved rapid nestling development in response to predation at the colony, especially those which do not live in burrows.

1.3. The comparative approach to assessing life-history strategies of closely related species

The study of life-history patterns often deals with comparisons rather than with absolutes (Begon *et al.* 1986). In ecological studies, life-histories of two or more species are usually compared in order to understand the differences between them with reference to their environments. For example, whilst it is often difficult to explain why one seabird species usually raises two chicks, it may be simpler to explain why it rears more than a similar species which only raises a single chick. Explanations for these differences could be obtained by comparing the rates at which these species feed their broods, how far the parents have to travel for food, the time that parents have to spend brooding their chicks and how much energy the chicks require for growth. Interspecific comparisons are also useful when contrasting the flexibility of life-history traits in response to variations in the environment.

1.4. Life-histories of terns

Within the range of seabirds there is a clear distinction between those species which forage far away from the shore and those which forage nearshore. The marine terns (*Sterna* sp.) are a genus of approximately 32 small seabird species which generally forage near to the shore at the sea surface on fish and marine invertebrates (Harrison 1983; Cramp 1985). They are one of the most widely distributed genera of seabirds; the Antarctic Tern *Sterna vittata* breeds in the low latitudes of Antarctica, the breeding range of the Arctic Tern *S. paradisaea* extends well into the high Arctic whilst the Sooty Tern *S. fuscata* breeds in the Tropics (Harrison 1983; Ricklefs &

White 1980; Hagemeijer & Blair 1997). Seven species of marine tern breed regularly in Europe (Hagemeijer & Blair 1997). In general, terns and other seabirds which forage nearshore produce more offspring annually, feed their chicks more regularly, reach maturity earlier and exhibit more rapid nestling development than pelagic species (Ricklefs 1972, 1982; Furness & Monaghan 1987). Many of these differences in life-history traits are thought to occur because those species feeding nearshore have to travel shorter distances to obtain their food and can therefore deliver food items to the nest at a faster rate than pelagic species. However, terns have little leeway in their energy budgets to increase the time they can spend foraging and have small potential foraging ranges (Pearson 1968; Monaghan *et al.* 1989; Becker *et al.* 1993). This makes them particularly prone to changes in environmental conditions such as short and long-term temporal and spatial variations in food supply.

Common Terns *S. hirundo* and Arctic Terns are two species of marine tern which breed sympatrically (and syntopically) at many coastal and offshore colonies in Europe where their two ranges overlap. Although the breeding distribution of the Arctic Tern is almost entirely coastal the Common Tern is also able to breed successfully at colonies well inland (Hagemeijer & Blair 1997). The European distribution of both species has a northerly bias (Cramp 1985). The Common Tern breeds irregularly as far south as North Africa but only regularly north of the Mediterranean. The most northerly colonies of this species breed in Finnmark (Hagemeijer & Blair 1997). In comparison, the Arctic Tern has a circumpolar distribution during the breeding season extending well into the boreal zone (Hagemeijer & Blair 1997). The breeding colonies in eastern Britain and the Netherlands represent the southerly limit to the breeding distribution of Arctic Terns. Both species also breed in North America at similar latitudes to those seen in

Europe (Cramp 1985). Both Arctic Terns and Common Terns are migratory. Common Terns from northern European colonies tend to winter offshore in sub-equatorial Africa (Cramp 1985). The Arctic Tern winters much further south and has the longest migration flight of any bird. Although some first-year Arctic Terns may winter in South Africa the majority continue down to Antarctica (Cramp 1985). There have been few changes in the numbers of Arctic Terns or Common Tern breeding in Europe since the 1970s (Hagemeijer & Blair 1997) yet both species are mentioned on Annex I of the European Birds Directive 79/409 which offers them special protection during the breeding season. These two species appear on this Annex not because they are particularly endangered but because both depend on relatively few breeding colonies in Europe. The main threats to these species come from human disturbance and predation at the colony, industrial fishing of their main prey (notably sandeels) and human predation at the wintering grounds (Lloyd *et al.* 1990; Hagemeijer & Blair 1997).

Although they are very closely related, Common Terns annually produce more offspring per nest than do Arctic Terns, the former laying modal clutches of three eggs the latter of two (Cullen 1957; Coulson & Horobin 1976; Bullock and Gomersall 1981; Monaghan *et al.* 1989; Uttley *et al.* 1989). Adult Common Terns are also larger, on average, than Arctic Terns, with average body masses of around 130g and 110g respectively (Cramp 1985). Little is known about the differences in life-history traits exhibited by these two species, especially the relationships between annual productivity, chick growth rates, provisioning rates, parental activity budgets and nestling energy requirements. It is also unclear how environmental conditions such as annual food supply, weather conditions and predation have shaped the life-history traits of these two species.

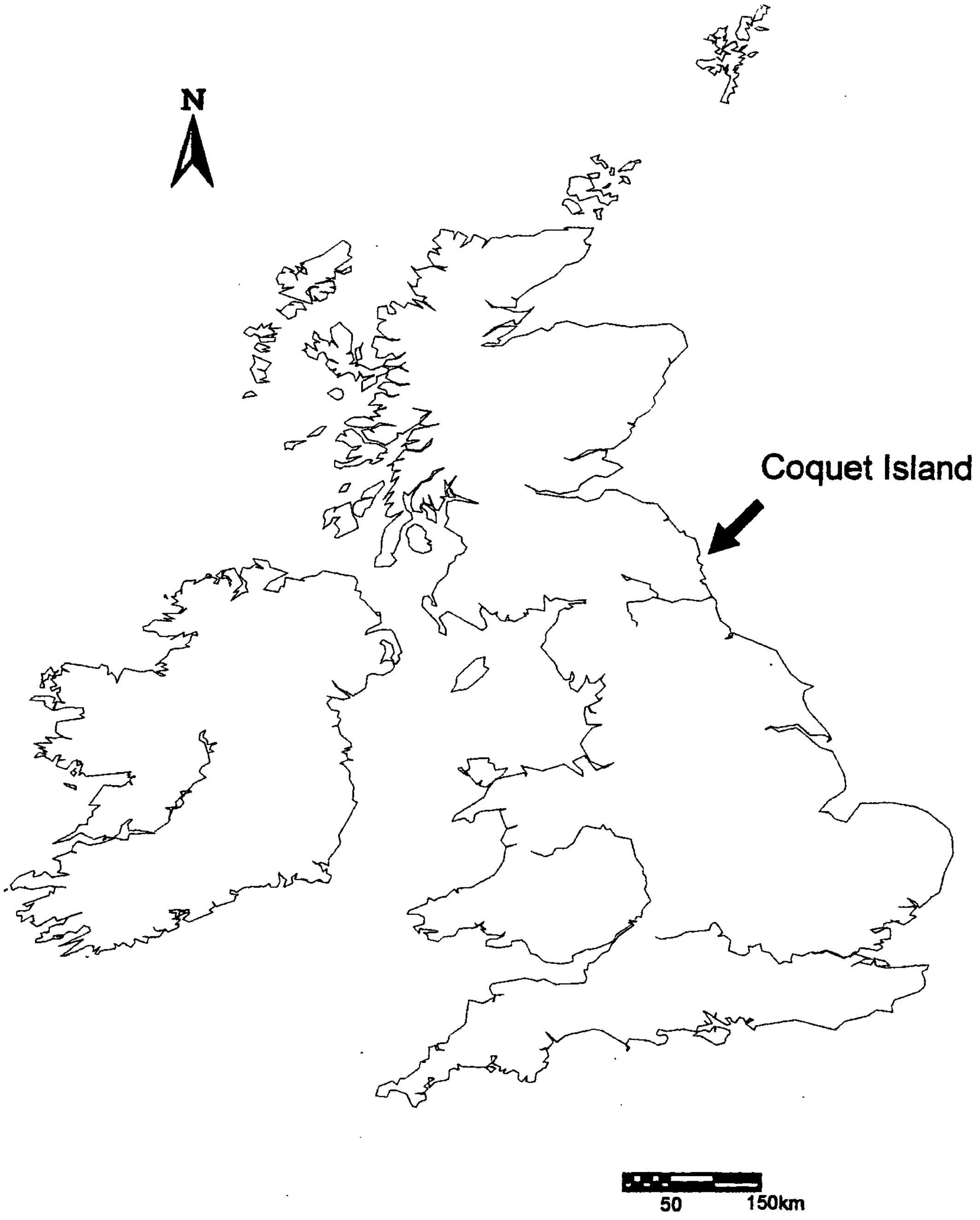
1.5. Study site

Fieldwork for this study was conducted at Coquet Island (55° 20'N, 1° 32'W) which is a small low-lying, island approximately 1km off the coast of Northumberland, N.E. England (Fig. 1.1). The island has been declared a Special Protection Area (SPA) under EC Directive 79/409 and is managed by the Royal Society for the Protection of Birds for it's important assemblage of breeding seabirds. Trinity House maintain the island's lighthouse which is currently operated automatically. Landings on the island are prohibited except for RSPB and Trinity House staff so that the seabirds breeding there experience very little disturbance from humans during the breeding season. Members of the public visit the island on specially organized boat trips and view the birds from the boat whilst moored at a small jetty to the north west of the island.

Eleven species of seabird regularly breed on Coquet Island during the summer months (Table 1.1) but this was not always the case. After the lighthouse had been constructed in 1834 the island was occupied by two lighthouse keepers and their families together with some sheep, cows and dogs. Parts of the island were also cultivated. Terns eventually deserted the island in 1882 due to disturbance from the activities of these human inhabitants. The first Common Terns returned to breed on Coquet Island in 1954 (J.C. Coulson pers. com.) whilst all the other current breeding species returned subsequently.

The island now hosts internationally important breeding populations of Sandwich Terns *S. sandvicensis* and Roseate Terns *S. dougallii.* Large numbers of Common

Fig 1.1. The location of Coquet Island in the British Isles.



Terns, Arctic Terns, Black-headed Gulls *Larus ridibundus,* Puffins *Fratercula arctica,* and Eiders *Somateria mollisima* together with smaller numbers of Fulmars *Fulmarus glacialis,* Kittiwakes *Rissa tridactyla,* Herring Gulls *Larus argentatus* and Lesser black-backed Gulls *Larus fuscus.* Several other bird species also breed regularly on the island, including Shelducks *Tadorna tadorna,* Oystercatchers *Haematopus ostralegus,* Ringed Plovers *Charadrius hiaticula* , Rock Pipits *Anthus spinoletta,* Starlings *Sturnus vulgaris* and Jackdaws *Corvus monedula.* The large gulls (Lesser black-backed and Herring Gulls) are disturbed regularly throughout the breeding season to prevent breeding attempts. The primary reason for this disturbance is to reduce the number of seabird chicks and Eider ducklings taken by these predatory gulls. During the winter months the plateau is used by several thousand roosting gulls (predominantly Herring Gulls and Greater black-backed Gulls *L. marinus*) whilst the rocky intertidal areas are utilized by several species of shorebirds for both foraging and roosting at high water.

Approximately 200 rabbits *Oryctolagus cunniculus* are present on the island during the summer. Rabbit mortality is particularly high during the winter months and numbers during this time often fall to around 20 individuals. The only other mammals which are recorded on the island are Grey Seals *Halichoerus grypus* and Common Seals *Phoca vitulina* which haul up in relatively large numbers (c.40) on the rocky intertidal areas during low water. Rats (*Rattus* sp.) and other small rodents are absent from the island.

Coquet Island is a low sandstone outcrop, c.30ft above sea level, which is topped with a plateau approximately 5ha in area. Most of the intertidal area is rocky with small coves of shingle beaches which provide nest sites for c.200 pairs of Arctic Terns. However, there is a small sandy beach to the south east of the island which is also utilized as a breeding area by this species (c.10 pairs). Both these areas are susceptible to tidal inundation during high spring tides and breeding failures due to flooding are common. The plateau is covered by a thin layer of top-soil on which grows a mixed sward of vegetation during the summer months. The dominant plant species include sow-thistle *Sonchus* sp., bugloss *Lycopsis arvenis*, stinging nettle *Urtica dioica*, annual nettle *Urtica urens* and several grass species. Over certain parts of the island the vegetation is managed for the benefit of the nesting terns. In late April and November traditional areas are strimmed and sprayed with conventional herbicides. This management technique converts dense areas of tall grasses and nettles into areas covered in predominantly short grasses, which are preferred by the nesting terns, surrounded by denser vegetation in which chicks can hide and shelter. It was within these areas that the study nests of Common and Arctic Terns for this study were chosen. The different species of tern that breed on the island tend to segregate spatially when egg-laying, except for individual pairs of Roseate Terns which sometimes nest within the Common Tern colony. Much of the rest of the island is honeycombed by the burrows of Puffins which, through their annual re-burrowing, are seriously eroding certain areas of the island.

1.6. Aims of this study

In this thesis I aim to compare life-history traits of two sympatric seabird species, the Common *Sterna hirundo* and Arctic Tern *S. paradisaea*, and the flexibility of these traits in relation to short term changes in environmental conditions. I will focus in particular on annual productivity, chick growth and energy budgets, adult time budgets and provisioning rates, and the relationships between these different aspects of reproductive ecology. In *Chapter 2* the provisioning rates and time budgets of parent terns and nestling energy requirements are compared in order to examine the adaptive significance of the difference in annual productivity of the two species. *Chapter 3* deals with the effects of brood size on provisioning and growth of nestlings within species and the trade-off between brood size and nestling growth rates. The flexibility of life-history traits in response to environmental conditions is addressed in *Chapter 4* and *Chapter 5*. In *Chapter 4* the daily variations in foraging success and brooding time allocation associated with changes in weather conditions are related to changes in chick growth rates. The response of these two tern species to a prolonged period (c.7 days) of bad weather is assessed, focusing particularly on flexibility of growth rate both during and after this period. In *Chapter 5* the effects of annual variations in food abundance, measured inshore, and predation on the breeding performance of Arctic and Common Terns are investigated. The use of these species as biomonitors of inshore marine food supplies is discussed. *Chapter5* and *Chapter 6* deal with the predation of tern chicks by rabbits and Black-headed Gulls and the effects that these predators have on breeding success. In *Chapter 7* I discuss the differences in life-history traits between these two tern species with respect to long-term evolutionary forces and immediate responses to the environment.

Table 1.1. Numbers of breeding seabirds at Coquet Island between 1996 and 1998.

	Estimated numbers of breeding pairs		
	1996	*1997*	*1998*
Common Tern	567	806	805
Arctic Tern	640	749	843
Sandwich Tern	1,511	1,659	1,897
Roseate Tern	24	25	29
Black-headed Gull	2,217	2,100	2,100
Eider	336	330	273
Puffin	10,200	not counted	11,460
Fulmar	62	71	59
Kittiwake	45	61	44
Herring Gull	9	11	25
Lesser black-backed Gull	22	20	95

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Chapter 2

Contrasting brood sizes in Common and Arctic Terns: nestling energy budgets, food provisioning rates and the role of parental brooding.

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2.1. Summary

Arctic Terns *Sterna paradisaea* and Common Terns *S. hirundo* are closely related species that breed sympatrically at a number of locations in northern Europe. They are similar in many aspects of their breeding ecology, but Common Terns generally lay three eggs per clutch whereas Arctic Terns lay only two. We used an energetics approach to assess whether this difference in annual productivity was related to the foraging ecology of parents or to nestlings' energy requirements. Parents of both species spent only 1-2% of the time during daylight hours together at the nest during chick-rearing, suggesting that they had little leeway to increase food provisioning rates without increasing the proportion of time that chicks were left unattended. Both species fed their chicks mainly on sandeels *Ammodytes marinus*, but Common Terns included a higher proportion of other species in the diet and a higher proportion of fish in larger size-classes. Common Terns also had a higher rate of food delivery to the nest and higher nest attendance, indicating that they made trips of shorter average duration. Daily metabolizable energy intake of chicks was about 30% higher in Common Terns than in Arctic Terns, yet the size-specific growth rates of the two species were almost identical, indicating a major difference between species in nestling energy budgets. Chicks were inactive most of the time and there was no difference between species in nestling time/activity budgets. Arctic Terns had higher thermal conductance due to smaller body size, and there was no difference between species in the proportion of time that chicks were brooded by their parents. Yet Common Terns apparently spent a higher proportion of daily energy intake on maintenance of body temperature, and we suggest that this was because parents could not brood three chicks as effectively as two. Thus energy savings to chicks through brooding by parents were probably higher for Arctic Terns than for Common Terns, as a result of the larger number of chicks per brood in Common Terns. Brooding appeared to play a less important role in the energy budgets of Common Terns, and the number of chicks that Arctic Terns could raise was probably limited not only by the rate at which parents could supply food to the nest but also by the requirements of chicks for brooding.

2.2. Introduction

Seabirds share a suite of extreme life-history characteristics including delayed reproduction and low annual productivity, which suggest that the rate at which parents can provide food for their offspring is severely limited. Small seabirds such as terns have less leeway in their annual energy budgets than do larger species and spend a greater proportion of their time foraging when they have offspring (Pearson 1968). This, coupled with their small foraging ranges (Boecker 1967; Becker *et al.* 1993; Duffy 1986), makes them very vulnerable to food shortages near the breeding colonies. Variation in food supply should therefore have a marked impact on tern productivity, and such effects have been demonstrated for individual species in the case of temporal variation in prey stocks at a colony (Safina *et al.* 1988; Monaghan *et al.* 1989). Evolved differences in annual productivity between species might also be related to differences in the maximum sustainable rate at which parents can deliver food to the nest. However, there is surprisingly little evidence for this (Ydenberg & Bertram 1989; Ricklefs 1990), and there are alternative explanations. For example, brood size may be limited by costs of egg production and incubation rather than chick-rearing (Heaney & Monaghan 1995).

Arctic Terns *Sterna paradisaea* and Common Terns *S. hirundo* are closely related species that breed sympatrically at a number of locations in northern Europe. Both are surface feeders, taking prey by plunge diving or by dipping, and both feed mainly on sandeels (Ammodytidae) and small clupeid fish during the breeding season (Langham 1972; Kirkham & Nisbet 1987; Uttley *et al.* 1989). However, Common Terns generally lay larger clutches than Arctic Terns. The former rarely lays fewer than two eggs in a clutch and often lays three-egg clutches, whereas the latter often lays one-egg clutches and seldom lays more than two eggs in a clutch (Coulson & Horobin 1976; Bullock and Gomersall 1981; Monaghan *et al.* 1989).

This difference in annual productivity is thought to arise from Arctic Terns having less flexibility in their foraging locations and choice of prey species during the breeding season (Uttley *et al.* 1989; Frank 1992; Becker *et al.* 1998). This implies that there should be a difference between species in food provisioning rates or nest attendance patterns of parents during the chick-rearing period, but there are few data for sympatric populations of these species to test these predictions. Moreover, chick provisioning rates and parental nest attendance need to be placed in the wider context of the chicks' overall energy requirements. For instance, brooding by parents can reduce a chick's energy requirements for maintenance of body temperature by up to 80%, and so parents may need to trade-off food provisioning against brooding (Uttley 1992; Klaassen *et al.* 1994). The difference between species in annual productivity suggests that such a trade-off may place a greater constraint on brood size in Arctic Terns than in Common Terns, particularly if Arctic Tern chicks have higher energy requirements for maintenance of body temperature, for instance due to smaller body size or more exposed nest-site locations. However the interactions between brood size, food provisioning rate and thermal requirements of chicks have seldom been studied.

This paper adopts an energetics approach to compare the provisioning and growth rates of chicks and the nest attendance and brooding behaviour of parents in sympatric populations of Common and Arctic Terns at a colony in N.E. England. We assess whether higher productivity of Common Terns results from a difference between species in parental foraging ecology or nestling energy requirements, focusing particularly on maintenance of body temperature and brooding by parents. Nestling growth rates and energy requirements vary allometrically with body mass and Common Terns are around 20% heavier than Arctic Terns (adult body mass = 130g and 110g respectively; Klaassen 1994; Wendeln & Becker 1996). We therefore accounted for differences in body size when comparing growth rates and metabolic energy requirements between species.

2.3. Methods

Fieldwork took place from 1 May to 20 July in 1996 and 1997 at a mixed colony of Common and Arctic Terns on Coquet Island, Northumberland (55° 20'N, 1° 32'W). Sample plots were established early in the breeding season of 1996 in the central areas of the Common and Arctic Tern colonies. To minimize disturbance and facilitate location of chicks, shortly before hatching 18 nests of each species from within these plots, with laying dates ± 2 days of the modal value, were surrounded by small wire-mesh enclosures *c.* 30 cm high, similar to those used in previous studies (Pearson 1968; Nisbet & Drury 1982; Monaghan *et al.* 1989). Data on hatching success and fledging success were then obtained for all study nests within the enclosures.

Chicks were individually marked shortly after hatching and were then weighed daily (to the nearest 1g using a Pesola balance) at midday until fledging. Growth rates were compared between species using rate constants of logistic equations fitted to mass growth data (Ricklefs 1968). In 1996, prey delivery rates to broods within enclosures were recorded from hides positioned within each colony. Each nest was observed for a total of 90 hours, divided over 30 three-hour periods spanning the first 20 days of the nestling period (until chicks attained asymptotic body mass; see below) and divided evenly across all hours of daylight (0430-2230h).

Adult terns deliver single prey items in their bills and the rate at which food was brought to chicks was assessed by direct observation. Prey items were identified as sandeel (predominantly *Ammodytes marinus*), clupeids (Herring *Clupea harengus* and Sprat *Sprattus sprattus*), gadids (predominantly Whiting *Merlangius merlangius* and Saithe *Pollachius virens*), rocklings (*Ciliata* sp.) and crustaceans. Fish were divided into four size categories (<3cm, 3.1-6cm, 6.1-9cm and >9cm) and the energy content of each prey item was estimated using conversion factors for appropriate species and sizes-classes from Harris and Hislop (1978) and Massias and Becker (1990). These data were then used to estimate energy delivery rates to each brood. The accuracy with which observers placed fish in different size categories was assessed at the start of the breeding season in 1996 using a mount of a common tern, with fish obtained from males at the colony during courtship display. After some practice, all observers placed fish into the correct size category on >90% of occasions.

In order to relate energy delivery rates for each species to mass-specific energy requirements of chicks, we converted chick body masses into estimates of basal metabolic energy expenditure, using equations derived for each species at colonies in the Netherlands, at a similar latitude to the colony in N.E. England (Klaassen 1994):

Arctic Tern: $\text{BMR}\,[\text{ml O}_2 \,.\, \text{g}^{-1}\,\text{h}^{-1}] = 0.42 + 0.098M - 7.625M^2 \,.\, 10^{-4}$

Common Tern: $\text{BMR}\,[\text{ml O}_2 \,.\, \text{g}^{-1}\,\text{h}^{-1}] = 1.17 + 0.038M - 2.365M^2 \,.\, 10^{-4}$

where M is body mass in grams.

Energy delivery rates were converted into metabolizable energy intake rates assuming an assimilation efficiency of 80% (Klaassen *et al.* 1992). We then calculated the ratio of metabolizable energy intake to energy required for basal metabolism, including growth and biosynthesis, for chicks of each species. This allowed us to compare rates of energy supply between species, controlling for interspecific and age-specific variation in body mass.

Parental attendance and chick activity were recorded for both species in 1997 using scan sampling (Martin & Bateson 1986). Food provisioning rates were not recorded simultaneously, but mass growth rates of chicks in 1997 were almost identical to those recorded in 1996 (Common Tern, 7.8 ± 0.2 g day^{-1} and 7.0 ± 0.3 g day^{-1} in 1996 and 1997 respectively; Arctic Tern, 7.1 ± 0.2 and 6.9 ± 0.3 g day^{-1} respectively). We observed 20 Common Tern and 16 Arctic Tern broods for a total of 54 hours between 0430h and 2230h, at intervals throughout chick-rearing, from hides within the colonies of the two species. The behaviour of each chick was recorded at 5 minute intervals, with activity divided between chicks being brooded by parents, quiescent but not brooded, preening, walking and other activities (calling, gullar fluttering or picking at vegetation).

To estimate the combined effects of ambient temperature, wind exposure and solar radiation on the potential energy requirements of chicks for maintenance of body temperature, we measured the operative temperatures (T_0) of Arctic and Common Tern chicks in two age-classes, 1-5 days and 21-25 days. T_0 is the temperature that an organism would attain if it lacked metabolic heat production and water loss (Bakken 1976) and the difference between T_0 and body temperature equals the net thermal gradient between an animal and its environment. Following Walsberg & Weathers (1986) and Klaassen (1994) we measured T_0 using four hollow copper spheres, each with a surface 1.5mm thick, painted matt grey and mounted on 35mm lengths of doweling set in wooden bases. Two spheres representing 1-5 day old chicks were 35mm in diameter and a further two representing 21-25 day old chicks were 55mm in diameter. Temperatures inside each sphere were measured by a thermocouple and recorded on a Squirrel data logger.

Operative temperatures were measured at 30 minute intervals throughout day and night on a total of 16 days during the chick-rearing period of 1997, giving eight days of data for each species and age-class of chick. For each species, the smaller sphere was used immediately after peak hatching and the larger sphere was used during peak fledging. The spheres were placed within either the Common or Arctic Tern colony, in typical microhabitats close to existing nests. Potential energy requirements for maintenance of body temperature over each recording period, in the absence of brooding by parents, were calculated from operative temperature recordings using equations in Klaassen (1994), assuming a core body temperature of 39°C.

$$E_{tr} = \sum_{i=1}^{n} E_{tr[i]} / n$$

where

$$E_{tr} = h\,(T_b - Te_{[i]}) - BMR$$

During this study, data were collected repeatedly over many days from the same individual chicks. To account for these repeated measures, the nestling period was divided into six five-day age-classes (1-5 days, 6-10 days, 11-15 days, etc.). Data for each age-class were aggregated into a single mean value for each chick, and test statistics were calculated from aggregated mean values, following Sokal & Rohlf (1981). Following Bolton (1995), we also adopted the conservative measure of adjusting the degrees of freedom for analysis of age-specific effects to the number of nests studied rather than the number of observations across all age-classes. For all data concerning food provisioning rates, degrees of freedom refer to the number of broods studied and not the number of individual chicks.

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2.4. Results

2.4.1. *Breeding success and chick growth*

Basic breeding statistics for Common and Arctic Terns are given in Table 2.1. Clutch size was significantly larger in Common Terns ($\chi^2_2 = 119.2$, $P < 0.01$) but there was no difference between species in hatching success ($\chi^2_1 = 0.1$, $P > 0.05$ using Fisher's exact test) or fledging success ($\chi^2_1 = 0.8$, $P > 0.05$). As a result of larger average clutch size, Common Terns fledged more chicks per pair than Arctic Terns ($\chi^2_2 = 7.7$, $P < 0.05$).

Figure 2.1 shows changes in body masses of chicks during growth. Data for both species closely fitted logistic growth curves (linear regression of logistic conversion factors for chick mass upon age; $R^2 = 0.92$ and 0.91 for Arctic Terns and Common Terns respectively), where chick mass (g) at age a days was given by the following equations:

Arctic Tern: $$\text{chick mass} = \frac{111}{1+e^{-0.29(a-8.5)}}$$

Common Tern: $$\text{chick mass} = \frac{123}{1+e^{-0.29(a-8.2)}}$$

where e is the base of natural logarithms. There was no difference between species in size-specific growth rate (0.29 in both cases; t-test using pooled variance estimate; $t_{73} = 0.01$, $P > 0.05$).

2.4.2. *Chick diets and food provisioning rates*

There was a significant difference between species in the proportion of the diet comprising sandeels, clupeids or other species ($\chi^2_2 = 223.1$, $P < 0.01$). Arctic Tern chicks were fed a higher proportion of sandeels than were Common Terns (95.7% of 2,498 meals and 82.2% of 2,699 meals respectively) and a lower proportion of Herring and Sprat (4% and 17% for Arctic and Common Terns respectively). Other items comprised <1% of the diet for both species. There was a significant difference between species in meal size ($\chi^2_2 = 27.0$, $P < 0.05$), with Common Tern chicks fed a higher proportion of fish in larger size-classes (84.4% of 3.1-6cm, 15.2% of 6.1-9cm and 0.4% of > 9cm) compared to Arctic Terns (89.1%, 10.9% and 0.1% respectively).

The frequency of food delivery by parents increased with average age of chicks in each brood up to 14 days post-hatching and was consistently higher in Common Terns than in Arctic Terns until chicks attained asymptotic body mass (Fig. 2.2; analysis of covariance of feeding frequency by species with chick age as a covariate; for effect of species, $F_{1,33} = 5.1$, $P < 0.05$; for effect of age, $F_{1,32} = 105.6$, $P < 0.01$). Combining data for meal size and feeding frequency, rates of energy supply per chick were also higher for Common Terns than for Arctic Terns (Fig. 2.2; ANCOVA; $F_{1,33} = 19.5$, $P < 0.01$) and increased as chicks grew, at least during the first half of the nestling period ($F_{1,32} = 36.1$, $P < 0.01$).

2.4.3. *Nestling energy requirements*

During the linear period of growth, mean daily metabolizable energy intake (MEI = 0.8 x energy supply rate per chick; see above) was 107.6 kJ per chick ($n = 18$ broods, S.D. ± 37.1) for Arctic Terns and 141.7 kJ per chick ($n = 18$, S.D. ± 54.8) for Common Terns. Over this period, the ratio of metabolizable energy intake to basal metabolic rate (BMR, estimated from chick body mass; see above) was significantly lower for Arctic Terns (1.49, n = 18, S.D. ± 0.4) than for Common Terns (2.14, n = 18, S.D. ± 0.8; $t_{34} = 7.5$, $P < 0.01$).

The operative environmental temperatures for Arctic and Common Tern chicks showed considerable diurnal variation but were always lower than core body temperature (Fig. 2.3). Estimated mean daily energy requirement for maintenance of body temperature in the absence of brooding by parents (E_{tr}) was 38.1 ± 17.2 kJ per chick for Arctic Terns aged 1-5 days and 34.4 ± 16.7 kJ per chick for Common Terns of this age-class. For chicks aged 15-20 days these values were 31.5 ± 53.5 kJ per chick and 22.8 ± 66.0 kJ per chick respectively. The ratio of E_{tr} to BMR was significantly higher for Arctic Terns and for young chicks of both species (Arctic Tern, ratio = 2.9 ± 1.4 at age 1-5 days and 0.3 ± 0.5 at age 15-20 days; Common Tern, ratio = 1.9 ± 0.9 at age 1-5 days and 0.2 ± 0.5 at age 15-20 days; two-way ANOVA; species, $F_{1,5} = 177.8$, $P < 0.01$; age, $F_{1,5} = 177.6$, $P < 0.01$; there was no interaction between species and age-class).

2.4.4. *Parental attendance and time/activity budgets of chicks*

Chicks were not brooded during the second half of the nestling period (see below). During the first two weeks post-hatching, the proportion of time when there was at least one adult at the nest decreased with brood age-class and was higher for Common Terns than for Arctic Terns (Common Tern, mean = 88.0%, n = 20, S.D. ± 19.9; Arctic Tern, mean = 73.6% , n = 16, S.D. ± 30.5; ANCOVA of arcsine transformed data with brood age as a covariate; species, $F_{1,33} = 5.01$, $P < 0.05$; age, $F_{1,32} = 18.13$, $P < 0.05$). This was despite higher average brood size and more frequent delivery of food to the nest in Common Terns (see above). The proportion of time when both adults were together at the nest was very low in both Arctic Terns (mean = 1.1% , $n = 16$, S.D. ± 2.0) and Common Terns (mean = 2.1%, $n = 20$, S.D. ± 3.13) and did not differ significantly between species ($F_{1,33} = 2.4$, $P > 0.05$) or chick age-classes ($F_{1,32} = 0.5$, $P > 0.05$).

The proportion of time for which chicks were brooded varied significantly with chick age ($F_{1,32} = 153.2$, $P < 0.01$) but did not differ between species ($F_{1,33} = 0.03$, $P > 0.05$). Over the first 15 days post-hatching, chicks of both species were brooded for c.60% of the time, quiescent but not brooded for c.30% of the time and spent <10% of their time in other activities (Fig. 2.4a). Beyond age 15 days, chicks spent c.70% of the time quiescent and c.15% of the time preening, but neither species were brooded by parents (Fig. 2.4b).

Table 2.1. Breeding performance of Arctic and Common Terns on Coquet Island in 1996.

	Arctic Tern			Common Tern		
	n	mean	S.D.	*n*	mean	S.D.
clutch size	120	1.94	0.62	110	2.56	0.51
hatching success (%)	18	86.1	23.0	18	87.2	20.8
fledging success (%)	18	90.3	27.4	18	82.9	30.8
chicks fledged per pair	18	1.56	0.56	18	1.89	0.58

*Mean clutch sizes at enclosed nests were 2.00 and 2.62 for Arctic and Common Terns respectively.

Fig. 2.1. Growth of Common (○) and Arctic Tern (■) chicks that survived to fledging on Coquet Island in 1996. *n* = 34 and 28 chicks respectively (0-22 days); 30 and 25 (23 days); 28 and 17 (24 days); 22 and 4 (25 days); 18 Common Terns (26 days), 15 (27 days); 9 (28 days). Error bars are ± 1 S.E.

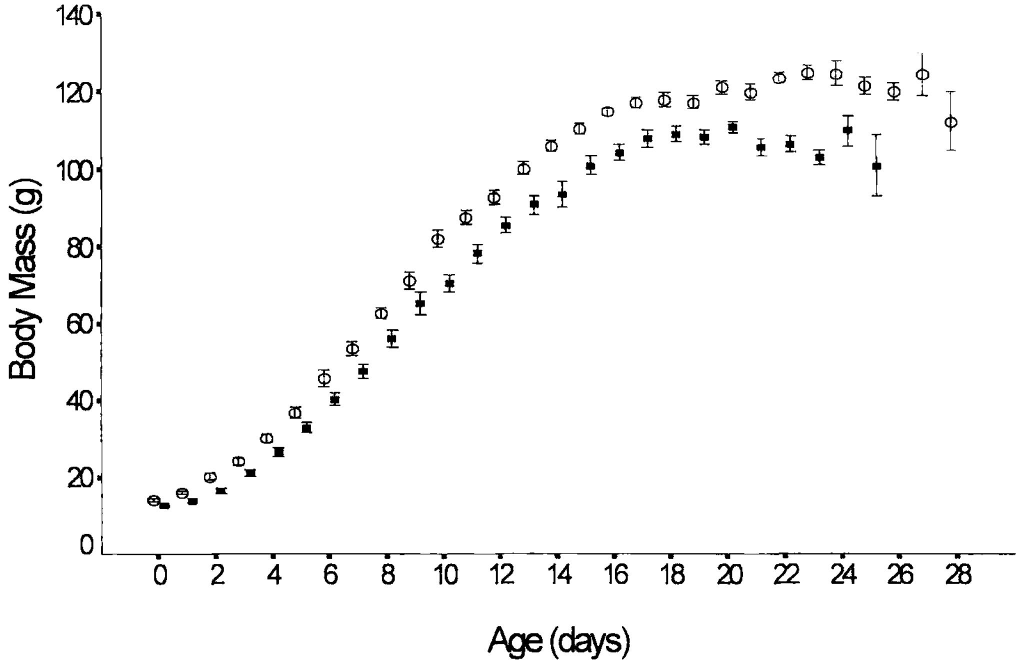
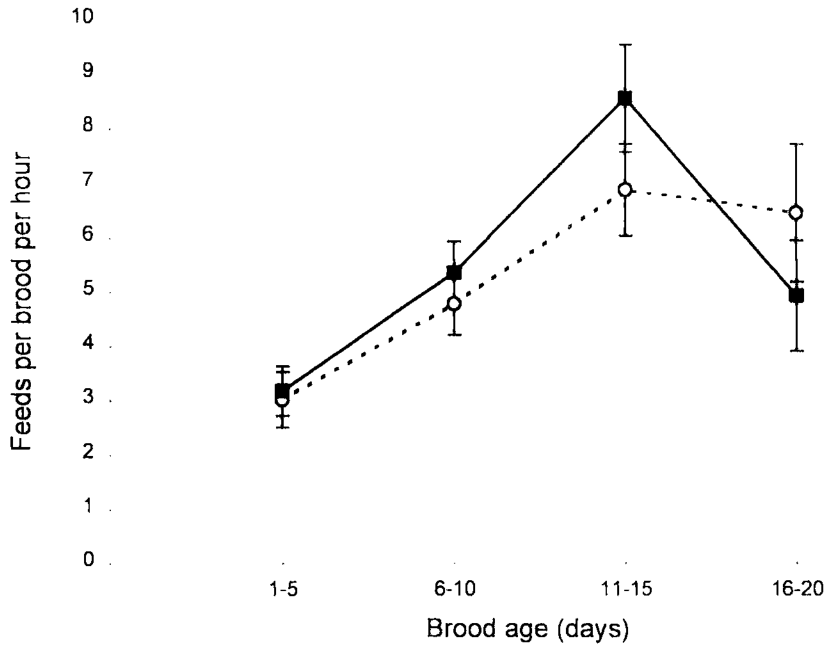


Fig. 2.2. Feeding frequency and daily energy intake of Arctic and Common Tern broods (open symbols and solid symbols respectively) as a function of average age of chicks in each brood. $n = 18$ broods of each species in each age-class. Error bars are ± 1 S.E.

(a) food delivery rate



(b) daily energy intake

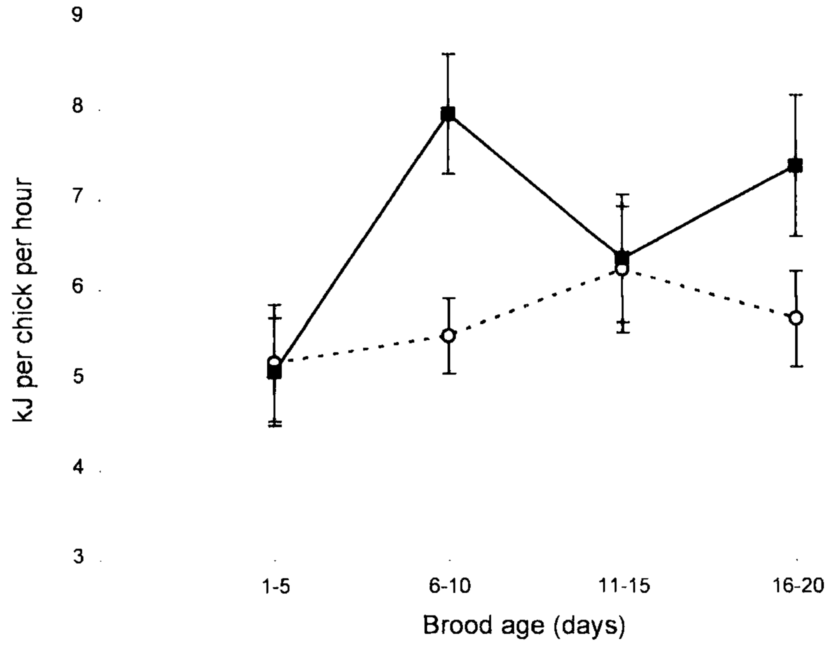
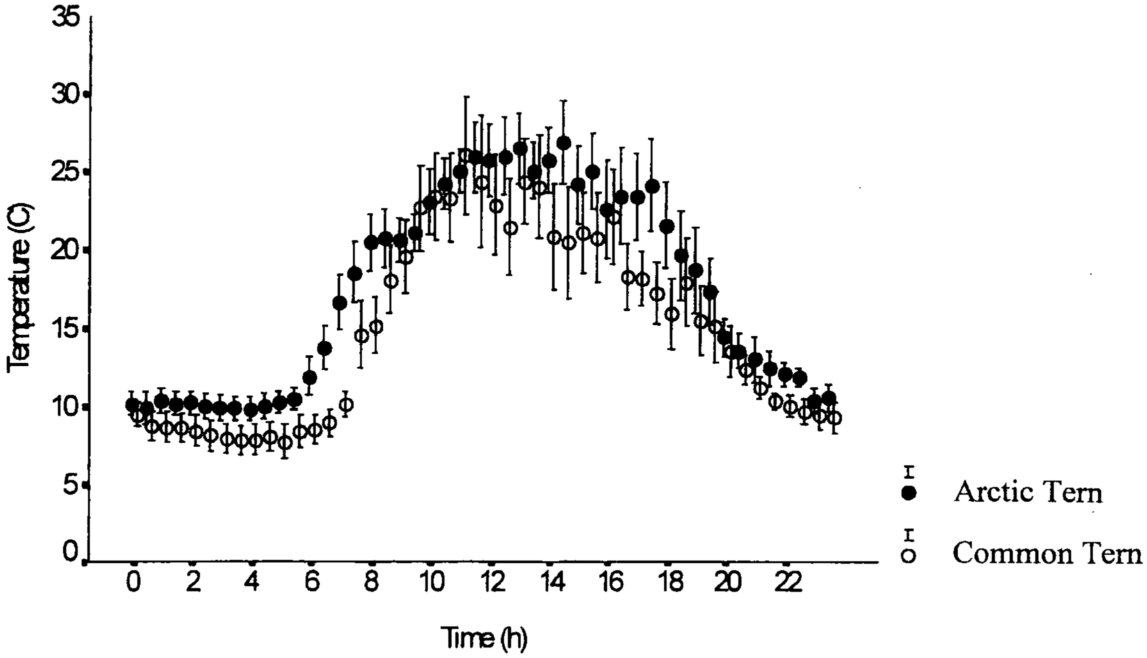


Fig.2.3. Operative temperatures for Arctic and Common Terns in two age-classes, as a function of time of day. Based on eight days of data for each species and age-class. Error bars are ± 1 S.E.

a) Age 1-5 days



b) Age 21-25 days

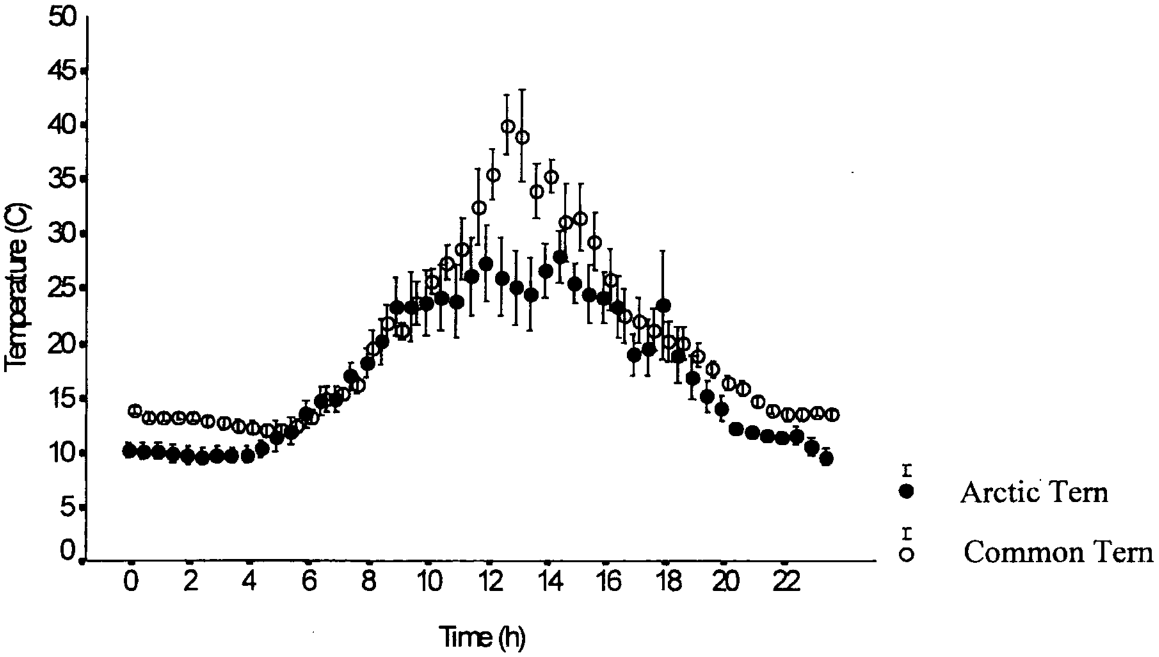
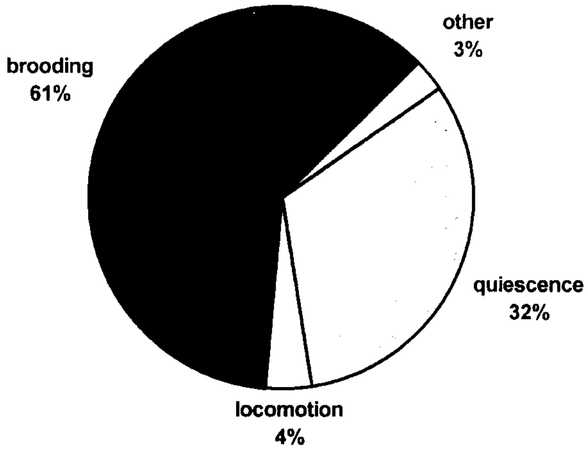


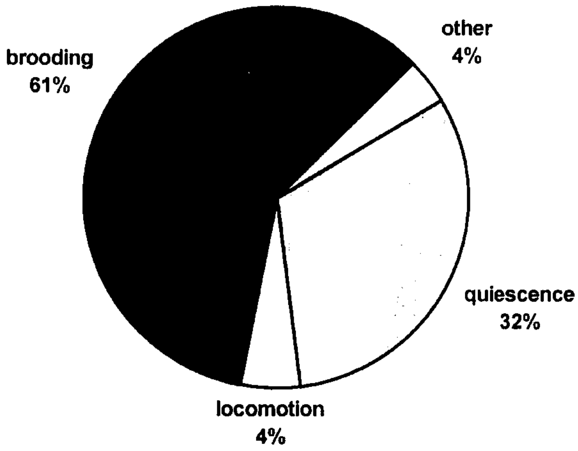
Fig. 2.4. Proportion of time spent in different activities by Arctic and Common Tern chicks, for two separate age-classes. n = 29 and 36 broods in each age-class for Arctic and Common Terns respectively.

(a) Chicks aged 1-14 days

Arctic Tern

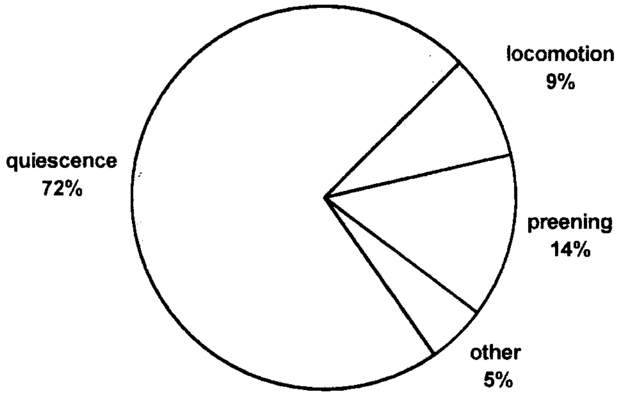


Common Tern

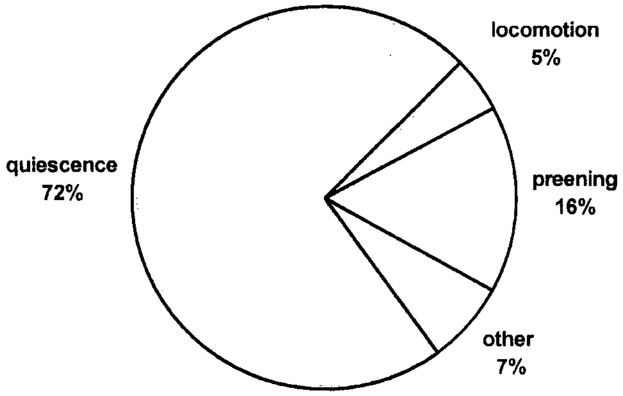


(b) Chicks aged 15-30 days.

Arctic Tern



Common Tern



2.5. Discussion

Breeding statistics for Common and Arctic Terns in this study (Table 2.1) were similar to those recorded previously in N.E. England and elsewhere during conditions of good food supply (Pearson 1968; Bullock and Gomersall 1981) and confirm the general pattern of higher annual productivity in Common Terns than in Arctic Terns. Both species fed their chicks mainly on sandeels of length 3.1-6 cm but Common Terns included a higher proportion of Herring and Sprat in the diet and a higher proportion of fish in larger size-classes. Above 6cm in length, Herring and Sprat have a higher caloric density than sandeels (Harris & Hislop 1978). The difference in species and size-classes of fish taken by Common and Arctic Terns in this study suggests greater flexibility of prey choice in Common Terns, and this is supported by data from Shetland, where clutch size, hatching success and chick growth rates of Common Terns were unaffected by a major reduction in stocks of sandeels, whereas for Arctic Terns both hatching success and chick growth rate were markedly reduced and most chicks died of starvation or exposure during the first week post-hatching (Uttley *et al.* 1989). This appeared to be due to only Common Terns being able to increase the proportion of other species in their diet to compensate for a lack of sandeels. However, at other colonies sandeels play a minor role in the diet of the Arctic Terns and crustaceans become more important (Frick & Becker 1995). This suggests that prey choice in these species is site-specific.

In this study, the proportion of time when both adults were together at the nest was very low for both species, and this was consistent with adults having little leeway in their time/activity budgets (Pearson 1968; Monaghan *et al.* 1989). Nest attendance by parents of both species declined as chicks grew, probably due to an increase in the food requirements of chicks, coupled with a decrease in the requirements for brooding by parents (see below) and a decrease in the vulnerability of unattended chicks to predation (Becker 1995; Robinson & Hamer 1998). Over the first two-weeks post-hatching, chicks were left unattended for up to 25% of the time during hours of daylight but Common Terns had significantly higher nest attendance, despite a higher average brood size and a higher frequency of food delivery to the nest (Fig. 2.2). This pattern suggests that Common Terns made shorter foraging trips than did Arctic Terns; although we did not record foraging trip durations by individual adults, a combination of higher feeding frequency and higher nest attendance is possible only by Common Terns making trips of shorter average duration. The two species have very similar flight speeds and foraging techniques (Gudmundsson *et al.* 1992; Wakeling & Hodgson 1992) and so these data strongly suggest that Common Terns were able to forage nearer to the colony than were Arctic Terns during this study. This is consistent with the notion that Common Terns generally tend to forage in more inshore waters than Arctic Terns (Uttley *et al.* 1989; Becker *et al.* 1997). Common Terns frequently kleptoparasitise Arctic Terns in the vicinity of the colony (Hopkins & Wiley 1972) and this may also have contributed to higher provisioning rates and shorter trip durations in Common Terns.

To some extent, the higher frequency of food delivery by Common Terns reflected the greater number of chicks per brood (see above). Nonetheless, as a result of more frequent delivery of larger meals with a higher average caloric density, the mean daily metabolizable energy intake (MEI) of Common Tern chicks was about 30% higher than that of Arctic Tern chicks (142 and 108 kJ chick^{-1} day^{-1} respectively; Fig. 2.2). After accounting for basal metabolic energy requirements, this difference increased to about 40% (2.1 and 1.5 times BMR respectively; see Results), as a result of higher mass-specific BMR in Arctic Terns (Klaassen 1994). These ratios were very similar to those derived by Klaassen (1994) from measurements of total and basal metabolic energy expenditure rather than daily energy intake, and this suggests that the energy budgets of terns in the Netherlands and N.E. England were broadly similar.

In spite of the large difference between species in the ratio of MEI to BMR, the size-specific growth rates of the two species were almost identical (Fig. 2.1), indicating a major difference in energy budgets. Energy requirements of chicks after accounting for basal metabolism and biosynthesis plus processing of food (which is only minor component of the energy budget) can be divided into energy accumulated in growing tissues (E_{tis}, which depends on growth rate and body composition) plus energy required for activity (E_{act}) and thermoregulation (E_{tr}). Common and Arctic Terns have similar body composition (Ricklefs & White 1981; Klaassen 1994), and so the higher MEI/BMR ratio in Common Terns did not result from higher E_{tis}. Nor did it result from higher $E_{act.}$ in Common Terns, because chicks of both species were inactive most of the time and there was no difference between species in nestling time/activity budgets (Fig. 2.4).

There was no difference in operative temperatures at Common and Arctic tern nests (Fig. 2.3), but Arctic Terns had higher estimated thermal conductance than Common Terns in each age-class, due to smaller body mass. As a result of this, the estimated energy required for maintaining body temperature in the absence of brooding by parents was higher in Arctic Terns than in Common Terns, particularly in young chicks, where E_{tr} greatly exceeded BMR (see Results). Potential savings in energy expenditure through brooding by parents were thus higher for Arctic Terns, particularly in the first half of the nestling period. Although there was no difference between species in the proportion of time that chicks were brooded by their parents

(Fig. 2.4) we suggest that Common Terns spent a higher proportion of daily energy intake on maintenance of body temperature, because parents could not brood three chicks as effectively as two. Broods of three-chicks were often more clearly visible beneath the parent than were broods of one or two (JAR pers. obs.), and this strongly suggests less effective thermal insulation for the larger broods. Thus energy savings to chicks through brooding by parents were probably higher for Arctic Terns than for Common Terns, as a result of the larger number of chicks per brood in Common Terns. In keeping with this, Klaassen *et al.* (1992) estimated from time budgets that energy savings to chicks through brooding were similar in the two species, whereas using energy budgets, Klaassen (1994) estimated that these savings were much higher for Arctic Terns (up to 67% of total energy required for maintaining body temperature) than for Common Terns (up to 38%). Chicks can potentially reduce E_{tr} in the absence of brooding through huddling behaviour (Mertens 1969, O'Connor 1975), but any such reduction is likely to be only small for tern chicks, which tend to sit under cover in vegetation when they are not being brooded rather than huddle together in the nest (Klaassen 1994; this study). Brooding appeared to play a less important role in the energy budgets of Common Terns, and the number of chicks that Arctic Terns could raise was probably limited not only by the rate at which parents could supply food to the nest but also by the requirements of chicks for brooding.

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Chapter 3

The effects of brood size on provisioning rates and chick growth rates in Common and Arctic Terns.

3.1. Summary

The effects of brood size on provisioning rates and chick growth rates of Common Terns *Sterna hirundo* and Arctic Terns *S. paradisaea* were studied at Coquet Island, N.E. England. Adult terns fed large broods more frequently than those containing fewer chicks but brood size had little effect on the species, sizes or energy content of individual meals delivered to the nest. Energy supply per nestling declined as brood size increased and as a result, chicks in large broods developed body mass at a much lower rate than those in small broods. Although brood size had no effect on fledging mass in either species, Common Tern chicks from large broods fledged later than those in small broods. Mass growth rate hierarchies did not occur within broods of either species and hatching position had no effect on the mass of fledglings. Brood size and hatching position had no effect on the rate at which chicks developed structurally or on final body size. These results suggest that flexibility of mass growth rates in Arctic and Common Terns may act as a fine-tuning mechanism, allowing parents to increase annual reproductive output through slower mass growth rates of chicks.

3.2. Introduction

Lack (1968) originally suggested that interspecific differences in brood size are partly related to the amount of food that parents are capable of supplying to the nest during the chick-rearing period. Differences in brood size also occur intraspecifically and may also relate to sustainable provisioning rates by parents during chick-rearing. Parental energy expenditure is usually highest during the chick-rearing period (Bryant & Westerterp 1980, Drent & Daan 1980). There is some evidence that, within species, parent birds have varying foraging capacity and that differences in energy expenditure between individuals may be linked to the number of chicks which can be successfully reared (Green & Ydenberg 1994). However, rates of parental provisioning are not always directly proportional to brood size and so per chick, nestlings in larger broods are often fed less frequently than those in smaller broods (Laido *et al.* 1998, Lozano & Lemon 1998).

The low annual reproductive output of seabirds is assumed to reflect the sparse and unpredictable distribution of marine food resources (Ashmole 1971), which places a low limit on the maximum rate at which parents can provide food for offspring. Thus adults presumably limit clutch size to the number of offspring that they can feed. However, as clutch size decreases, this becomes an increasingly imprecise way of regulating reproductive effort, because each unit decrease in clutch size is a progressively larger proportionate decrease. One way in which adults can adjust their reproductive investment more precisely is by manipulating growth rates of chicks. For instance, in terns, a 50% reduction in chick growth entails about a 40% reduction in a nestling's daily energy requirement (Klaassen *et al.* 1992). Thus adults might to be able to increase their annual reproductive output by reducing the growth rate of the whole brood or of particular members of the brood.

There are, however, potential disadvantages to slow nestling development. Coulson & Porter (1985) showed that Kittiwake *Rissa tridactyla* nestlings which developed slowly showed reduced post-fledging survival. Slow chick growth often results in stunting at fledging which has also been related to poor future survival (Perrins *et al.* 1973; Jarvis 1974; Boag 1987; Richner *et al.* 1989). Protracted development also increases the period of time during which nestlings are susceptible to land-based predators (Lack 1968).

Arctic Terns *Sterna paradisaea* and Common Terns *S. hirundo* are closely related species that breed sympatrically at a number of locations in Britain. Common Terns lay clutches of up to three eggs whereas Arctic Terns rarely lay more than two and chicks of both species hatch asynchronously (Cullen 1957, Pearson 1968, Coulson & Horobin 1976, Bullock & Gomersall 1981; Cramp 1985). Data on provisioning rates and chick diet are easily obtained for these species because chicks are fed within or near to the nest with discrete prey items which can be identified and measured by observations.

Although brood size may be limited by costs of egg production (Heaney & Monaghan 1995) adult terns have little extra time in their activity budgets to increase foraging during chick-rearing (Pearson 1968, Monaghan *et al.* 1989; *Chapter 2*) and so brood size may also be limited by parental provisioning effort. Although much is known about the foraging ecology of terns (e.g. Frank 1992, Becker *et al.* 1993), very little is known about the affects of brood size on parental provisioning or the potential trade-off between chick growth rates and productivity in these species.

The aims of this study were i) to investigate how brood size influences parental provisioning and energy supply rates to Arctic and Common Terns, and ii) to determine the consequences of variations in provisioning rates on the growth rates and fledging weights and sizes of individual chicks within and between broods of different sizes.

3.3. Methods

Fieldwork took place from 1 May to 20 July 1996 at a mixed colony of Common and Arctic Terns on Coquet Island, Northumberland (55° 20'N, 1° 32'W). Sample plots were established as described in *Chapter 2.*

Chicks were individually marked shortly after hatching and were then weighed daily (to the nearest 1g using a Pesola balance) at midday until fledging. Wing length (minimum wing chord, including down, measured to the nearest 1mm with a slotted metal ruler) and head plus bill length (from the tip of the upper mandible to the back of the head, measured to the nearest 0.1mm using Vernier callipers) were also measured at around midday every three days until fledging. Regression equations were fitted to growth data collected during the periods of linear growth of each variable (5-14 days post-hatching for body mass and head plus bill length; after 5 days post-hatching for wing length in both species) for chicks from different brood sizes and hatching positions within broods (i.e. *a*: first hatched, *b*: second hatched and *c*: third hatched chick). These equations were compared using ANCOVA which tests for differences in slope (i.e. growth rates) and elevation. Body masses and head plus bill lengths of fledglings were estimated from mean masses and lengths of individual Common Tern and Arctic Tern chicks over 23 and 21 days post-hatching respectively (Cramp 1985). Data on provisioning rates and chick diets were collected as described in *Chapter 2*.

As in *Chapter 2*, data for individual chicks were collected repeatedly over many days. To account for these repeated measures, the linear period of growth period was divided into two five-day age-classes, 6-10 days and 11-15 days. Data for each age-class were aggregated into a single mean value for each chick, and test statistics were calculated from aggregated mean values, following Sokal & Rohlf (1981). Degrees of freedom were adjusted for analysis of age-specific effects to the number of nests studied rather than the number of observations across all age-classes (see Bolton 1995). For all data concerning food provisioning rates, degrees of freedom refer to the number of broods studied and not the number of individual chicks.

3.4. Results

3.4.1. *Chick diets and provisioning rates*

Over 99% of the diets of both species comprised sandeels and clupeids (see *Chapter 2* for a breakdown of diets). Arctic Tern one-chick broods received a similar proportion of sandeels in their diet ($n = 196$, 98.0%) to two-chick broods ($n = 2300$, 95.5%, $\chi^2_1 = 2.6$, $P > 0.05$). Common Tern broods of a single chick received the highest proportion of sandeels ($n = 93$, 86.5%), three-chick broods the next highest proportion ($n = 1718$, 81.5%) and two-chick broods the lowest proportion ($n = 864$, 72.5%; $\chi^2_1 = 36.8$, $P < 0.01$). There was no significant difference between brood sizes in the sizes of fish fed to chicks of either species (Common Terns; $\chi^2_4 = 1.91$, $P > 0.05$; Arctic Terns; $\chi^2_3 = 4.2$, $P > 0.05$), the majority of fish delivered to all broods being between 3 and 9cm in length (Common Terns: 1-chick: 98%; 2-chick: 99%; 3-

chick: 99%; Arctic Terns: 1-chick: 99%; 2-chick: 99%; sample sizes as above). There was also no significant difference between brood sizes in the energy content of individual feeds delivered to nestlings (Table 3.1; ANOVA; Common Terns; $F_{2,2673} = 1.5$, $P > 0.05$; Arctic Terns; $F_{1,2494} = 0.8$, $P > 0.05$)

During the period of linear mass growth, the frequency of food delivery increased with both brood size and brood age in both Common Terns (Table 3.2; analysis of covariance of feeding frequency by brood size with chick age as a covariate; brood size; $F_{2,14} = 30.9$, $P < 0.01$; age; $F_{1,13} = 63.1$, $P < 0.01$) and Arctic Terns (Table 3.2; ANCOVA; brood size; $F_{1,15} = 33.1$, $P < 0.01$; age; $F_{1,14} = 42.7$, $P < 0.01$). Per nestling, feeding frequency declined with increasing brood size in Common Terns (ANCOVA; $F_{2,14} = 7.0$, $P < 0.01$; $P < 0.01$) and Arctic Terns (ANCOVA; $F_{1,15} = 7.7$, $P < 0.05$). Combining data for feeding frequency and meal size, rates of energy supply per nestling increased with brood age but were lower for larger broods in Common Terns (Table 3.2; ANCOVA; $F_{2,14} = 4.0$, $P < 0.05$; age; $F_{1,13} = 9.3$, $P < 0.01$) and Arctic Terns (Table 3.2; ANCOVA; brood size; $F_{1,15} = 8.9$, $P > 0.01$; age; $F_{1,14} = 22.4$, $P < 0.01$).

3.4.2. *Chick Growth*

Chick mass growth rates declined with increasing brood size in both species (Table 3.3; ANCOVA; Common Terns: $F_{2,15} = 5.3$, $P < 0.05$; Arctic Tern; $F_{1,16} = 9.7$, $P < 0.01$) but there was no significant difference between the mass growth rates of chicks of different hatching positions within broods containing more than one nestling (Table 3.4; Arctic Tern; $F_{1,16} = 0.4$, $P > 0.05$; Common Tern; $F_{2,15} = 1.5$, $P > 0.05$).

In neither species did brood size have an effect on the rate of head plus bill growth (Table 3.3; ANCOVA; Common Tern: $F_{2,15} = 0.2$, $P > 0.05$; Arctic Tern; $F_{1,16} = 0.01$, $P > 0.05$) or wing growth (Table 3.3; Common Tern: $F_{2,15} = 1.0$, $P > 0.05$; Arctic Tern; $F_{1,16} = 0.1$, $P > 0.05$). Hatching position also had no effect on the growth of head plus bill length (Table 3.4; Common Tern; $F_{2,15} = 1.9$, $P > 0.05$; Arctic Tern; $F_{1,16} = 0.3$, $P > 0.05$) or wing length (Table 3.4; Common Tern; $F_{2,16} = 0.6$, $P > 0.05$; Arctic Tern; $F_{1,16} = 0.1$, $P > 0.05$).

There were no significant effects of brood size or hatching position on the body masses of fledglings (Tables 3.5 and 3.6; Common Tern: brood size; $F_{2,15} = 0.2$, $P > 0.05$; hatch position; $F_{2,15} = 0.6$, $P > 0.05$; Arctic Tern: brood size; $F_{1,16} = 0.2$, $P > 0.05$; hatch position; $F_{1,16} = 1.0$, $P > 0.05$) or head plus bill length of fledglings (Tables 3.5 and 3.6; Common Tern: brood size; $F_{2,15} = 0.4$, $P > 0.05$; hatch position; $F_{2,15} = 4.1$, $P > 0.05$; Arctic Tern: brood size; $F_{1,16} = 0.0$, $P > 0.05$; hatch position; $F_{1,16} = 3.4$, $P > 0.05$). Common Tern chicks from larger broods reached fledging mass significantly later than those from smaller broods (Table 3.7; $F_{2,15} = 4.1$, $P < 0.05$) but brood size did not have any effect on the time it took Arctic Tern nestlings to reach fledging mass (Table 3.7; $t_{16} = 0.0$, $P > 0.05$).

Table 3.1. Mean caloric value (kJ) of individual meals delivered to Arctic and Common Terns in relation to brood size on Coquet Island in 1996.

		n	kJ feed^{-1} ± S.D.
Arctic Tern	1-chick	196	2.65 ± 5.14
	2-chick	2300	2.51 ± 3.11
Common Tern	1-chick	93	3.56 ± 5.02
	2-chick	864	4.15 ± 6.57
	3-chick	1718	4.43 ± 8.38

Table 3.2. Mean number of feeds brood^{-1} h^{-1} and kJ chick^{-1} h^{-1} for Arctic and Common Tern broods of mean age 6-10 days and 11-15 days post-hatching which survived until fledging on Coquet Island in 1996.

				Brood age	
		Brood size	*n*	6-10 days	11-15 days
feeds brood^{-1} h^{-1}	Arctic Tern	1 chick	5	3.80 ± 1.37	4.89 ± 2.47
		2 chick	13	5.78 ± 3.57	8.88 ± 4.70
	Common Tern	1 chick	3	4.17 ± 2.63	5.50 ± 3.79
		2 chick	5	5.73 ± 2.79	8.08 ± 4.25
		3 chick	10	6.17 ± 1.95	12.17 ± 4.62
kJ chick^{-1} h^{-1}	Arctic Tern	1 chick	5	5.75 ± 1.93	5.96 ± 2.26
		2 chick	13	5.23 ± 1.63	5.50 ± 3.34
	Common Tern	1 chick	3	8.25 ± 4.56	6.71 ± 3.21
		2 chick	5	8.16 ± 2.73	6.51 ± 3.14
		3 chick	10	7.45 ± 1.18	6.29 ± 2.65

Table 3.3. Mean growth rates of Arctic and Common Tern nestlings which survived until fledging in relation to brood size on Coquet Island in 1996.

			Growth rates		
	Brood size	*n*	Body mass (g d^{-1} ± S.D.)	Head plus bill length (mm d^{-1} ± S.D.)	Wing length (mm d^{-1} ± S.D.)
Arctic Tern	1 chick	5	6.87 ± 0.30	1.58 ± 0.76	8.12 ± 3.55
	2 chick	13	6.75 ± 0.05	1.56 ± 0.32	8.43 ± 1.41
Common Tern	1 chick	3	8.42 ± 0.30	1.84 ± 0.47	8.70 ± 1.97
	2 chick	5	7.64 ± 0.07	1.68 ± 0.22	7.56 ± 0.80
	3 chick	10	7.12 ± 0.13	1.76 ± 5.88	7.11 ± 2.37

Table 3.4. Mean growth rates of Arctic and Common Tern nestlings which survived until fledging in relation to hatching position on Coquet Island in 1996 (*a* = first hatched, *b* = second hatched, *c* = third hatched).

			Growth rates		
	Position within brood	*n*	Body mass (g d^{-1} ± S.D.)	Head plus bill length (mm d^{-1} ± S.D.)	Wing length (mm d^{-1} ± S.D.)
Arctic Tern	*a*	13	7.04 ± 0.05	1.64 ± 0.47	8.62 ± 1.91
	b	13	6.74 ± 0.07	1.53 ± 0.47	8.40 ± 2.06
Common Tern	*a*	15	7.82 ± 0.09	1.87 ± 0.41	7.12 ± 1.22
	b	15	7.61 ± 0.08	1.56 ± 0.45	7.55 ± 1.63
	c	15	6.22 ± 0.14	1.55 ± 1.23	7.15 ± 3.14

Table 3.5. Mean body masses and head plus bill lengths of Arctic and Common Tern fledglings in relation to brood size on Coquet Island in 1996.

	Brood size	*n*	Body mass (g ± S.D.)	Head plus bill length (mm ± S.D.)
Arctic Tern	1 chick	5	106.19 ± 5.83	60.73 ± 1.52
	2 chick	13	107.37 ± 10.40	60.59 ± 2.37
Common Tern	1 chick	3	120.19 ± 14.75	67.60 ± 1.21
	2 chick	5	120.35 ± 12.16	65.82 ± 1.70
	3 chick	10	121.71 ± 10.07	65.70 ± 2.70

Table 3.6. Mean body masses and head plus bill lengths of Arctic and Common Tern fledglings in relation to hatching position on Coquet Island in 1996 (*a* = first hatched, *b* = second hatched, *c* = third hatched).

	Position within brood	*n*	Body mass (g ± S.D.)	Head plus bill length (mm ± S.D.)
Arctic Tern	*a*	13	104.79 ± 10.38	61.28 ± 2.27
	b	13	107.35 ± 10.80	59.51 ± 2.22
Common Tern	*a*	15	119.22 ± 28.12	66.24 ± 1.43
	b	15	124.62 ± 8.48	65.59 ± 1.99
	c	15	124.50 ± 3.39	61.80 ± 1.82

Table 3.7. Mean age at which Arctic and Common Tern nestlings first reached fledging mass, 107g and 123 g respectively, in relation to brood size on Coquet Island in 1996.

	Brood size	*n*	Age at which chicks first reached fledging mass (mean no. of days post-hatching ± S.D.)
Arctic Tern	1-chick	5	17.67 ± 2.52
	2-chick	13	17.72 ± 2.96
Common Tern	1-chick	3	16.50 ± 2.08
	2-chick	5	20.05 ± 2.65
	3-chick	10	21.17 ± 2.86

3.5. Discussion

Brood size had a major influence on the feeding frequency of Common and Arctic Terns on Coquet Island in 1996 (Table 3.2). In both species, the number of feeds delivered to the nest increased with the number of chicks in the brood. This relationship between food delivery and brood size has also been documented in many other species (von Haartman 1954; Henderson 1975; Bryant & Gardner 1979; Nur 1984; Filliater & Breitsisch 1997; Olsen *et al.* 1998), although not all (Emms & Verbeek 1991; Nishimismi *et al.* 1996; Schadd & Ritchison 1998).

Feeding frequency is often higher per nestling for small broods than for large broods (Laido *et al.* 1998; Lozano & Lemon 1998), but adults can compensate for this constraint by delivering larger food items per trip to larger broods (Eybert *et al.* 1998; Siikamaki *et al.* 1998; Meyer *et al.* 1997; Wright *et al.* 1998). In other species parents rearing large broods delivered food per nestling at the same rate as those with fewer young (Rytkonen & Koivula 1996). In the present study, brood size had very little effect on the species, sizes, and most importantly, energy content of meals delivered to Arctic and Common Tern nestlings. Adult Arctic and Common Terns with large broods supplied energy at a lower rate per nestling than those rearing a small broods (Table 3.2).

In most bird species increased brood size has a negative effect on nestling growth (see Klomp 1970 for a review). However, there are some exceptions in which brood size has no effect (Platteeuw *et al.* 1995; Scolaro *et al.* 1996), or a positive effect (Markman *et al.* 1995) on the pace of chick development. At Coquet Island, Arctic and Common Tern chicks from large broods increased mass more slowly than those from small broods (Tables 3.3). This presumably reflected the brood-size related differences in per nestling energy supply of the two species during the linear period of chick mass growth, individual nestlings in large broods received less energy than those in small broods (Klaassen *et al.* 1992). However, brood size had no effect on structural growth rates, final body size, or final body mass in either species (Tables 3.3 and 3.5). Previous studies have shown that small body size at fledging may reduce fecundity (Boag 1987; Richner *et al.* 1989). I suggest that in Arctic and Common Terns, resources may be preferentially allocated to the growth of structural features at the expense of mass retardation so that normal final body size is successfully reached.

In many species, chicks reared in broods containing more than one nestling grow at different rates (Furness 1983; Nisbet *et al.* 1995) due to unequal distribution of food caused by asymmetrical sibling competition (Magrath 1990; Ricklefs 1993). In the present study, the hatching position of a tern chick within a brood had no effect on the rate at which it developed (Table 3.4) or its final fledging mass or size (Table

3.6). Although it was not possible to measure the amount of food that individual chicks within a brood received, the growth data indicated that within large broods energy was distributed equally to nestlings.

Although mass growth rates were lower, chicks from larger broods fledged at similar weights and sizes to those from small, faster growing broods (Table 3.5). However, Common Tern nestlings from larger broods took longer on average to reach fledging mass (Table 3.7). This protracted nestling period potentially increased the period during which Common Tern nestlings were susceptible to ground based predators. However, tern chick predation events usually occur very early in the nestling period (Uttley *et al.* 1989; Robinson & Hamer 1998; *Chapter 5*) so a longer fledging period probably does not lead to increased predation in these species.

The results of this and previous studies have demonstrated that avian nestling growth rates decline with increasing brood size (see above). This trend suggests that parental provisioning rates to broods of different size are a compromise between the energy requirements of the nestlings and the effort that parents make whilst collecting food. 'Optimal Working Capacity' (proposed by Royama (1966)) sets to explain this compromise in terms of life-history theory and predicts that parents normally work at a capacity beyond which they would suffer risks to future survival and reproductive output. From the results of the present study it appears that Common and Arctic Terns balance nestling requirements and parental foraging capacity and that this capacity may be higher in those parents raising large broods. This balance is particularly important in terns because they have little leeway in their activity budgets to increase the proportion of time they spend foraging during the chick-rearing period (Pearson 1968; Monaghan *et al.* 1989; *Chapter 2*). By manipulating mass growth rates these two species may be able to maximize reproductive output without having to increase foraging effort to their detriment. However, brood size had no effect on fledging mass in these species so the overall energy needed to raise an individual nestling may have been the same or higher in larger, slow growing broods (see Drent & Daan 1980; Weathers 1992; *Chapter 7*).

There is some evidence that more experienced adult Common Terns become more efficient at delivering food i.e. they can increase provisioning rate without increasing their daily energy expenditure (Galbraithe *et al.* 1999). It is possible that those terns rearing large broods deliver food more efficiently than those with small broods so that any potential cost of increasing brood size to the parent is offset.

Retarded nestling growth may incur fitness costs to seabirds by increasing post-fledging mortality (Coulson & Porter 1985). However, this cost may be offset if chicks are able to fledge at the same weights as those chicks which grow more rapidly, something which was true for Arctic and Common Terns on Coquet Island in 1996. The relationships between growth rate, fledging mass, fledging size and post-fledging survival need to be measured for terns before the trade-off between brood size and nestling fitness can be properly assessed.

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Chapter 4

Environmental foraging constraints and developmental plasticity in Arctic and Common Terns.

4.1. Summary

The flexibility of nestling growth in Arctic Tern *Sterna paradisaea* and Common Tern *S. hirundo* was investigated during moderate and extreme environmental conditions at a mixed colony at Coquet Island in N.E. England. Moderate environmental conditions imposed constraints on the provisioning rates of both of these tern species but had little effect on the rates of chick growth; both species of tern appear to be well adapted to small, daily variations in food availability. Prior to a 7-day period of extreme environmental conditions in the second half of the chick-rearing period of 1997, chicks of both species developed mass and structural features at similar rates to those recorded in 1996. During the period of prolonged bad weather, chick mortality in both species was particularly high and mass growth rates of nestlings which survived to fledging were retarded during this period by over 50%. Growth retardation and high mortality during this period probably resulted from reduced provisioning and increased energy requirements for thermoregulation. Structural growth rates were not retarded during this period and nestlings of both species fledged at similar body sizes in the two years. Both species fledged at similar masses in both years but reached fledging mass several days later in 1997. Mass growth rates were not accelerated during the period of realimentation.

The ability of Common and Arctic Terns to retard mass growth and to prolong the fledging period may, in combination with brood reduction, allow these species to cope with pronounced short-term reductions in food availability.

4.2. Introduction

In most bird species, there is little flexibility in the time it takes for hatchlings to reach adult body size. Although growth in body mass may vary considerably with food supply, physiological and structural development each tend to occur at species-specific rates (Lack 1968; Ricklefs 1968, 1983; Prince & Ricketts 1981; O'Connor 1984). However, environments characterized by temporal variation in food availability to growing chicks over a time scale of days to weeks should select for behavioural, morphological or physiological adaptations that reduce the impact of poor feeding conditions on the chick's survival and long-term development (Schew & Ricklefs 1998; Wernham & Bryant 1998). Retardation of growth resulting from reduced alimentation may be a non-adaptive passive response (termed phenotypic modulation by Smith-Gill (1983)). Alternatively, nestlings may respond adaptively to reduced alimentation by retarding their physiological development and then resuming normal growth when feeding conditions improve (O'Connor 1977).

Body mass development would be expected to be more flexible than structural growth, because structural characters such as the skeleton and flight feathers are more important to survival than non-structural elements such as body fat to the long-term survival of the chick (Ashmole 1962; Harris 1966, 1969; LeCroy & Collins 1972). Such plasticity of structural growth has been demonstrated for birds in the laboratory (McCance 1960; Schew 1995), and in some cases in the field (Lack &

Lack 1951; Bryant 1975; Ricklefs 1976; Emlen *et al.* 1991). Such an adaptation would reduce energy requirements of the chick by reducing the requirements for biosynthesis and differentiation of tissues (Konarzewski *et al.* 1996). However, in those species which experience more predictable food supply, periods of poor food availability have resulted in permanent stunting suggesting a lack of adaptive developmental plasticity (Boag 1987; Richner 1989; Konarzewski *et al.* 1996). In these species growth rates may be limited by physiological or anatomical constraints rather than by food availability.

Flexible development has been demonstrated in aerial insectivorous species (Lack & Lack 1951; Bryant 1975; Ricklefs 1976; Emlen *et al.* 1991), which exploit food supplies that are temporally and spatially unpredictable (Bryant 1975). The prey resources of many seabirds are similarly unpredictable and this is a particular problem for specialized surface feeders with limited foraging ranges and little leeway in their activity budgets to increase the time they spend foraging (Furness & Ainley 1984). Terns (*Sterna* sp.) are small, piscivorous seabirds that fit this description well. They feed by plunge-diving or dipping at the surface (Kirkham & Nisbet 1987), forage close to colonies during the chick-rearing period (Pearson 1968; Becker *et al.* 1993) and have little ability to spend extra time foraging (Pearson 1968). Much recent attention has focused on the effects of annual variation in food availability on the reproductive performance of terns (Safina *et al.* 1988; Monaghan *et al* 1989; Uttley *et al.* 1989; Mlody & Becker 1991). However, little attention has focused on the effects of day-to-day variation in food availability within individual breeding seasons (see Becker & Specht 1991). In particular, the adaptive responses of nestlings to short-term variation in food provisioning are poorly understood, although changing environmental conditions are known to affect both parental foraging success and chick growth rates (Hawksley 1957; Boecker

1967; Lemmetyinen 1972; LeCroy & LeCroy 1974; Dunn 1973; Becker & Finck 1985; Becker & Specht 1991; Mlody & Becker 1991).

Arctic Terns *S. paradisaea* and Common Terns *S. hirundo* breed sympatrically at mixed colonies around the British Isles. Arctic Terns forage almost exclusively on marine fish caught offshore, whereas Common Terns forage much closer to the land and often inland over freshwater (Uttley *et al.* 1989; Frank 1992; Becker *et al.* 1997). At high windspeeds Common Terns are less successful at foraging at sea than are Arctic Terns (Anon 1968) but they may compensate for this by exploiting freshwater prey from more sheltered inland sites (Frank 1992; Becker *et al.* 1997). There is some evidence that brooding of chicks may be more important for Arctic Terns than for Common Terns (*Chapter 2*). Common Terns may therefore be able to spend more time away from the nest foraging in comparison to Arctic Terns when ambient temperatures are low. However, there are few data on the effects of environmental conditions on the attendance of parents at the nest.

In this chapter the responses of Common and Arctic Tern adults and chicks to day-to-day variation in environmental conditions are examined over the course of a single nestling period. In addition, responses to a period of extreme weather during the second half of the nestling period in one year are also examined.

4.3. Methods

Fieldwork was carried out at Coquet Island in N.E. England (55° 20'N, 1° 32'W) in June and July of 1996 and 1997. Between 500-800 pairs of Common Terns and Arctic Tern nested on Coquet Island in these two years. Sample plots were established as described in *Chapter 2*. 18 nests of each species in 1996 and 30 Arctic Tern plus 35 Common Tern nests in 1997 were enclosed in this way shortly before hatching. Only nests with laying dates ± 2 days of the modal value each year were used, the laying dates for both species being similar.

In both years, chicks were individually marked at hatching and were then weighed daily (to the nearest 1g using a Pesola balance) at midday until fledging. Wing length (minimum wing chord, including down, measured to the nearest 1mm with a slotted metal ruler) and head plus bill length (from the tip of the upper mandible to the back of the head, measured to the nearest 0.1mm using Vernier callipers) were measured at around midday every three days until fledging.

During 1996 prey delivery and energy supply rates to enclosed broods were observed from hides positioned within the colonies as described in *Chapter 2*. Observations of chick brooding were recorded for both species during 1997. Food provisioning rates were not recorded simultaneously but, during the time when brooding time was being investigated, mass growth rates of chicks in 1997 were almost identical to those recorded in 1996 (Common Tern, 7.8 ± 0.2 g day^{-1} and 7.0 ± 0.3 g day^{-1} in 1996 and 1997 respectively; Arctic Tern, 7.1 ± 0.2 and 6.9 ± 0.3 g day^{-1} respectively). 29 Arctic Tern and 36 Common Tern nests of mean chick age 5-14 days post-hatching were observed between 0430h and 2230h from hides within the colonies of the two species. Individual nests were observed over a total of 36 hours and the presence or absence of a brooding parent at a nest was recorded at 5 minute intervals.

To allow ordination of differences in food provisioning rates, brooding times and chick growth associated with weather conditions, the following data were obtained from the meteorological station at Boulmer, Northumberland (approximately 10km from Coquet Island): mean windspeed (knots), rainfall (mm), sunshine (hours), mean temperature (°C) and minimum temperature (°C) for every day during June and July 1996. These data were analysed by a Principal Components Analysis (PCA; Norusis 1990). The position of this station, close to the sea and the study site, suggests that the conditions measured there were representative of those in the vicinity of the study site.

To assess the effects of weather conditions on chick growth, indices of relative growth were calculated by regressing body mass, head plus bill length and wing length upon chick age during the linear period of growth (5-14 days for body mass and head plus bill length; 5 days to beyond fledging for wing length; see Fig. 4.1). For each of these variables a relative growth index (RGI) was calculated from the following equation:

$$\mathrm{RGI} = \frac{G_{obs} - G_{exp}}{G_{exp}} \times 100,$$

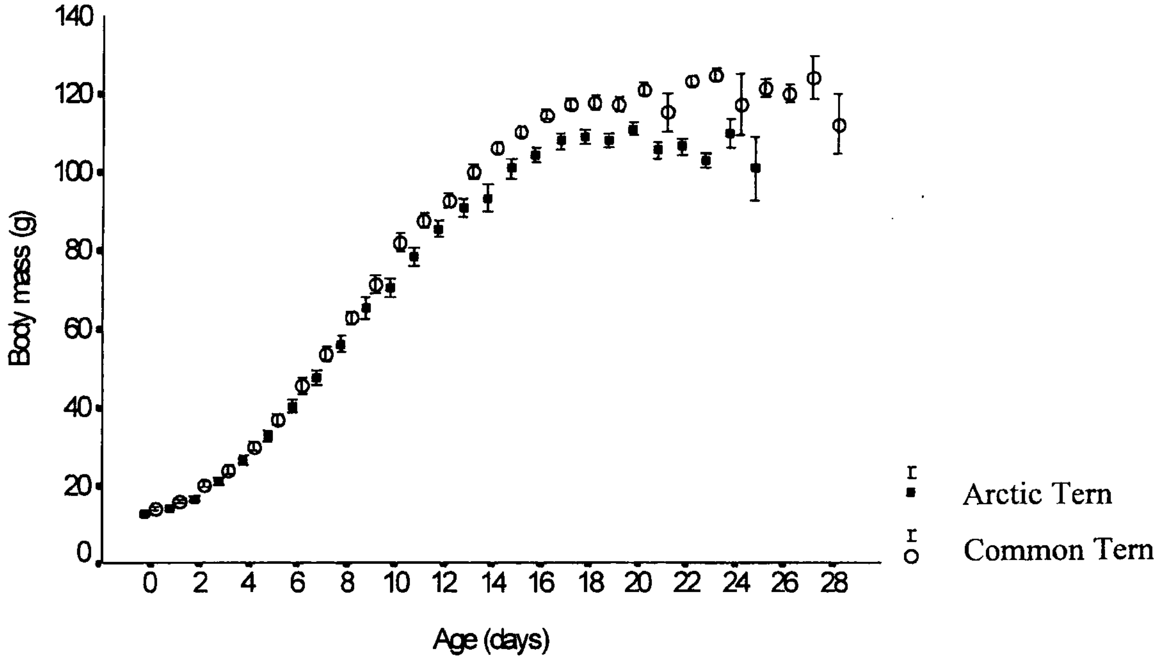
where G_{obs} and G_{exp} are observed and predicted measurements respectively.

In 1997, a period of extremely bad weather, characterized by high windspeeds, high rainfall and low temperatures, occurred between June 25 and July 2 (Fig. 4.2). This provided a 'natural experiment', allowing the effects of an extreme bad weather event on chick growth to be measured. During this period chick mortality was similarly high for both species (42.9% (n = 42) of Arctic Tern nestlings and 49.1% (n = 57) of Common Tern nestlings at study nests died during this period; $\chi^2_1=0.4$, $P > 0.05$). However, a sample of chicks of both species survived this period of bad weather and their growth was measured during this time and during the subsequent period of realimentation. Regression lines were fitted to the linear periods of growth before and during the period of bad weather as described above. The slopes of these lines (i.e. growth rates) were compared to those measured for chicks in 1996 using ANCOVA. 1996 was considered to be a year of good food supply because breeding success was high for both species (see *Chapter 2*). Unfortunately, the island had to be vacated during the period of bad weather due to logistical problems and therefore provisioning rates could not be measured. For this reason I was also unable to include 1997 weather data into the Principal Components Analysis.

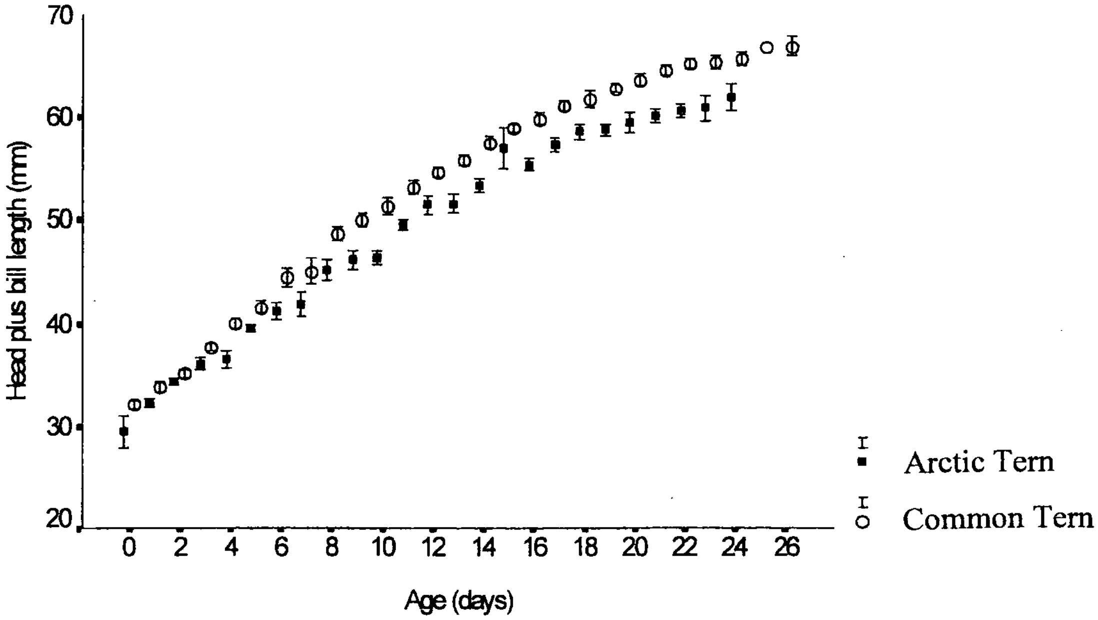
The masses and head plus bill lengths of Common and Arctic Tern fledglings in 1996 and 1997 were estimated from mean values of individual chicks over 24 days and 21 days post-hatching respectively (Cramp 1985). The age at which chicks reached fledging mass was determined as that when Common and Arctic Terns had reached 123g and 107g, respectively. To account for the effects of repeated measures, the degrees of freedom in analyses concerning growth data refer to the number of chicks measured rather than to the number of individual measurements.

Fig. 4.1. Growth of Common and Arctic Tern chicks that survived to fledging on Coquet Island in 1996; *n* = 34 and 28 chicks respectively. Error bars are ± 1 S.E.

i) body mass



ii) head plus bill length



iii) wing length

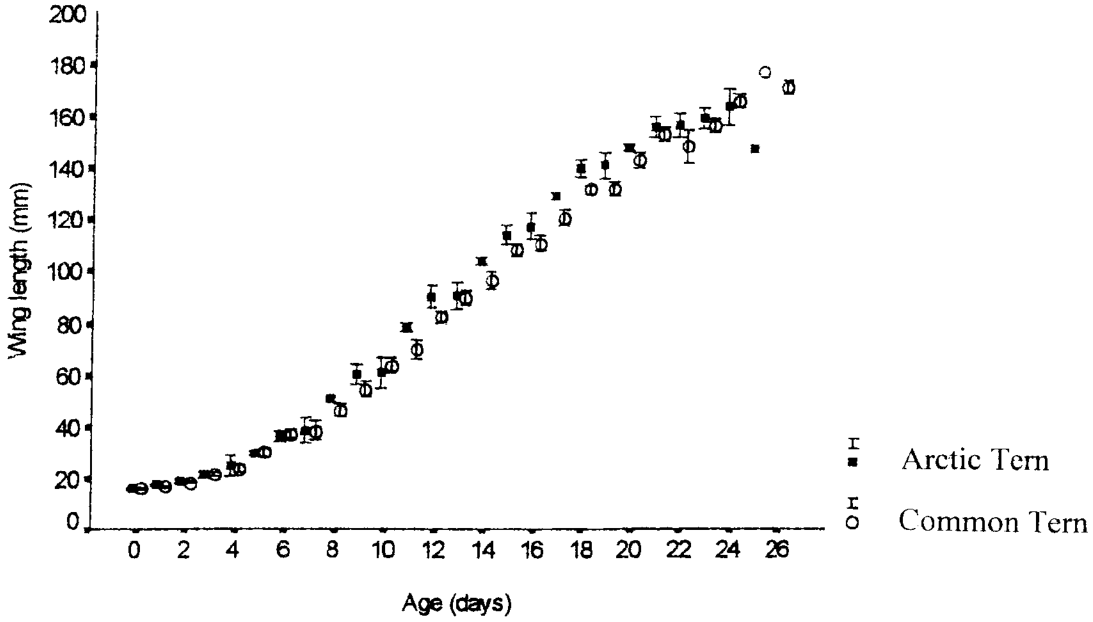
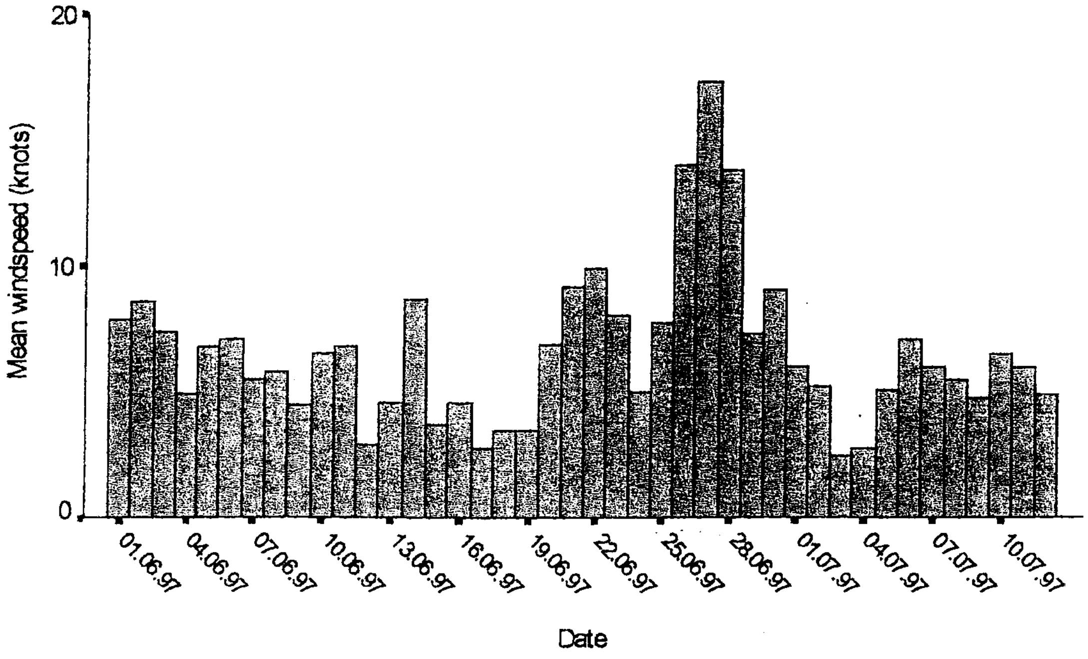
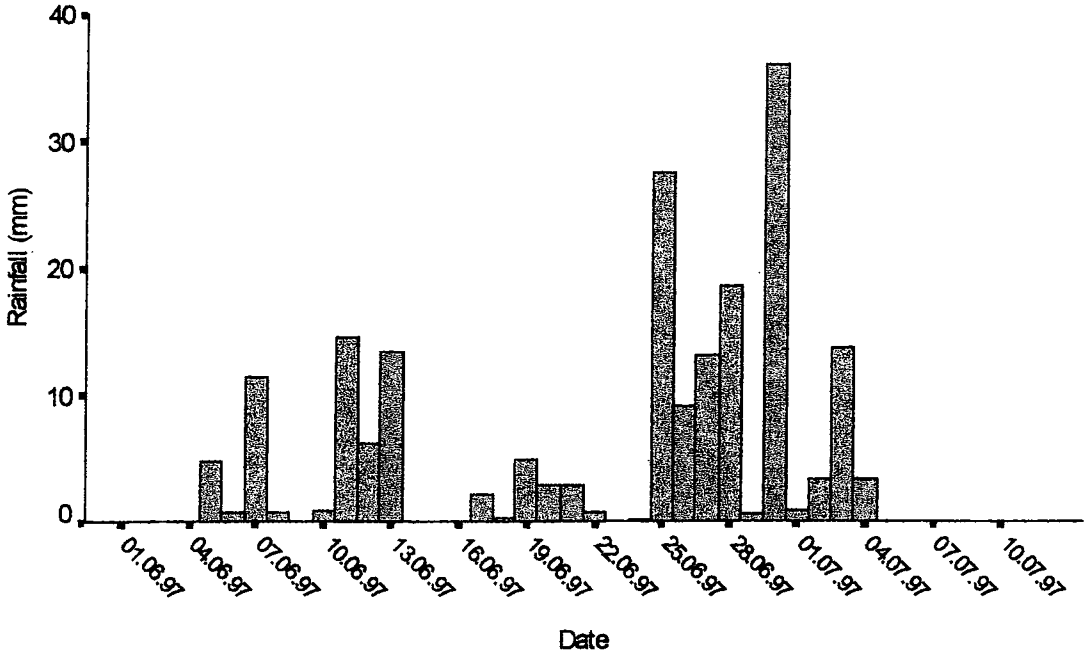


Fig. 4.2. Environmental variables in the vicinity of Coquet Island, N.E. England during June and July 1997.

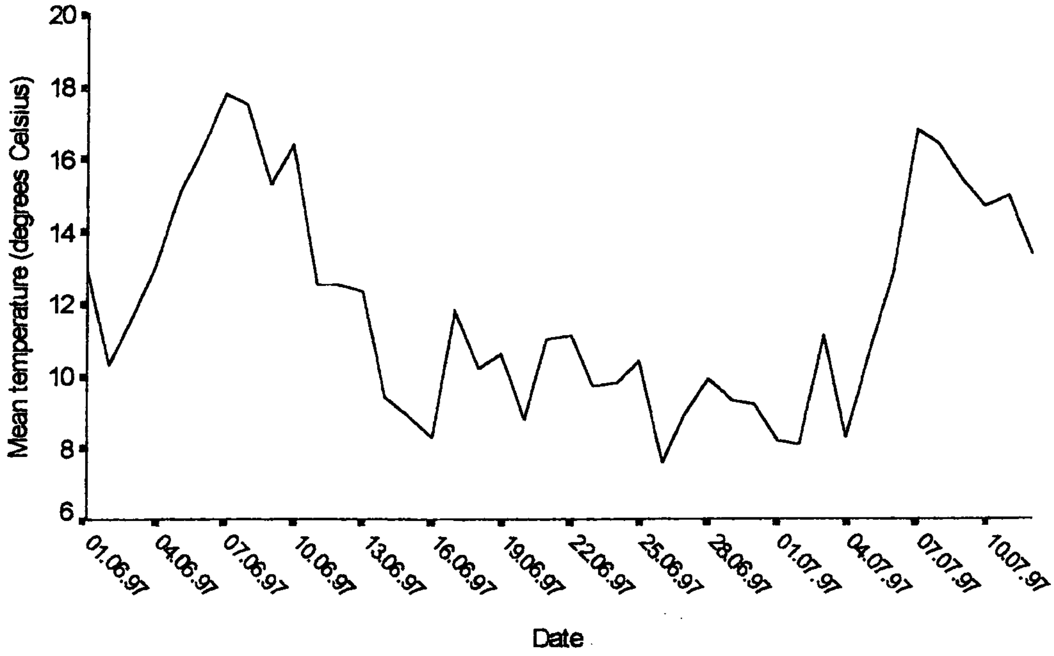
a) mean daily windspeed



b) rainfall



c) mean daily temperature



4.4. Results

4.4.1. *Effects of environmental conditions on chick provisioning, time allocation to brooding and chick growth*

Table 4.1 shows the ranges of environmental variables measured in N.E. England during the 1996 breeding season (June and early-July). There were no periods of extremely bad weather in 1996; prevailing conditions were moderate. PCA extracted two components of variation, here termed WET and WINDY, which accounted for 39% and 23% of the variability in the data set, respectively. The WET score increased with (in order from greatest to least importance) increasing minimum temperature, increasing mean temperature, increasing rainfall, decreasing windspeed and decreasing sunshine. A high WET score therefore represented calm rainy days of high mean and minimum temperatures. The WINDY score increased with increasing windspeed, decreasing rainfall, decreasing mean temperature, increasing sunshine and decreasing minimum temperature. High WINDY scores indicated windy dry days with low temperatures.

Stepwise multiple regression was used to examine how daily feeding frequency ($\log_{10}$ number of feeds per chick per hour), energy supply rate ($\log_{10}$ kJ per chick per hour) and proportion of time brooded (arcsine transformed) were related to the two weather variables above plus brood age. In order to reduce the effects of brood size only the most commonly occurring brood sizes for each species (Common Tern broods of three chicks and Arctic Tern broods of two chicks; see *Chapter 2*) were used in the analyses. In the regression equations presented below all coefficients are presented ± one standard error.

4.4.1.1. *Common Tern*

The two weather variables had no effect on how frequently Common Terns delivered food items to their broods. Brood age had a positive effect on feeding frequency ($R^2 = 0.14$; $F_{1,175} = 36.0$, $P < 0.05$), according to the following equation:

$\log_{10}$ number of feeds per chick per hour = 0.02 (brood age) (S.E. ± 0.00) + 0.15 (S.E. ± 0.03).

Neither the weather variables nor chick age explained any of the variation in energy supply rate to Common Tern broods ($P > 0.05$).

The proportion of time that Common Terns spent brooding their chicks increased with increasing values for WET ($R^2 = 0.14$; $F_{1,175} = 15.1$, $P < 0.05$), according to the following equation:

brooding time = 0.13 WET (S.E. ± 0.03) + 0.43 (S.E. ± 0.06)

None of the variation in Common Tern chick mass or structural growth was accounted for by the two weather variables or chick age ($P > 0.05$).

4.4.1.2. *Arctic Tern*

Arctic Terns fed their broods less frequently with increasing values for WET whilst brood age had a positive effect on feeding frequency ($R^2 = 0.16$; $F_{2,180} = 18.7$, $P < 0.05$), according to the following equation:

$\log_{10}$ number of feeds per chick per hour = -0.02 WET (S.E. ± 0.01) + 0.02 (brood age) (S.E. ± 0.00)+ 0.14 (S.E. ± 0.03)

Brood age accounted for 14% of the variation in feeding rate, but WET accounted for only an additional 2%. WET had no effect on the energy supply rate to Arctic Tern broods, whilst brood age had a positive effect ($R^2 = 0.07$; $F_{1,181} = 10.1$, $P < 0.05$):

$$\log_{10} \text{kJ per chick per hour} = 0.03 \text{ (brood age) (S.E.} \pm 0.01) + 0.14 \text{ (S.E.} \pm 0.07)$$

The time that adult Arctic Terns allocated to brooding their chicks, and chick mass and structural growth were all unrelated the two weather variables and brood age ($P > 0.05$).

4.4.2. *Chick growth in 1996 and 1997*

Prior to June 24 1997, there was no significant difference between years in mass growth rates of Arctic Terns (Table 4.2; ANCOVA; $F_{1,46} = 0.5$, $P > 0.05$) or Common Terns (Table 4.2; $F_{1,59} = 0.5$, $P > 0.05$). Nor was there a difference between years in head plus bill length growth rate (Table 4.2; Arctic Tern; $F_{1,46} = 0.0$, $P > 0.05$; Common Tern; $F_{1,59} = 0.8$, $P > 0.05$) or wing length growth rate (Table 4.2; Arctic Tern; $F_{1,46} = 0.0$, $P > 0.05$; Common Tern; $F_{1,59} = 0.0$, $P > 0.05$)

Between June 25 and July 2 chicks of both species developed mass more slowly in 1997 than in 1996. (Table 4.2; Arctic Tern: $F_{1,46} = 81.9$, $P < 0.01$; Common Tern: $F_{1,59} = 175.2$, $P < 0.01$) but there was no significant difference between years in nestling head plus bill length growth rates (Table 4.2; Common Tern: $F_{1,59} = 0.7$, $P > 0.05$; Arctic Tern: $F_{1,46} = 0.0$, $P > 0.05$) or wing length growth rates (Table 4.2; Arctic Tern: $F_{1,46} = 0.8$, $P > 0.05$; Common Tern: $F_{1,59} = 0.1$, $P > 0.05$).

After the bad weather had ended individuals of both species had almost completed the linear period of mass development (mean body mass of nestlings on July 2; Arctic Tern, $n = 20$, 95.7g ± 11.9; Common Tern, $n = 27$, 107.6g ± 14.7) and therefore growth rates could not be compared using ANCOVA. There was no significant difference between years in the fledging masses of Common Terns (mean fledging mass ± S.D.; 1996: $n = 34$, 121.4g ± 21.4; 1997: $n = 27$, 119.0g ± 12.0; $t_{46} = 0.9$, $P > 0.05$) or Arctic Terns (mean fledging mass ± S.D.; 1996: $n = 28$, 107.2g ± 9.8; 1997: $n = 20$, 119.0g ± 12.0; $t_{59} = 0.8$, $P > 0.05$). However, chicks of both species reached fledging mass much later in 1997 than in 1996 (Common Tern: $t_{59} = -8.5$, $P < 0.05$; Arctic Tern: $t_{46} = -5.8$, $P < 0.05$); Common Tern nestlings reached 123g approximately 6 days later in 1997 than they had in 1996 (mean age of chicks on first reaching 123g = 17.9 days, $n = 34$, S.D. ± 2.7 in 1996; 23.8 days, $n = 27$, S.D. ± 2.7 in 1997) whilst Arctic Tern nestlings reached 107g approximately 4 days later in 1997 than in 1996 (mean age of chicks on first reaching 107g = 15.9 days, $n = 28$, S.D. ± 2.2 in 1996; 20.2 days, $n = 20$, S.D. ± 2.6 in 1997).

There was no significant difference between years in head plus bill lengths of fledgling Common Terns (mean fledgling head plus bill length = 63.7mm, $n = 34$, S.D. ± 1.7 in 1996; 63.8mm, $n = 27$, S.D. ± 2.3 in 1997 ; $t_{59} = 0.4$, $P > 0.05$) or Arctic Terns (mean fledgling head plus bill length = 60.4mm, $n = 28$, S.D. ± 2.3 in 1996; 60.0mm, $n = 20$, S.D. ± 3.1 in 1997 ; $t_{46} = -0.3$, $P > 0.05$). Wing growth continues beyond fledging in these two species so measurements at fledging were not compared.

Table 4.1. Environmental conditions in the vicinity of Coquet Island, N.E. England during June and July 1996.

	Mean ± S.D.	Minimum	Maximum
Mean daily temperature (°C)	13.4 ± 2.4	10.1	18.9
Minimum daily temperature (°C)	10.1 ± 2.3	6.0	15.9
Daily rainfall (mm)	1.0 ± 1.5	0.0	4.8
Sunshine (hours)	6.3 ± 4.2	0.3	15.0
Mean daily windspeed (knots)	5.6 ± 3.3	0.5	12.1

Table 4.2. Mean mass and structural growth rates of Arctic Tern and Common Tern nestlings which survived to fledging in 1996 and 1997 (Sample sizes: 1996; 28 Arctic Terns; 34 Common Terns; 1997; 20 Arctic Terns; 27 Common Terns).

		1996	*1997* (prior to June 24)	*1997* (between June 25 and July 2)
	Growth Rates	mean ± S.D.	mean ± S.D.	mean ± S.D.
Common Tern	mass (g d^{-1})	7.79 ± 0.20	7.24 ± 0.03	2.64 ± 0.04
	head plus bill (mm d^{-1})	1.81 ± 0.35	1.82 ± 0.02	1.74 ± 0.02
	wing (mm d^{-1})	7.00 ± 1.28	6.45 ± 0.35	5.91 ± 0.04
Arctic Tern	mass (g d^{-1})	7.10 ± 0.20	6.91 ± 0.06	3.30 ± 0.04
	head plus bill (mm d^{-1})	1.61 ± 0.37	2.11 ± 0.06	1.89 ± 0.01
	wing (mm d^{-1})	7.58 ± 0.06	7.97 ± 0.36	7.21 ± 0.05

4.5. Discussion

4.5.1. *The effects of environmental conditions on chick provisioning, chick growth and the time that parents allocated to brooding.*

Principal components analysis is particularly useful when dealing with a large number of variables which may be inter-related because it extracts a small number of meaningful variables which are fully independent. In the present study two weather variables were extracted by this method. High values for the first variable represented principally wet, mild days (WET), and high values for the second corresponded with windy, dry days (WINDY).

Neither of these two components of weather conditions had any effect on the mass or structural growth indices of Arctic or Common Tern chicks. Previous studies have shown that terns feed their broods less frequently on rainy days (LeCroy & LeCroy 1974; Feare 1976; Becker *et al.* 1985), possibly due to raindrops churning up the surface of the sea making prey location more difficult. In the present study increasing values for WET were associated with reductions in the feeding frequency of Arctic Terns, although the effect was slight (WET accounted for only 2% of the variation in feeding rate). WET had no influence on food delivery rates in Common Terns. The latter spent less time brooding chicks on days when rainfall was high, suggesting they may have had more difficulty foraging in the rain and had to spend more time foraging to sustain their rate of provisioning. There is also some evidence that brooding of chicks may be more important for Arctic Terns than for Common Terns because the rate at which the former can supply energy to the nest is more constrained by foraging range and diet (*Chapter 2*). This may explain why Arctic Terns did not reduce the time they allocated to brooding in order maintain provisioning rates on days with high WET values. However, both species were able to maintain energy supply as WET changed and so chick growth was buffered against the observed changes in this variable.

Previous studies have shown that Common Terns and Arctic Terns find it more difficult to forage in high windspeeds (Dunn 1973; Dunn 1975; Taylor 1983; Frank 1992). However, adverse effects are usually only observed at windpeeds well over 20 knots (Boecker 1967; Frank 1992) which were much higher than any windspeeds experienced by terns on Coquet Island in 1996. This was probably the reason why no significant relationships were found between the WINDY variable and parental provisioning rates, chick growth indices or the time allocated to brooding in either species.

The results of the first part of this study indicate that although moderate day-to-day changes in weather may influence the foraging and brooding behaviour of these tern species to some extent, parents are able to maintain energy supply and chick growth is buffered under such conditions.

4.5.2. *Chick growth before, during and after a short-term period of bad weather in 1997.*

In the second half of the chick-rearing period in 1997, a seven day period of continually high windspeeds, high rainfall and low daily temperatures occurred at the colony (Fig. 5.2). A high proportion of the nestlings of both species died during this period, presumably from starvation or hypothermia (see methods).

Prior to the period of bad weather Arctic and Common Tern chicks were increasing mass at the same rate as they had in 1996 (Table 4.2), indicating that food supply prior to the period of the bad weather in 1997 was similar. During the 7-day period of extreme weather conditions the mass development rates of both species were retarded by over 50% (Table 4.3). Although I was not able to observe nests during this period, increased time spent brooding chicks combined with unfavorable foraging conditions were probably responsible for reducing the rate of food supply and hence slowing chick mass development (see Boecker 1967; Dunn 1972; LeCroy & Collins 1972; Becker & Specht 1991; Frank 1992; Uttley *et al.* 1989; Uttley 1992; Becker *et al.* 1998).

Neither species experienced retarded structural growth rates during the period of adverse weather (Table 4.3). A similar lack of response of nestling structural growth to undernutrition has been observed in other birds (Rofstad 1986; Konarzewski *et al.* 1996). Structural chick growth rates appeared to be maintained, presumably at the expense of mass growth retardation when conditions were unfavorable. The benefits of this trade-off are unclear but may be related to post-fledging survival (Boag 1987; Richner *et al.* 1989), particularly if structural growth retardation results in permanent stunting.

On July 2 the period of adverse weather ended and no more chick mortality of either species occurred subsequently that year. As mass growth rates had been reduced by 50% during the 7-day period of bad weather in 1997, fledging masses were expected to be reached approximately 4 days later than normal if mass growth during the period of realimentation had returned to normal. In fact, Arctic and Common Tern nestlings reached fledging mass 4 and 6 days later than normal, respectively, indicating that neither species was able to accelerate mass growth rates during the period of realimentation.

The energy required for growth is an important component of a chick's daily energy expenditure (approximately 20% in terns and other larids; Drent *et al.* 1992). Increased mass development rates involve high energy expenditure; for instance a doubling of growth rate increases peak daily energy requirements of chicks by up to 61% (Klaassen *et al.* 1992; Weathers 1992). Energy supply is limited by the amount of food that parent birds are able to supply to their chicks, and adult terns are unlikely to be able to increase the amount of energy they supply to the nest. However, in the present study all Common and Arctic Tern broods studied lost at least one chick during the period of bad weather and therefore more energy should have become available to those chicks still alive when foraging conditions improved. This raises the question why nestlings did not develop faster during the period of realimentation.

Growth rates may be limited by physiological constraints in addition to proximate food supply. Firstly, tissue growth is limited by the rate at which cells can proliferate (Ricklefs 1979). Secondly the conversion of food into biomass is controlled by the rate chicks can process the food (Konarzewski *et al.* 1989, 1990). The conversion of food is controlled largely by the size of the gut and small chicks convert nutrients and energy less rapidly than large chicks (Kirkwood & Prescott 1984). Thirdly, mass growth may be limited by the growth dynamics of the skeleton (Carrier & Leon 1990). In relation to the data available for Arctic and Common Tern chicks measured on Coquet Island in 1997 none of these explanations can be dismissed.

There evidence from previous studies that during the breeding season adult terns are in poorer condition than normal, as indicated by low body mass, during periods of unfavorable foraging conditions (Monaghan *et al.* 1989; Frank & Becker 1992;

Wendeln & Becker 1996). Although I was unable to weigh adult terns in 1997 they may have been in much worse condition after the period of bad weather than they were prior to this period and were therefore unable to sustain the normal rate of provisioning. However, it remains unclear why these species were unable to increase chick mass growth during the period of realimentation.

Reduced nestling growth rates may have considerable negative repercussions for nestling and post-fledging survival (Coulson & Porter 1985; Hamer *et al.* 1991; Nisbet *et al.* 1995). Prolonged nestling periods also increase the time during which chicks are susceptible to ground based predators. However, at times when food availability is low a strategy of brood reduction, reduced mass growth rates and delayed fledging may maximize annual productivity in birds (Emlen *et al.* 1991). Growth rate flexibility increases the probability of nestling survival when food shortages occur over short time spans but brood reduction ensures that when food supply is low over longer periods of time the brood requirements can be modified further. The results of the present study suggest that Arctic and Common Terns also employ this type of strategy in response to poor feeding conditions. However, future work is required in order to determine whether the strategy of growth plasticity is adaptive or purely a consequence of undernutrition in these species.

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Chapter 5

Annual variation in the breeding performance of Common and Arctic Terns in relation to inshore food availability and predation.

5.1. Summary

The reproductive performance of Arctic Terns *Sterna paradisaea* and Common Terns *S. hirundo* breeding sympatrically at Coquet Island in N.E. England was assessed in 1996, a year of relatively high fish abundance, and 1998, a year of relatively low fish abundance in the vicinity of the colony. Both species utilized inshore fishing grounds to some extent, but Arctic Terns tended to forage further offshore than did Common Terns. Both species laid larger clutches in 1996 than in 1998 whereas fledging success, egg sizes, egg volumes and structural growth rates were similar in both years. Common Tern chick mass growth rates were higher in 1996 than in 1998 whereas those of Arctic Tern chicks were similar in both years. Egg predation in both species was highest in 1998, whereas chick predation was low in both years. Evidence from this study suggests that mass growth rates of Common Tern nestlings may be the most sensitive indicators of inshore fish abundance particularly where the effects of predation and bad weather on breeding success are difficult to measure.

5.2. Introduction

The annual reproductive output of many seabirds has been shown to be closely linked to marine food supply (Crawford & Shelton 1991; Anderson *et al.* 1982; Furness 1982; Ricklefs *et al.* 1984; Coulson & Thomas 1985; Hunt *et al.* 1986; Monaghan *et al.* 1989; Uttley *et al.* 1989; Hamer *et al.* 1991; Hamer *et al.* 1993). The relationships between food availability and parameters of seabird behaviour such as breeding success, chick growth, colony attendance and activity budgets suggest that seabirds can be used as indicators of marine food supplies (Cairns 1987; Montevecchi 1983). However, individual breeding parameters are likely to vary at different levels of food availability so to be able to utilize seabirds as accurate biomonitors it is necessary to assess which parameters are most sensitive to variations in food supply at different levels.

To study the relationship between seabird breeding performance and prey stocks it is necessary to measure the abundance of prey types directly. In some cases, the yields of trawlers or research vessels have provided useful indices for quantifying the availability of prey species during the breeding season (Monaghan *et al.* 1992; Safina *et al.* 1988). However, in many cases these data are not obtainable. Clearly, a method of assessing fish stocks for which there is no need to leave the mainland, which provides fishery-independent data, and which is relatively inexpensive would be valuable for the study of this type of predator-prey interaction.

Measurement of fish abundance at cooling water intake screens has been undertaken at many industrial power stations around the British Isles as a tool for quantifying inshore fish populations and community structure (Henderson 1988). By measuring the rate at which fish are impinged on these screens it is possible to obtain an index of the abundance of different species available to marine predators which feed inshore.

Common Terns *Sterna hirundo* and Arctic Terns *S. paradisaea* breed sympatrically at colonies throughout Britain. They forage over small ranges (at maximum 20km and 25km radius around the colony for Common and Arctic Terns respectively; Pearson 1968; Becker *et al.* 1993; Breakwell *et al.* 1996), feed near to the surface by plunge-diving (Kirkham & Nisbet 1987), and have very little extra time to increase foraging effort during the chick-rearing period (Pearson 1968; Monaghan *et al.* 1989; *Chapter 2*). This makes these terns particularly sensitive to changes in food availability (Furness & Ainley 1984). Common Terns breeding in Northern Europe forage predominantly inshore (Becker *et al.* 1993; Craik 1998), feeding chicks on a diet comprised of clupeids (sprats *Sprattus* and herrings *Clupea harrengus*) and sandeels Ammodytidae (Pearson 1968; *Chapter 2*). Arctic Terns feed their chicks a diet almost entirely composed of sandeels and may feed further offshore than do Common Terns (Hopkins & Wiley 1972). However, it is unclear whether the breeding ecology of Common Terns is more sensitive to changes in inshore food availability than that of Arctic Terns.

Much recent attention has focused on the breeding performance of Common and Arctic Terns when faced with annual variations in food supply (Safina *et al.* 1988; Monaghan *et al.* 1989; Uttley *et al.* 1989; Monaghan *et al.* 1992; Uttley 1992). In general, egg production, breeding success and chick growth rates are limited by food availability (Nisbet 1973; Nisbet 1977; Safina *et al.* 1988; Monaghan *et al.* 1989; Klaassen *et al.* 1992). Parental attendance may also decline especially during chick-rearing (Barret & Runde 1980; Uttley 1992; Hamer *et al.* 1993), allowing predators more opportunity to take tern chicks when food supply is low.

Black-headed Gulls *Larus ridibundus* are the main predators of tern chicks and eggs on Coquet Island (pers. obs.). Although Black-headed Gulls feed predominantly on earthworms (Lumbricidae) and other terrestrial invertebrates, some individuals are kleptoparasitic taking fish from a range of seabird species (Cramp 1983; Ratcliffe *et al.* 1997). In the event of reductions in marine food supplies it is possible that Black-headed Gulls may take more tern chicks and eggs at colonies where they nest in close proximity to terns as a way of compensating for the lack of fish which can be stolen from terns and other seabirds.

In this study we test the hypotheses that during the breeding season: a) Common Terns are more sensitive to annual changes in inshore food abundance than are Arctic Terns because they feed further inshore; and b) some breeding parameters of these species act as useful indicators of variations in inshore food supply.

5.3. Methods

5.3.1. *Measurement of inshore fish abundance*

Fish abundance was determined by sampling from cooling water intake screens at Lynemouth power station, Northumberland, NE England. This power station is approximately 10km south of Coquet Island (see below) and extracts sea water at a constant rate from 1500m off the coast. Fish and other marine organisms are carried in the cooling water as it is extracted from the sea and are screened off at grids of aperture 8-10mm so that only fish eggs, larvae, small invertebrates and small juvenile fish pass through the system (Dempsey 1988). Fish impinged on the screens are then washed into skips.

In 1996 and 1998 a framed net was placed at the outlet to the waste skip so that all the fish that had been drawn from the sea were caught. Fish were sampled in this manner over 3 hour periods between April and August, at the time when Common and Arctic Terns were breeding on Coquet Island. To minimize the effect of tide and time of day, sampling was started at low tide and always between 0930h and 1030h. At the end of each sampling period the numbers and sizes of each fish species caught in the net were recorded. Only fish up to 9cm long (which comprised >99% of the diet; see Results) were included in further analysis.

5.3.2. *Breeding performance and foraging locations*

Diets of both species were assessed in each year using the methods described in *Chapter 2*. To assess foraging locations used by the two species, adult terns returning to Coquet Island from different directions were observed at intervals throughout the chick-rearing period of 1998. Observation points facing due east, north, south and west were determined prior to the chick-rearing period using a magnetic compass (Fig. 5.1.). The numbers of Common and Arctic Terns carrying fish within 90° of each observation point were counted over ten 1-hour long periods of observation randomized throughout hours of daylight (0430h-2230h). The types and size-classes of fish being carried were determined as above. Inshore feeders were defined as those terns returning from the west, whilst offshore feeders were defined as those returning from the east.

Clutch sizes of both species were measured annually as described in *Chapter 2*. The lengths and widths of eggs in the study nests were measured to the nearest 0.1mm on clutch completion using Vernier callipers. Egg volume (cm^3) was calculated from the equation in Bolton (1991):

$$\text{Volume} = 0.000476 \times \text{length} \times \text{width}^2$$

Data on hatching success (chicks hatched per egg laid) and fledging success (chicks fledged per chick hatched) were obtained for all study nests in each year. Nests of both species were checked daily and the numbers of corpses and eggs/chicks removed by predators were recorded. Predators were identified opportunistically in both years.

Chicks were individually marked on hatching and were then weighed daily (to the nearest 1g using a Pesola balance) at midday until fledging. I also measured wing length (minimum wing chord, including down, measured to the nearest 1mm with a slotted metal ruler), tarsus plus toe length (from the back of the tibiotarsus to the skin at the nail, to the nearest 1mm with a slotted metal ruler) and head plus bill length (from the tip of the upper mandible to the back of the head, measured to the nearest 0.1mm using Vernier callipers) at around midday every three days until fledging.

Regression equations were fitted to growth data collected during the periods of linear growth of each parameter in each year (in both species: 5-14 days post-hatching for body mass and head plus bill length growth, 2-9 days post-hatching for tarsus and toe growth and after 5 days post-hatching for wing length growth). Between-year differences in the rates of linear growth were examined using analysis of covariance (ANCOVA). The masses, head plus bill lengths and tarsus and toe lengths at fledging were estimated from mean measurements of individual Arctic and Common Tern chicks more than 21 and 23 days old respectively (Cramp 1985). Wing length was not measured in this way because flight feathers continue to grow beyond fledging. Between-year variations in fledging values were examined using

ANOVA. In all cases degrees of freedom were derived from the number of chicks measured rather than from the number of individual measurements to account for the effects of repeated measures.

5.4. Results

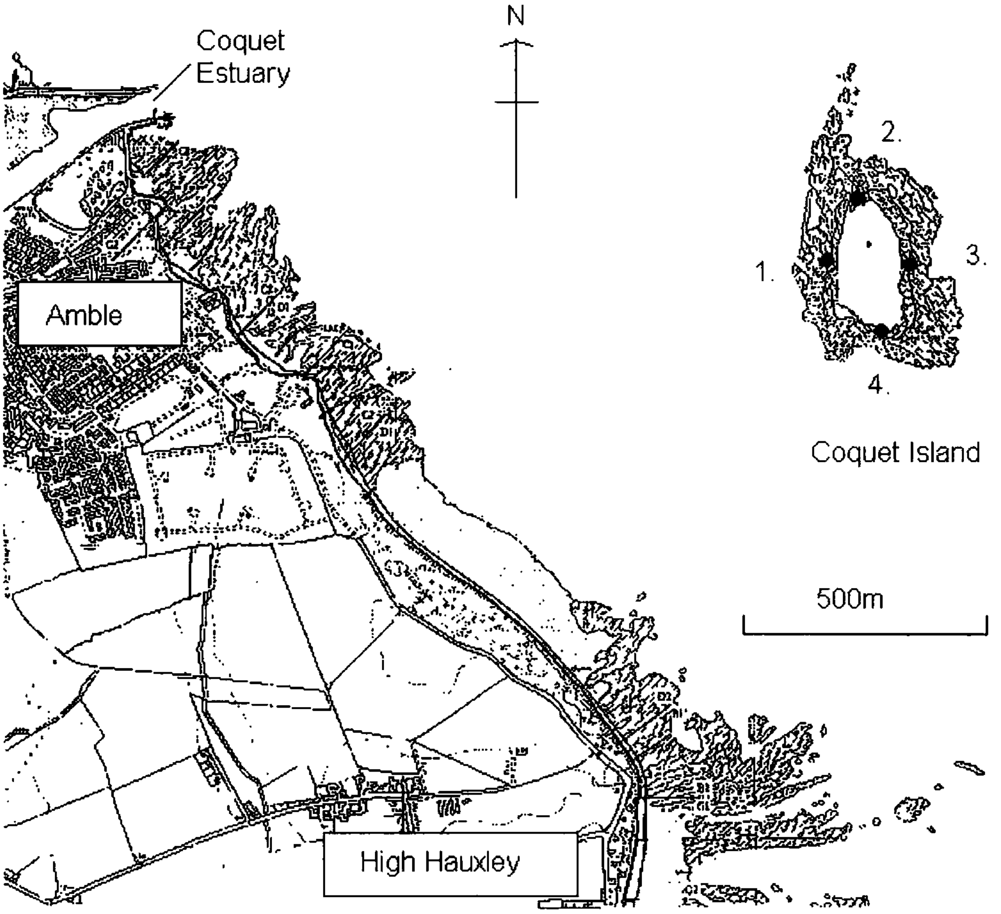
5.4.1. *Inshore fish abundance*

The rate at which small fish of prey species (<9cm) were impinged on the cooling water intake screens of Lynemouth power station was c.10 times greater in 1996 than in 1998 for both sandeels and clupeids (Fig. 5.2; two-way ANOVA; $F_{1,18}$ = 4.63, $P < 0.05$) but did not differ between prey types: ($F_{2,18} = 0.13$, $P > 0.05$). There was no significant interaction between year and prey type ($P > 0.05$).

5.4.2. *Diets and foraging distributions*

In both 1996 and 1998, Common and Arctic Terns fed their chicks almost exclusively (<99%) a diet of sandeels and clupeids. In both years, Arctic Terns fed their chicks a higher proportion of sandeels than did Common Terns (1996: Arctic Terns 95.7%, n = 2498; Common Terns 82.2%, n = 2699; $\chi^2_2 = 223.1$, $P < 0.01$. 1997: Arctic Terns 75.3%, n = 455; Common Terns 33.4%, n = 504; $\chi^2_2 = 172.5$, $P < 0.01$.). Although the majority of fish delivered were between 3 and 6 cm long (Table 5.1), Common Terns delivered a higher proportion of fish in the larger size-classes in both years (Table 5.1; 1996; $\chi^2_2 = 27.0$, $P < 0.01$; 1998; $\chi^2_2 = 93.7$, $P < 0.01$).

Fig. 5.1. Coquet Island and the adjacent coastline at low water. Closed circles indicate the observation points from which Arctic and Common Terns were recorded returning from 1.) westerly, 2.) northerly, 3) easterly, and 4.) southerly foraging locations in 1998.



During the chick-rearing period of 1998, Common Terns returned almost twice as frequently as Arctic Terns from inshore feeding grounds to the west of the island (Fig. 5.3; $\chi^2_3 = 237.1$, $P < 0.01$). Similar proportions of the two species returned with fish from northerly and southerly directions.

Arctic Terns and Common Terns returning to the island from offshore feeding grounds carried a higher proportion of sandeels than did those returning from inshore areas (Arctic Terns; 78.0% of 221 returns from offshore, 56.4% of 234 returns from inshore; $\chi^2_1 = 15.5$, $P < 0.01$: Common Terns; 51.1% of 141 returns from offshore, 32.7% of 245 returns from inshore; $\chi^2_1 = 12.7$, $P < 0.01$). Whether returning from offshore of inshore fishing grounds, Arctic Terns brought a higher proportion of sandeels back to the island than did Common Terns (offshore: $\chi^2_1 = 28.1$, $P < 0.01$; inshore: $\chi^2_1 = 27.4$, $P < 0.01$).

5.4.3. *Breeding success*

Clutch sizes of both tern species were higher in 1996 than in 1998. (Table 5.2; Common Tern, $\chi^2_2 = 118.7$, $P < 0.01$; Arctic Tern, $\chi^2_2 = 45.4$, $P < 0.01$). However, there were no significant differences between years in the widths, lengths or volumes of eggs laid by Arctic Terns (Table 5.3; t tests using pooled variance estimates; width: $t_{84} = -1.5$, $P > 0.05$; length: $t_{84} = 0.0$, $P > 0.05$; volume: $t_{84} = -0.8$, $P > 0.05$) or Common Terns (Table 5.3; width: $t_{185} = -0.1$, $P > 0.05$; length: $t_{185} = -2.3$, $P > 0.05$; volume: $t_{185} = -1.6$, $P > 0.05$). Common Tern hatching success was similar in the two years (Table 5.2; $\chi^2_4 = 0.9$, $P > 0.05$) but, Arctic Tern hatching success was higher in 1996 than in 1998 (Table 5.2, $\chi^2_4 = 19.6$, $P < 0.01$). Egg predation was higher in 1998 than in 1996 for Common Terns (eggs predated; 0% ($n = 40$) in 1996; 14% ($n = 81$) in 1998; $\chi^2_1 = 6.0$, $P < 0.05$) and Arctic Terns (0% ($n = 35$) in 1996; 33% ($n = 81$) in 1998; $\chi^2_1 = 14.6$, $P < 0.01$).

Fledging success of both species was similar in the two years (Table 5.2; Common Tern, $\chi^2_4 = 5.9$, $P > 0.05$; Table 5.2; Arctic Tern, $\chi^2_4 = 4.5$, $P > 0.05$). Chick predation was similar in both years for Common Terns (chicks taken; 3% ($n = 37$) in 1996; 5% ($n = 67$) in 1998; $\chi^2_1 = 0.2$, $P > 0.05$) and Arctic Terns (3% ($n = 35$) in 1996; 13% ($n = 24$) in 1998; $\chi^2_1 = 2.1$, $P > 0.05$). All chicks taken by predators were fewer than 5 days old. From observations, all Common and Arctic Tern eggs ($n = 2$ and 3 respectively) and chicks ($n = 6$ and 10 respectively) during 1996 and 1998 were taken by Black-headed Gulls.

5.4.4. *Chick growth*

Body mass development of Common Tern chicks progressed at a slower rate in 1998 than in 1996 (Table 5.4; ANCOVA; $F_{1,74} = 17.9$, $P < 0.01$). However, rates of Common Tern skeletal and wing growth were similar in 1996 and 1998 (Table 5.4; head plus bill length: $F_{1,74} = 2.6$, $P > 0.05$; wing length: $F_{1,74} = 0.4$, $P > 0.05$; tarsus plus toe length: $F_{1,74} = 0.4$, $P > 0.05$). Fledgling masses of Common Terns were higher in 1996 than in 1998 (Table 5.5; $t_{74} = 4.2$, $P < 0.01$) but, head plus bill lengths and tarsus plus toe lengths of Common Tern fledglings were similar in the two years (Table 5.5; head plus bill length: $t_{74} = 0.4$, $P > 0.05$; tarsus plus toe length: $t_{74} = 1.9$, $P > 0.05$).

Arctic Tern rates of mass, skeletal and wing growth were similar in 1996 and 1998 (Table 5.4; body mass: $F_{1,49} = 1.8$, $P > 0.05$; head plus bill length: $F_{1,49} = 0.1$, $P > 0.05$; wing length: $F_{1,49} = 0.7$, $P > 0.05$; tarsus plus toe length: $F_{1,49} = 2.8$, $P > 0.05$). Masses of Arctic Tern fledglings were also similar in 1996 and 1998 (Table 5.5; $t_{49} = 0.5$, $P > 0.05$), whereas head plus bill lengths and tarsus plus toe lengths at fledging were greater in 1998 (Table 5.5; head plus bill length: $t_{49} = 3.6$, $P < 0.05$; tarsus plus toe length: $t_{49} = 7.7$, $P < 0.05$).

Table 5.1. Proportions (%) of different size-classes of fish fed to Arctic Tern and Common Tern broods on Coquet Island in 1996 and 1998.

			% of size-class in diet			
		n	<3cm	3.1-6cm	6.1-9cm	>9cm
Common Tern	1996	2699	0.0	84.4	15.2	0.4
	1998	455	1.8	79.1	18.1	1.0
Arctic Tern	1996	2498	0.0	89.1	10.9	0.1
	1998	504	4.9	93.9	1.2	0.0

Table 5.2. Clutch sizes, hatching success and fledging success (means ± S.D.) of Common Terns and Arctic Terns at Coquet Island in 1996 and 1998. Sample sizes refer to the number of nests monitored.

	Common Tern				Arctic Tern			
	n	1996	*n*	1998	*n*	1996	*n*	1998
Clutch size	110	2.56 ± 0.51	120	1.98 ± 0.67	110	1.94 ± 0.62	120	1.70 ± 0.50
Chicks hatched per egg laid	18	0.87 ± 0.21	35	0.79 ± 0.36	18	0.86 ± 0.23	31	0.43 ± 0.46
Chicks fledged per chick hatched	18	0.83 ± 0.34	35	0.68 ± 0.31	18	0.90 ± 0.56	31	0.79 ± 0.43

Table 5.3. Mean lengths, widths and volumes (± S.D.) of Common Tern and Arctic Tern eggs laid on Coquet Island in 1996 and 1998. Sample sizes refer to the number of eggs measured.

		n	Mean length (mm)	Mean width (mm)	Volume (cm^3)
Common Tern	1996	40	40.56 ± 1.78	30.15 ± 0.97	17.57 ± 1.39
	1998	80	40.74 ± 4.49	30.29 ± 0.92	17.81 ± 2.31
Arctic Tern	1996	35	39.97 ± 1.24	29.34 ± 0.80	16.39 ± 0.95
	1998	51	40.39 ± 1.29	29.33 ± 0.86	16.56 ± 1.09

Table 5.4. Mean rates of mass, head plus bill length, tarsus plus toe length and wing length development during the linear phase of growth of Common and Arctic Tern chicks which survived to fledging on Coquet Island in 1996 and 1998. Rates are presented ± S.D.

		1996		1998	
	Growth parameter	*n*	Mean ± S.D.	*n*	Mean ± S.D.
Common Tern	mass (g d^{-1})	34	7.79 ± 0.20	42	6.73 ± 1.43
	head plus bill (mm d^{-1})	34	1.81 ± 0.35	42	1.66 ± 0.45
	tarsus plus toe (mm d^{-1})	34	0.91 ± 0.52	42	0.98 ± 0.52
	wing (mm d^{-1})	34	7.00 ± 1.28	42	7.23 ± 2.01
Arctic Tern	mass (g d^{-1})	28	7.10 ± 0.20	23	6.65 ± 1.11
	head plus bill (mm d^{-1})	28	1.61 ± 0.37	23	1.65 ± 0.44
	tarsus plus toe (mm d^{-1})	28	0.69 ± 0.63	23	0.82 ± 0.44
	wing (mm d^{-1})	28	7.58 ± 0.06	23	7.24 ± 1.11

Table 5.5. Mean body masses, total head lengths and tarsus and toe lengths (± S.D.) of Common and Arctic Tern fledglings at Coquet Island in 1996 and 1998.

	Year	*n*	Body mass (g)	Tarsus and toe length (mm)	Total head length (mm)
Common Tern	1996	34	121.2 ± 9.6	42.7 ± 1.7	63.7 ± 1.7
	1998	42	105.9 ± 21.9	42.0 ± 1.6	63.5 ± 2.7
Arctic Tern	1996	28	107.2 ± 9.8	37.0 ± 1.5	60.4 ± 2.3
	1998	23	109.4 ± 17.3	41.4 ± 2.4	63.0 ± 2.8

Fig. 5.2. Relative inshore abundance (fish impinged hr^{-1}) of sandeels (open columns) and clupeids (filled columns) April-August 1996 and 1998 as measured at the cooling water intake screens of Lynemouth power station.

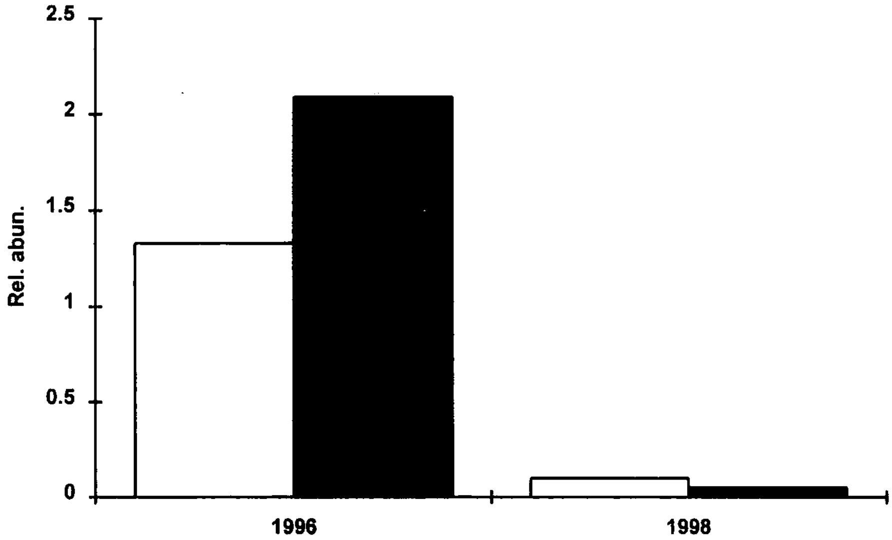
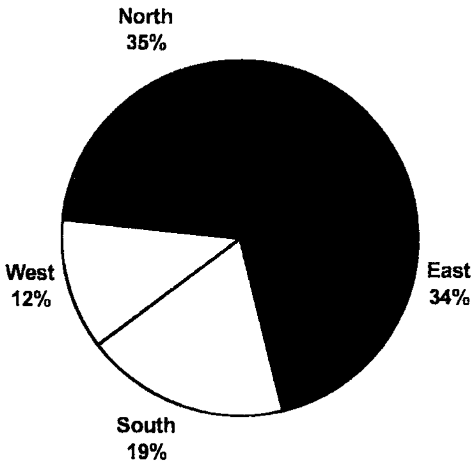
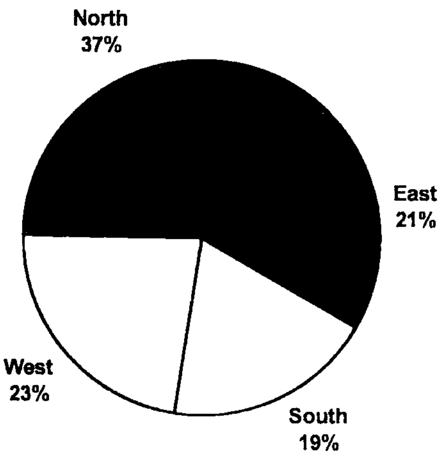


Fig. 5.3. Percentage (%) of adult Arctic Terns and Common Terns returning to Coquet Island with fish from different directions in 1998.

i) Arctic Tern (n = 652)



ii) Common Tern (n = 666)



5.5. Discussion

In the present study the effect of food abundance on the breeding performance of Common and Arctic Terns was measured in only two breeding seasons. However, there are indications from the results of this study that some aspects of tern breeding ecology at Coquet Island were strongly influenced by food availability in these two years.

Results from the present and previous studies show that Arctic and Common Terns are almost entirely reliant on sandeels and clupeids during the chick-rearing period, but that Common Terns feed their chicks on a higher proportion of clupeids (Pearson 1968; Uttley *et al.* 1989). Changes in the rate at which these fish species impinged on the cooling water intake screens at Lynemouth power station indicated that the abundance of sandeels and clupeids in inshore waters around Coquet Island was almost ten times higher in 1996 than in 1998 (Fig. 5.2).

There appeared to be some overlap in the feeding areas utilized by sympatric Arctic and Common Terns during the study (Fig. 5.3) and this agrees with previous data from Coquet Island and elsewhere (Fig 5.3.; Boecker 1967; Pearson 1968; Hopkins & Wiley 1972; Breakwell *et al.* 1998). In the Wadden Sea feeding rates of Arctic terns are higher than those of the Common Terns and observations suggest the former feed further inshore (Frick & Becker 1995). However, Arctic Terns at Coquet Island did show a tendency to fish further offshore than did Common Terns (Fig.5.2). Therefore, it was expected that the breeding performance of Common Terns would be affected more by inshore food abundance than that of Arctic Terns at this colony.

Although foraging distribution around Coquet Island partly explained why Arctic Terns took more sandeels than did Common Terns it was clear that the former preyed on a higher proportion of sandeels than the latter even when fishing in the same area. This suggests either that the two tern species select different prey types or that differences in their foraging techniques (Kirkham & Nisbet 1987) influence which species of fish they normally catch.

Clutch size may be determined by the reserves accumulated by females prior to laying (Ankey & McInnes 1978; Houston *et al.* 1983). Larger clutches are sometimes laid when females are given supplementary food (Hogstedt 1981; Dijkstra *et al.* 1982) but not always (von Bromssen & Jansson 1980; Poole 1985). Nisbet (1977) showed that clutch sizes of Common Terns are related to courtship feeding rates and therefore indirectly to food availability around the colony. Safina *et al.* (1988) similarly showed that Common Terns laid smaller clutches in years of poor food supply. In contrast, Monaghan *et al.* (1989) found no differences between years of high and low food abundance in the sizes of clutches laid by Arctic Terns. At Coquet Island terns of both species laid more eggs per clutch in 1996 when sandeel and clupeid abundance inshore was higher (Table 5.2). Although the results of the present study indicate that clutch size may be influenced by food supply it remains unclear precisely how nutrition limits egg production in terns. Experimental studies involving supplemental feeding and observational studies of courtship feeding and diets are required to clarify this matter. Clutch size is however unlikely to be a sensitive indicator of food supply simply because the integer steps of adjusting clutch size are very crude in birds such as terns which lay small clutches.

In common with the results of some previous studies (Morris 1986; Monaghan *et al.* 1989; Safina *et al.* 1989) but contrary to others (Nisbet 1973, 1977, 1978), there was no difference between years in the sizes of eggs laid by either species in this study (Fig 5.3). In general it appears that these tern species may reduce clutch size rather than egg size in response to annual variations in food supply, probably because egg size was more important in influencing chick survival (Parsons 1970; Nisbet 1973, 1978; Davis 1975; Quinn & Morris 1986; Bolton 1991). Therefore egg size is probably not a good indicator of food supply in terns.

A higher proportion of Arctic Tern and Common Tern eggs were taken by predators in 1998 than in 1996. A consequence of this was that hatching success was lower in 1998 for Arctic Terns (Table 5.2). However, hatching success of Common Terns was similar in the two years (Table 5.2) because whilst predation was responsible for most Common Tern egg losses in 1998, the majority of losses in 1996 were due to infertility or chilling. This suggests that for Common Terns at least, different causes of egg failure are not fully additive.

Black-headed Gulls were the main predators of tern eggs in this study. Terns spend longer away from the nest feeding themselves when food availability is reduced (Frank & Becker 1992) but the proportion of time that eggs are incubated is unlikely to change (Uttley 1992). Therefore, the period of time that eggs are left unguarded is unlikely to be affected by changes in food supply. Increased predation during years of poor food supply may be related to reductions in the prey available to predators (Regehr & Montevecchi 1997; Uttley *et al.* 1989). It is possible that with reductions in the amount of fish available to kleptoparasitic Black-headed Gulls during years of low food abundance, this species exploit tern eggs to a greater degree to supplement it's diet.

Fledging success of Common and Arctic Terns was similar in both years (Table 5.2) indicating that food supply did not fall to the levels which caused high chick mortality in these species (Safina *et al.* 1988; Monaghan e*t al.* 1989). Although egg predation was higher in 1998, the proportions of chicks of both species taken by predators were similar in both years. Predation of tern chicks by Black-headed Gulls is uncommon, especially for older chicks, possibly because tern chicks have the ability to hide when danger approaches and avoid detection or are simply too large for these gulls to handle beyond the first few days post-hatching. Potential predators which take larger tern chicks at other colonies, such as Herring Gulls *L. argentatus* and Great black-backed Gulls *L. marinus* (Nocera & Kress 1996; Becker 1995), were not observed taking tern chicks on Coquet Island in 1996 and 1998 although nocturnal predation by these species cannot be ruled out (Nocera & Kress 1996).

Common Tern chicks have been shown to develop body mass at a much slower rate when food supply is low (LeCroy & Collins 1972; Safina *et al.* 1989; Becker *et al.* 1998). This is thought to be largely due to adults having little extra time to increase foraging effort during the chick-rearing period (Pearson 1968; Monaghan et al. 1989; *Chapter 2*). It has also been shown that captive Common Tern chicks which are fed small amounts of energy develop mass at a slower rate than those which are fed large amounts (Klaassen *et al.* 1992). In 1996, when food availability was higher, Common Tern chicks on Coquet Island developed mass at a higher rate and fledged heavier than in 1998 (Tables 5.4 and 5.5). Although provisioning rates were not measured it is assumed that this was due to lower food supply in 1998 compared to 1996. However, growth rates of structural parameters and fledging sizes of Common Terns were the same in the two years (Tables 5.4 and 5.5). The successful growth of the skeleton and flight feathers may be more important to the survival of the Common Terns chicks than the development of body mass (also see *Chapter 4*), and so structural growth may be more conserved than mass growth. This plasticity in body mass growth may allow resources to be allocated preferentially to the structural growth in years when food supply is poor. As fledging success did not differ between years it appears that Common Terns are able to maintain productivity at the cost of reduced mass growth, which results in lowered post-fledging survival (Coulson & Porter 1985; Hamer *et al.* 1991).

Arctic Tern chicks in Shetland grew at much slower rates during periods of poor food supply and succumbed to starvation prior to fledging (Monaghan *et al.* 1989). Arctic Tern chicks on Coquet Island developed mass at similar rates and fledged at the similar weights in 1996 and 1998 (Tables 5.4 and 5.5). The development of Arctic Tern chick skeletal measurements and flight feathers also progressed at similar rates in both years although skeletal size at fledging was higher in 1998 (Tables 5.4 and 5.5). As fledging success and chick growth rates of Arctic Terns were similar in 1996 and 1998 it appears that inshore food supply had no direct effect on the breeding performance of this species.

It is clear from the results of this study that care must be taken when examining the effects of low food abundance on seabird reproductive success. Terns may be especially useful as indicators of marine fish stocks because they do not utilize offal and other discards to the same extent as other seabirds (Hudson & Furness 1988). During the chick-rearing period Arctic Terns feed further offshore and results from the present study show that changes in inshore food supply did not have an effect on this species. Common Terns are more dependent on inshore fishing grounds than are Arctic Terns and data from this study suggest that although chick mortality did not increase, mass growth rates of Common Terns declined when inshore fish abundance declined. Therefore, Common Tern chick growth rates may be the most sensitive indicator of inshore fish abundance.

Clearly, more years of data are necessary before the relationship between food abundance and Common Tern chick mass growth rates can be quantified. However, such calibration may allow annual variations in inshore food supply to be estimated without the need to monitor fish populations directly. In less intensive studies the number of visits to tern colonies will almost certainly be limited and the accurate assessment of chick age may not be possible. Because structural growth rates of Common Terns are relatively insensitive to food supply and environmental conditions it may be possible to use these measurements as indirect indicators of chick age against which body mass development can be compared.

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Chapter 6

Predation of Arctic Tern chicks by rabbits in Northeast England.

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6.1. Summary

In 1997, Arctic Tern chicks at Coquet Island, northeast England were observed with injuries that were highly characteristic and very similar to those inflicted elsewhere by sheep. Observations at the colony indicated that only chicks 1-5 days old were attacked and that the animals responsible were rabbits, which were probably making up nutrient deficiencies by eating chicks. All attacks eventually proved fatal but losses were low compared to other causes of mortality. We suggest that at Coquet Island, predation of tern chicks by rabbits may be a novel habit involving only a small number of individuals. Nonetheless rabbits breed sympatrically with terns at many colonies and the possibility of such predation occurring elsewhere should not be overlooked.

6.2. Introduction

Recent attention has focused on the impacts of introduced predators on populations of ground-nesting seabirds (Fitzgerald & Veitch 1985; Uttley *et al.* 1989; Ashmole *et al.* 1994; Burger & Gochfeld 1994; Craik 1995) but considerably less attention has focused on impacts of other introduced species. Both domestic sheep *Ovis* and red deer *Cervus elaphus* have been recorded to prey upon nestlings of a variety of species including Arctic Skua *Stercorarius parasiticus*, Arctic Tern *Sterna paradisaea* and Manx Shearwater *Puffinus puffinus* (Wormell 1969; Furness 1988a,b) but to our knowledge there are no records of such predation by other species of herbivore. This chapter describes the likely predation of Arctic Tern chicks by rabbits *Oryctolagus cunniculus* at Coquet Island, Northumberland, northeast England, and assess the likely impact of this predation upon productivity at the colony.

6.3. Locality and methods

Coquet Island (55° 20'N, 1° 32'W) is a small low-lying island situated off the coast of Northumberland, northeast England. About 750 pairs of Arctic Terns nest on the island annually, in grassy areas with a mixed sward including sow-thistle *Sonchus* spp., bugloss *Lycopsis arvenis*, stinging nettle *Urtica dioica* and annual nettle *Urtica urens* that provide cover for chicks after hatching. There are also colonies of other ground-nesting seabirds on the island, including Common Tern *S. hirundo*, Sandwich Tern *S. sandvicensis* and Black-headed Gull *Larus ridibundus*. Rabbits feed in close proximity to nests of all these species, sometimes provoking aggressive responses from breeding adults.

The breeding ecology of Arctic Terns on Coquet Island is monitored annually. In particular, breeding productivity is monitored each year at a sample of *ca.* 130 nests within a walled enclosure attached to the island's lighthouse. Shortly after the onset of hatching in 1997, for the first time tern chicks within this enclosure were noticed which had been attacked in a particularly characteristic manner strongly resembling that recorded at colonies in Shetland by Furness (1988a) as a result of predation by sheep. We therefore made careful searches of the entire tern colony throughout the chick-rearing period and recorded all cases of live or dead chicks showing these mutilations, along with all cases of dead chicks that were not mutilated. We also made observations from a suitable vantage point within the lighthouse complex and recorded the presence of putative predators within the colony. The ages of chicks showing mutilations were determined where possible from measurements of wing or tarsus length calibrated against growth in chicks of known age (J.A. Robinson & K.C. Hamer unpublished data).

6.4. Results and discussion

Chicks that had been attacked (n = 15) had between one and four limbs cleanly severed. In most cases one or both legs had been removed, whilst severed wings were less common. Chicks did not survive these attacks, although in six cases were one leg had been severed when the chicks was first encountered, death occurred several days after the injuries were first recorded. There was no further damage to the body except in two cases where the beak had been severed. The chicks attacked were all newly hatched (1-5 days old) and attacks always coincided with occasions when one or more rabbits had been observed feeding in close proximity to the nest, although we were not able to observe predation events directly.

In total 229 eggs were laid at 130 Arctic Tern nests in the enclosure in 1997. Hatching success was 97%, producing 222 chicks. None of the failed eggs were eaten by rabbits. Fledging success was 46.9% (104 chicks) and of the 118 chicks that died before fledging, 15 (12.7%) had injuries indicative of attack by rabbits. Such injuries were not observed at Arctic Tern nests elsewhere on the island and no other tern or gull species were affected in this way.

There are no sheep or deer at Coquet Island and mammalian predators such as mink *Mustela vison*, otters *Lutra lutra* and hedgehogs *Erinaceus europaeus* are also absent, as are small rodents. Moreover the injuries inflicted on chicks were quite different from those caused by these predators or by predatory birds (e.g. see Craik 1995). The only putative predators observed feeding in the colony were rabbits and the injuries to the terns were highly characteristic of those caused by herbivores at other colonies (Furness 1988a, b). It is therefore highly probable that the injuries inflicted on chicks were caused by rabbits.

The parts of chicks that were removed were those with high bone content but little flesh, skin or feathers, and the method used to extract these parts was very precise and remarkably similar to that adopted by sheep and deer at seabird colonies elsewhere (Furness 1988a, b). The proportion of chicks killed by rabbits was small compared to total chick mortality prior to fledging. However, fledging success was unusually low in 1997 due to a severe and prolonged storm during the second half of the chick-rearing period. Fledging success of Arctic Terns at Coquet Island is usually around 70% (Uttley *et al.* 1989) and in these circumstances predation by rabbits at the level observed in 1997 would represent a substantial proportion of overall chick mortality. Nonetheless only 6.5% of chicks within the walled enclosure were killed by rabbits in 1997 and no such predation was observed anywhere else on the island. This intensity of predation is unlikely to have a large effect on annual productivity at the colony, although it may influence the choice of nest site by terns in future years.

The fact that predation by rabbits was recorded only within the walled enclosure suggests that at most a few individual rabbits were involved, although instances of such predation may have been overlooked elsewhere on the island where longer vegetation made dead or injured chicks harder to locate. The mineral status of rabbits at Coquet has not been investigated but it seems probable that the attacks on chicks were carried out in order to obtain calcium. Coquet is formed of sandstone and most of the dominant plant species are characteristic of poor quality light soils. Sheep and deer that prey upon seabird chicks also appear to use them as a source of calcium (Furness 1988b, Uttley *et al.* 1989) and other herbivores have also been observed to eat animals in order to obtain nutrients not available from plants in nutrient-poor habitats (Wallisdevries 1996).

To our knowledge, killing of birds by rabbits has not been previously documented. This suggests that it is likely to be a rare phenomenon, occurring only in unusual circumstances where rabbits are feeding on mineral-deficient vegetation in proximity to seabirds nesting at high density. Moreover, no chicks were apparently attacked beyond the first week post-hatching, suggesting that older individuals can successfully deter or avoid attack. The same is likely to be true of larger species of seabird. The fact that predation by rabbits at Coquet was apparently confined to a small part of the colony and has not been previously observed there suggests that it may be a novel habit involving only a small number of individual rabbits. Nonetheless rabbits breed sympatrically with terns at many colonies and the possibility of such predation occurring elsewhere should not be overlooked.

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Chapter 7

General discussion

7.1. Life-history traits of Common and Arctic Terns - the relationships between annual productivity, parental foraging capacity and chick requirements

Many of the prime examples of optimization of life-history traits have come from studies of avian clutch size (see Partridge 1989; Roff 1992; Stearns 1992). For terns, the results of this and previous studies have shown that, on average, Common Terns lay larger clutches and fledge more chicks per brood than do the Arctic Terns (Coulson & Horobin 1976; Bullock & Gomersall 1981; Monaghan *et al.* 1989). One of the central aims of this thesis was to determine why these two closely related species differ in this way, by comparing other traits such as the pace of chick development, chick energy expenditure and the rates at which parents deliver food to their offspring. Previous work has shown that the number of Common Tern chicks that can be successfully reared is constrained to some extent by the costs of egg production and incubation to the parents (Heaney & Monaghan 1995). However, little detailed information existed previously on the limiting factors operating during the chick-rearing period.

In *Chapter 2* it was shown that parents of both species have little extra time to increase chick provisioning rates above observed levels (see also Pearson 1968;

Monaghan *et al.* 1989) without increasing the proportion of time that nestlings are left unattended and it was suggested that this constraint on provisioning rate at least partly explained the lower productivity of Arctic Terns. It may be valuable in future years to conduct experiments to reduce the foraging capacity of these species, by clipping flight feathers or adding additional weights to adults, to assess experimentally whether they do normally forage at or near to their maximum sustainable rate. If terns cannot or do not increase the energy they expend during chick-rearing above observed levels, then provisioning rates would be reduced, chicks would develop more slowly and in extreme cases, brood size would need to be reduced.

Nestlings of the two study species developed at similar rates once the effects of body size had been accounted for. Yet Common Terns supplied energy at a higher rate than Arctic Terns in relation to resting metabolism, by delivering larger food items at a faster rate, which was probably achieved by foraging nearer to the colony. Radio-tracking of foraging adults in the future could confirm this apparent difference in the foraging ranges of the two species (e.g. Becker *et al.* 1993). The thermoregulatory costs of Common Tern nestlings were apparently higher than those of the Arctic Terns even though gross costs, neglecting the compensatory effects of parental brooding, were higher for the latter. Heated mounts placed in the nest, which measure energy consumption for thermoregulation (e.g. Klaassen 1994), could be used in the future to examine whether Common Tern chicks do in fact expend a higher proportion of their metabolizable energy intake on keeping warm than do Arctic Tern chicks. Brooding appeared to play a less important role in the energy budgets of Common Tern nestlings, and the number of chicks that Arctic Terns could raise was probably limited not only by the rate at which parents could supply food to the nest but also by the requirements of chicks for brooding. To test this hypothesis more rigorously, one approach might be to increase the brood sizes of Arctic Terns by one and supplementally feed those broods to cover the food requirements of the extra offspring, assuming no reduction in the efficiency of parental brooding. If the costs of thermoregulation were in fact increased, due to a reduction in brooding efficiency, then either the energy allocated to chick growth or chick activity would fall or the brood size would be reduced.

Variations in the phenotypic characteristics of the parents, and especially the female of the pair, are likely to play an important role in reproductive decisions during a breeding season. In some species, age, breeding experience, body size and nutrient reserves prior to egg formation all affect clutch size, timing of reproduction and breeding success (e.g. Perrins 1979; Newton *et al.* 1983; Sydeman *et al.* 1991). In most birds, reproductive performance increases with age in the initial breeding attempts, reaches a plateau at middle age and generally declines in older birds (Clutton-Brock 1988; Newton 1989). One explanation for this age-dependent change in reproductive success is that as residual reproductive value decreases with the age of a bird due to decreased life expectancy or reproductive potential, so the level of reproductive effort should increase with age (Williams 1966). However, this theory of age dependent reproductive effort only holds if all individuals of the same age are equivalent (McNamara & Houston 1996). Wendeln & Becker (1999) demonstrated that the quality of an individual Common Tern, as indicated by its body mass during breeding, was more important than age in determining the success of a breeding attempt indicating a state dependent, rather than age dependent, pattern of reproductive effort. However, prior to the present study the relationship between provisioning rates and chick growth rates (indirect measures of annual reproductive effort) and brood size (an indirect measure of breeding success) in Common and Arctic Terns was poorly understood.

In *Chapter 3* of this thesis I present evidence that Common and Arctic Terns that rear large broods do so by providing more food per brood per day than those rearing small broods but less food per chick per day. If parents were able to adjust brood size exactly in accordance with their foraging capacity, then food provisioning rate per chick would be independent of brood size. This was not the case for Common or Arctic Terns in this study because individual chicks in larger broods received less food per day than those in small broods. This illustrates the inexact nature of the parent tern's ability to adjust their reproductive output. Faced with a high brood size, parents can limit the required increase to their daily workload to some extent by bringing less food per chick which results in slower mass growth. However, this flexibility is limited, because chicks do not seem to reduce their structural growth (see also *Chapter 4*), possibly because they are physiologically incapable, or because the costs to parents and offspring are too high to make it a tenable strategy (i.e. chicks would be of poor quality with low post-fledging survival; Coulson & Porter 1985; Nisbet *et al.* 1995). Because of this limited flexibility in chick growth, parents that still have an excessively high food demand, even with retarded mass growth of chicks, have no option but to reduce the number of chicks, even though they may have some spare capacity for increasing their rate of provisioning. It would be interesting to know if brood reduction occurs in terns because parents preferentially feed particular chicks in the brood during unfavorable conditions or because some chicks in the brood are more successful at obtaining feeds than are others: the asynchronous hatching of broods may facilitate the former by making individual chicks easier to recognize and the latter by creating a size hierarchy within the brood.

Interestingly, parents with small broods do not reduce their food provisioning exactly to match these reduced food requirements. This suggests that retarded chick growth may be costly to parents i.e. slow growth leads to more days of growth before fledging which increases the amount of food required by a nestling in total. Using the equation given by Klaassen *et al.* (1992), which relates growth rate to daily energy intake, it was possible to estimate the amount of energy an individual Common Tern chick on Coquet Island required to reach fledging mass in relation to brood size (Table 7.1). The results show that nestlings from two and three-chick broods require more energy to reach fledging mass than single, rapidly growing chicks. However, costs for two and three-chick broods are remarkably similar.

Table 7.1 The amount of energy required by Common Tern nestlings to reach fledging mass in relation to brood size.

Brood size	Mean growth rate (g d^{-1})	Mean time taken to reach fledging mass (d)	Estimated amount of energy (kJ) required by an individual nestling to reach fledging mass
1-chick	8.42	16.5	1,970
2-chick	7.64	20.0	2,350
3-chick	7.12	21.2	2,330

The relationship between brood size and the condition of adults through the nestling period needs to be quantified in the future in order for these costs to adults to be assessed more directly. In this context, there is some evidence that more experienced adult Common Terns become more efficient at delivering food i.e. they can increase provisioning rate without increasing their daily energy expenditure (Galbraithe *et al.* 1999). It would also be interesting to see if those terns rearing large broods delivered food more efficiently than those with small broods so that any potential cost of increasing brood size to the parent was offset. Supplemental feeding experiments could also be used in the future to determine whether and to what extent parents adjust the rate of food delivery in response to changes in the brood's nutritional requirements. If parents rearing large broods do face a cost in terms of retarded chick growth, then supplementary feeding should result in an increase in chick growth rates before parents reduce their provisioning rates.

Retarded growth may also be costly to the chicks because slower growth reduces nestling and post-fledging survival (e.g. Coulson & Porter 1985; Hamer *et al.* 1991; Nisbet *et al.* 1995) or increases the likelihood of predation before fledging. The evidence from *Chapter 5* and *Chapter 6* suggests that only very young tern nestlings are susceptible to predators and therefore this latter cost may not be high in these two species at Coquet Island. However, the situation may be different at colonies where larger gulls are responsible for taking many larger chicks (Becker 1995; Nocera & Kress 1996). The effects of retarded mass growth on post-fledging survival in Arctic and Common Terns requires attention in the future.

7.2. Plasticity of life-history traits in a stochastic environment

The costs and benefits of reproductive effort vary both spatially and temporally for species which live in changing environments (Partridge 1989). Life-history theory predicts that iteroparous organisms will trade-off current against future reproductive effort so that lifetime reproductive success is maximized (Williams 1966; Winkler & Wilkinson 1988). Reproductive investment, defined as an individual's contribution to the production and survival of current offspring (Low 1978), is likely to be resource limited so when resource levels are low any method by which annual reproductive output could be maximized without increasing the level of parental investment may be selected for. Evidence from Shetland in the 1980s showed that when resources are at exceptionally low levels, terns abandon the breeding attempt when risks to their own survival become too great (Monaghan *et al.* 1989). However, when resources are reduced to a lesser extent, the flexibility of a life-history trait such as chick growth may be adaptive in order to maximize annual productivity, because it permits reduction in the daily amount of energy necessary to fuel development, easing the daily burden on the parents at the expense of increasing energy supply necessary over the entire nestling period. This may be particularly important at times when foraging conditions are unfavorable, when adult terns are likely to be in poorer condition than normal (Monaghan *et al.* 1989; Frank & Becker 1992; Wendeln & Becker 1996) and normal provisioning rates are not achievable. Although Arctic and Common Terns exhibit distinct differences in some of their life-history traits I suggested in the introduction to this thesis that some of these traits may well be flexible enough to compensate for the temporal and spatial changes which occur frequently in the marine environment. The results of this study suggest that chick mass growth is especially flexible in response to these changes in environmental conditions.

The effects of daily and annual variation in food availability on the breeding ecology of Common and Arctic Terns were assessed in *Chapter 4* and *Chapter 5*. Weather conditions can limit foraging success and therefore food availability in these species over short periods of time (LeCroy & LeCroy 1974; Dunn 1973; Dunn 1975; Taylor 1983; Becker *et al.* 1985; Frank 1992; *Chapter 4*). In the present study moderate daily changes in weather conditions had little effect on chick growth in either species, probably because conditions were not as unfavorable for foraging terns as those recorded in previous studies. During a 7-day period of particularly bad weather in 1997 many Arctic and Common Tern chicks died of starvation or hypothermia. However, surviving chicks had been able to retard their mass growth during the period of bad weather, then resumed normal growth when conditions improved, although they did fledge later than those chicks monitored in 1996. Structural growth was maintained during this period presumably at the expense of mass growth retardation or because not doing so would have led to chick death (see above). Hierarchical allocation of resources to different growth parameters is likely to be a means by which those structures which are most important to a bird, such as the skeleton or brain, are protected to some extent from the effects of undernutrition. It remains unknown whether successful structural development confers any advantage to terns once they have left the nest as it does in other species (Boag 1987; Richner *et al.* 1989) and whether chicks that are not nourished sufficiently to be able to develop structural features successfully die during the nestling period. There is clearly some scope for further research in this area.

The effects of annual changes in inshore food abundance on Common and Arctic Tern reproductive performance were assessed in *Chapter 5*. Common Terns caught prey more regularly inshore and exploited a higher number of species, other than sandeels, than did Arctic Terns. Therefore it was perhaps no surprise that, of the two species, Common Terns were affected more by changes in the food available inshore than were Arctic Terns. Food supply in 1998 was not low enough to cause increased chick mortality as has occurred elsewhere (Safina *et al.* 1988; Monaghan *et al.* 1989) but it did have an impact on chick mass growth in Common Terns. By slowing development, Common Tern nestlings were able to survive during a season when food supply was low, without any need for brood reduction. This provides further evidence that the chick growth strategies of marine terns may be related to the unpredictability of their food supply and that growth rate flexibility is an adaptation to maximize annual productivity when food becomes less abundant. Common Terns may have been unable to supply food at the same rate in 1997 as they had in 1996 because food was more difficult to obtain and adults were possibly in poorer condition (Wendeln & Becker 1996). Clutch size may also be affected by annual changes in food supply but this relationship will be difficult to measure until the contribution of courtship feeding to egg production has been more fully assessed.

The impact of predators on reproductive success was assessed in *Chapter 5* and *Chapter 6*. In the year of low food supply it was shown that tern egg predation was particularly high. This was attributed to the behaviour of Black-headed Gulls which may have been forced to exploit alternative food supplies other than those obtained from kleptoparasitism in a year when the food brought back to the colony by terns was limited. Chick predation by gulls was similar in years of good and poor food supply. Predation by rabbits was discussed in *Chapter 6*. Rabbits were shown to have only a small effect on the breeding success of Arctic Terns and probably in only a very small area of the colony. None of the Common Tern nestlings monitored on the island suffered attacks from rabbits. Soon after hatching, tern chicks seem to be too large or too difficult for Black-headed Gulls and rabbits to handle; predation of older chicks was thus rare and was apparently independent of marine food supply.

7.3. Growth rates in comparison with other species

Compared to more pelagic seabird species, the nestlings of nearshore foraging marine terns develop rapidly for their size (Ricklefs 1979, 1990). It is possible that this rapid development is an adaptation to reduce the time that nestlings spend in the nest when they are most susceptible to land-based predators (Lack 1968; Craik 1995). However, most predation of tern chicks occurs in the first few days after hatching, and so the selective pressure to grow fast from this factor may not be great. The rapidity of tern development in comparison to more highly pelagic species is almost certainly linked at least in part to the rate at which food can be delivered to the nest. The constraints imposed by a short breeding season may also favour high growth rates in these small migratory terns. Both species return to British colonies in late April, lay eggs in early May and nestlings start to fledge from around the middle of June (Cramp 1985). Although failed breeders often relay, second broods are exceptionally rare and migration back to wintering grounds begins soon after the chicks have fledged. Food supply may also decline later in the season. This time constraint may favour those terns which can complete the breeding period quickly so that fledglings can practice flight and foraging techniques before the long flight ahead of them.

7.4. General Conclusions

Arctic and Common Terns differ consistently in annual productivity and this can be explained by differences between species in foraging areas and food provisioning rates of parents and in the brooding requirements of nestlings. Within species, parents supply food at a higher rate to larger broods but chicks develop mass more slowly than those in smaller broods. There may be costs associated with retarded growth to both the parents (increased energy demand over the entire nestling period) and to the chicks (reduced survival). Both species are affected by temporal changes in environmental conditions and predation at the breeding grounds and are equally well adapted to the foraging constraints imposed by short periods of bad weather and changes in annual food supply. Under adverse conditions, adults reduce their food provisioning rates an chicks exhibit retarded growth which protracts the fledging period. This adaptation maximizes annual productivity but there may be costs to the chick and adults similar to those associated with retarded growth of chicks in large broods.

This thesis deals only with life-history traits that can be measured during the breeding season. To fully understand the breeding strategies of Arctic and Common Terns I suggest that long-term studies measuring the relationship between annual reproductive investment and lifetime reproductive success in these species are required. This type of research would hopefully provide answers to some important questions which I was unable to cover. For example, does annual reproductive output influence lifespan in these species, and are differences in annual productivity between individuals consistent between years (e.g. Coulson & Porter 1985; Catry *et al.* 1999; Wendeln & Becker 1999). With the wealth of information already gathered on the breeding ecology of terns and their robustness to intensive studies I suggest they will continue to provide excellent species for testing predictions of life history theory for some years to come.

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