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LIVING WITH GULLS

Eric W.M. Stienen

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RIJKSUNIVERSITEIT GRONINGEN

LIVING WITH GULLS
Trading off food and predation in the Sandwich Tern *Sterna sandvicensis*

PROEFSCHRIFT

ter verkrijging van het doctoraat in de
Wiskunde en Natuurwetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de
Rector Magnificus, dr. F. Zwarts,
in het openbaar te verdedigen op
vrijdag 20 januari 2006
om 14.45 uur

door

Eric Willem Maria Stienen

geboren op 21 januari 1967
te Melick en Herkenbosch

Promotor: Prof. Dr. R. H. Drent

Contents

Voorwoord

Wanneer ik de uren optel die ik turend door een kleine opening van een schuiltent aan de rand van een sternenkolonie of bij een baltsplaats op Griend heb besteed en wanneer ik daarbij de uren bij optel die ik schuilend in Afrikaanse, Deense en Belgische kolonies heb doorgebracht, kom ik tot de conclusie dat ik ten minste een half jaar van mijn leven heb doorgebrcht in een tochtige ruimte niet veel groter dan 1 m^3. Toch heb ik het altijd als een enorm voorrecht ervaren dat ik het dynamische kolonieleven van de Grote Stern van zo dichtbij mocht aanschouwen. De nooit aflatende strijd om voedsel die wordt gevoerd tegen de elementen en de natuur, en vooral de strijd met en tegen de kokmeeuwen blijft fascineren. Na 13 jaren onderzoek aan Grote Sterns heb ook ik leren leven met meeuwen.

Ik heb Griend eigenlijk bij toeval leren kennen in mijn studententijd aan de Katholieke Universiteit van Nijmegen toen Piet van Tienen mij in 1990 vroeg om een doctoraalstudie naar energiebehoefte van sterns te doen. Hoewel ik toen dacht voorbestemd te zijn om aquatisch oecoloog te worden, trok het primitieve leven op een onbewoond eiland temidden van vele tienduizenden vogels me enorm aan. Dankzij en met Piet, heb ik een onvergetelijke tijd op Griend beleefd.

Marcel Klaassen heeft mij geïntroduceerd in het sternenonderzoek op Griend. Zijn passie voor en bedrevenheid in dierecologisch onderzoek heb ik zeer gewaardeerd, Marcel heeft daarmee de basis gelegd voor mijn blijvende fascinatie voor de ornithologie. Het is Jan Veen geweest die me vanwege mijn weigerachtigheid tegenover legerdienst de mogelijkheid heeft geboden om een onderzoek naar de Grote Stern te starten. Hij kreeg het in 1992 voor elkaar dat ik - in het kader van een literatuurstudie nota bene - drie maanden het vogelleven op Griend kon bestuderen en ook nog eens twee maanden onderzoek kon doen naar overwinterende sterns in Guinee Bissau. Jan heel erg bedankt voor de mogelijkheden die je me hebt geboden en de uiterst prettige manier van samenwerken.

Heel veel heb ik te danken aan Allix Brenninkmeijer. Met veel plezier denk ik terug aan de zomers die we samen hebben doorgebracht op Griend, de expeditie naar Guinee Bissau, werkbezoeken aan Duitsland en Denemarken, of gewoon de tijd samen met de andere collega's op het instituut in Arnhem en later in Wageningen. Zijn ervaring met vogelstudies, zijn werklust, positieve levenshouding en vriendschappelijkheid waren onmisbaar. Zonder zijn inzet was dit boekje nooit tot stand gekomen.

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De noodzakelijke, maar niet altijd vanzelfsprekende wekelijkse bevoorrading met voedsel, drank, post en gasten vanaf Terschelling werd tijdens de eerste jaren op Griend verzorgd door Cees de Boer en na zijn overlijden overgenomen door Dirk de Boer, Dirk van Hollik en Peter van Tellingen. Ook de bemanning van de Phoca (Dirk Kuiper en Jan van Dijk) en de Rijkspolitie te Water te Harlingen vonden we vaak bereid om mensen of materialen over te zetten van of naar het vasteland.

Heel veel collega-onderzoekers, studenten en vrijwilligers hebben geholpen tijdens het veldwerk en hebben feitelijk grote delen van de onderliggende gegevens gegenereerd, genoteerd of gedigitaliseerd. Anne-Jelle Lyklema à Nijholt, Arie Spaans, Aswin Bouwmeester, Chris Klok, Frank Hoffman, Gijs Doeglas, Hans Schekkerman, Hans van den Berg, Jan de Jong, Jan van der Kamp, Jan Veen, Johan Krol, John Habraken, John Schobben, Joost Roelse, Karin Geschiere, Noël van Rens, Maaike Raaijmakers, Marcel Kersten, Marcel Klaassen, Paul Erftemeijer, Peter van Beers, Peter Boerkamp, René Oosterhuis, Teun Baarspul, Thor Veen en Wouter Bulthuis heel erg bedankt voor jullie inzet. Uiteraard waren Thea Smit en Wilma Dijkman onze meest trouwe bezoekers. Zonder hun steun in aan- en afwezigheid was dit onderzoek niet mogelijk geweest.

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Chapter 1

General introduction

RATIONALE FOR THE STUDY

The low-lying, sandy areas along the Dutch coast offer important breeding opportunities for Sandwich Terns *Sterna sandvicensis*. Throughout the twentieth century Sandwich Terns nested here in fluctuating numbers. The Dutch population suffered from a major kill in the 1960s due to pesticide pollution causing the number of breeding pairs to drop from over 35 000 in the 1950s to 875 in 1965. After the spill of pesticides had stopped the numbers slowly increased but after 40 years the population has not yet fully recovered. The slow and incomplete recovery of the Dutch population was a source of concern and the present study aimed at a better understanding of the factors regulating the size of the Dutch Sandwich Tern population. Following the crash in 1960s, the size of the Dutch population positively correlated with the amount of young herring present in the North Sea (Brenninkmeijer & Stienen 1994). This relationship suggests that the Dutch Sandwich Tern population is limited by food availability. For this reason we concentrated the study on the feeding ecology of Sandwich Terns, hoping to find links with population dynamics.

OUTLINE OF THE THESIS

In this thesis, I concentrate on the feeding ecology of Sandwich Terns during the breeding season and how Black-headed Gulls *Larus ridibundus* interfere with the food input into the colony and consequently shape the foraging decisions of the terns. The impact of variation in food availability and the impact of the gulls are dealt with in terms of fitness costs. Although some data were gathered in a Danish breeding colony and some in the wintering areas of the terns, the study is largely based on observational data that were gathered in the breeding colony on Griend, The Netherlands. This island of about 57 ha is situated in the Dutch part of the Wadden Sea, and harbours Europe's largest population of Sandwich Terns. During the study period (1992-1999), the number of pairs fluctuated between 5,000 and 8,300, but further increased afterwards to 11,275 pairs in 2004. For the study I could elaborate on the study of Veen (1977), who very precisely described various functional aspects of the nest distribution in Sandwich Terns on Griend. Veen studied the associative nesting behaviour of the terns and found that the non-aggressive terns profit from the presence of Black-headed Gulls (or other aggressors) for the protection of their eggs and chicks. For that reason Sandwich Terns intentionally settle near or in the middle of a Black-headed Gull colony. The associative nesting with the gulls means that the gulls themselves sometimes rob a tern egg or a chick and steal fish that is meant for the tern chicks.

During the breeding season Sandwich Terns are highly gregarious and breed in large, very dense colonies. Within a (sub)colony egg laying is highly synchronised and consequently most chicks hatch at about the same date. The chicks are semi-precocial and some days after hatching the social structure of the colony slowly disintegrates. Parents and their chicks start walking around and seek new hiding places; first inside the colony but soon also in its direct surroundings. This behaviour makes it very difficult to study individual chick feedings and growth for a longer period. Previous studies on feeding ecology of Sandwich Tern chicks therefore only describe short periods and often involved smaller chicks (e.g. Pearson 1968, Isenmann 1975, Veen 1977, Campredon 1978, Garthe & Kubetzki 1998). To prevent the chicks from leaving the colony site we held them inside enclosures of chicken wire, where they could be followed from hatching until fledging.

Food specialists

Being strictly piscivorous, Sandwich Terns are near the top of the marine food chain. They predominantly feed on an exclusive diet dominated by a few marine fish species with a high nutritive value. This restricted choice makes them extremely vulnerable to variation in the abundance and/or the availability of their food. This makes the Sandwich Tern a good indicator of the prevailing food situation. In **chapter 2** we describe some general patterns in the amount and the composition of the food that is transported to the Sandwich Tern colony on Griend. Due to the specialised food choice of the parents and the fact that they bring fish to the colony one by one, changes in the availability of the prey fish are likely to be instantly reflected in the diet composition of the chicks.

Kleptoparasitising gulls

Sandwich Terns are single prey loaders that carry the fish one at a time to their nestlings holding it crosswise in the bill with the fish's head held on one side. The feeding areas may be up to 25 km from the colony and in some colonies even further. When arriving in the colony prey-carrying parents are often heavily attacked by Black-headed Gulls that try to steal the fish. Prey stealing or kleptoparasitism is relatively common in seabirds (Brockmannn and Barnard 1979, Furness 1987). Gulls are frequent kleptoparasites, whereas species that nest in highly concentrated colonies and conspicuously carrying their prey are frequent victims (Brockmann and Barnard 1979, Duffy 1980, Barnard and Thompson 1985). Sandwich Terns evoke kleptoparasitism even more than other hosts, because they intentionally seek the presence of Black-headed Gull colonies to build their nests. As a consequence they are forced to live with the consequences of high rates of food loss to kleptoparasitising Black-headed Gulls. In **chapter 3** the consequences of the prey stealing behaviour of the gulls are treated from the perspective of a tern chick. We describe how prey stealing evolves with the aging of the tern chicks and how it depends on the food choice of the adult terns as well as on weather conditions. Finally the effects of prey loss to the gulls are expressed in terms of growth and survival of the chicks.

It is assumed that animals seek to maximise forage intake and that individuals that forage more effectively than others will be at an advantage (Schoener 1971, Krebs 1973, Charnov 1976). Animals that must return to a central place in order to feed their young are restricted by travel time costs because they must perform round-trips between the breeding ground and the foraging patches. Single prey loaders must return to a central place each time they catch a prey and are thus even more restricted (Orians and Pearson 1979, Lessels and Stephens 1983). Sandwich Terns are specialist central place foragers with a restricted choice of prey species and prey size. They are single prey loaders that perform long foraging trips and face additional costs of losing prey to kleptoparasitising gulls when arriving in the colony. In **chapter 4** it is explained how this influences the foraging decisions of Sandwich Tern parents nesting on Griend. Parent terns are largely able to buffer fluctuations in food availability and counterbalance the negative effects of the food losses to the gulls.

Birds have adopted several behavioural strategies to reduce food loss through kleptoparasitism (Barnard 1984). They may tolerate the losses, compensate for them by increasing their foraging effort or evade the attacks. The avoidance strategy includes faster handling of prey, shifting the diet, synchronizing feeding activities and increasing the distance from the pirates (Amat 1990). Sandwich Tern parents often lead their chicks away from the nesting site (Cullen 1958; Chestney 1970; Veen 1977, Campredon 1978) and thus away from the kleptoparasitising gulls, but the reason for this behaviour is not well understood. In **chapter 5** we experimentally tested whether leaving the colony site might be an evasive strategy that leads to a reduced incidence of robbery by the gulls.

Because seabirds depend on highly unpredictable food resources that show large temporal and spatial variations one would expect them to be very flexible in the growth of their chicks. In many bird species slow growth can, however, increase chick mortality and may have negative effects on post-fledging survival or recruitment (Gebhardt-Henrich & Richner 1998). In **chapter 6** the fitness consequences of growth rate variation in Sandwich Tern chicks are explored. We suspected that the chicks had wide margins within which body mass could vary without having strong effects on pre- or post-fledging mortality. We also examined if variation in growth rate during the nestling phase had effects on the size an individual reached as an adult. In **chapter 7** we focus on the various causes of chick loss in relation to the laying sequence of the egg from which the chick originated and the chick's rank within the brood. We try to answer the question why Sandwich Terns that lay normally two egg-clutches seldom raise two chicks to fledging.

Wadden Sea versus wintering area

Sandwich Terns spend most of the year in the wintering areas and only a few months in the breeding colonies. Most European Sandwich Terns winter along the west coast of Africa, with Ghana and Senegal being the major strongholds (Müller 1959, Møller 1981, Noble-Rollin & Redfern 2002). A minority of the birds spend the winter in The Mediterranean and some travel around South Africa to winter along the African east coast. In chapter 8 we search for evidence of food stress in the wintering areas and for that reason we studied the feeding ecology of terns in the coastal waters of Guinea Bissau. These waters hold important numbers of western Palaearctic terns as well as local tern species. The different feeding strategies of Little Tern *S. albifrons*, Sandwich Tern and Royal Tern *S. maxima* are discussed and placed in an energetic context.

In the final chapter of this thesis the underlying causes for population fluctuations in the Sandwich Tern are examined in the light of my own study. My conclusion is that the recovery of the Dutch population after the collapse in the 1960s due to the pollution of the coastal waters with organochlorine was initially halted by poor prey stock availability. Afterwards, marked changes in the Dutch Wadden Sea population correlated with fluctuations in the availability of herring and sprat indicating that the growth of the population is limited by the availability of prey fish. The distribution of Sandwich Terns over the different populations in Europe is probably determined by changes in the North Atlantic Oscillation being the driving force that changes the distribution and composition of fish stocks in the North Sea and ultimately determines food availability for European Sandwich Terns.

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Chapter 2

Reflections of a specialist: patterns in food provisioning and foraging conditions in Sandwich Terns *Sterna sandvicensis*

Eric W.M. Stienen, Peter W.M. van Beers, Alex Brenninkmeijer, John M.P.M. Habraken, Maaike H.J.E. Raaijmakers & Piet G.M. van Tienen

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ASTRACT

Highly specialised piscivorous seabirds, like Sandwich Terns *Sterna sandvicensis* have limited capacity to switch to alternative prey species when the availability of a particular prey species is low. Therefore, variations in the diet of such species are likely to reflect fluctuations in food availability. We studied food provisioning of Sandwich Tern chicks on Griend in 1992-98. The chicks were predominantly fed with Clupeidae and Ammodytidae. About 75% of the fish brought to the colony were eaten by the chicks. The rest was lost, mainly to robbing Black-headed Gulls *Larus ridibundus*. Parents met the increasing energy demands of the growing chicks by adjusting prey size, rather than increasing the rate of prey transport to the chicks. Distinct patterns in food transport rate, diet composition and prey size were associated with weather conditions and diurnal or tidal rhythms. Food transport to the colony was severely curtailed by strong winds, but was also relatively low at low wind speeds. Wind speed also had a large impact on prey size and diet composition, with a decreasing proportion of Clupeidae brought to the chicks as foraging conditions became worse. Distinct diurnal rhythms in food transport coincided with diel vertical migration patterns in Clupeidae and Ammodytidae. Clupeidae were mostly brought to the colony early in the morning and late in the evening, while the transport of Ammodytidae was highest around noon. Tidal patterns in food delivery rate were probably related to tide-specific foraging areas used by the terns. A fish-monitoring programme showed considerable variation in food abundance within the foraging area of the terns. Especially Clupeidae had a patchy distribution and most clupeids were caught in the coastal areas around Vlieland. In accordance to the pattern found in the colony, Clupeidae caught in 1996 and 1997 towards fledging of the chicks and in 1998 just after hatching of the chicks in 1998 were relatively small.

INTRODUCTION

Seabirds are highly susceptible to changes in food availability, in particular during the breeding season, when they are confined to feeding areas relatively close to the colony, and perhaps work close to the limits of their capacity. They have evolved several life history strategies that may help to overcome difficulties in foraging. Compared to other birds, seabirds lay smaller clutches, have a delayed maturation and are long-lived (Lack 1968). Moreover, they often breed in dense colonies, which may enhance their chances of finding sufficient food for their offspring when food is irregularly distributed (Evans 1982; Waltz 1987; Götmark 1990). Despite these adaptations several well-documented cases describe marked changes in breeding performance and population size of seabirds due to the collapse of components of their food stock (e.g. Heubeck 1988; Monaghan *et al.* 1989; Vader *et al.* 1990; Bailey 1991; Suddaby & Ratcliffe 1997). Generalists among seabirds may be able to buffer fluctuations in the availability of a particular prey species by switching to alternative prey. Highly specialised piscivorous seabirds like Sandwich Terns *Sterna sandvicensis*, however, face the disadvantage of restricted choice, which makes them particularly vulnerable to temporal and spatial variation in one of their food components. During the breeding season, Sandwich Terns predominantly feed on a few high quality prey species (e.g. Isenmann 1975; Campredon 1978; Shealer 1998); in the southern North Sea these prey are mainly *Clupeidae* and *Ammodytidae* (Pearson 1968; Veen 1977; Garthe & Kubetzki 1998).

Many marine fish exhibit a specific rhythmicity of activity (Thorpe 1978). Diurnal and tidal patterns in the behaviour of the fish may force seabirds to adjust their activities to the cyclic behaviour of their prey in order to raise successfully their chicks (Daan 1981). Short-term changes in the accessibility of one of the Sandwich Tern's prey species must be tackled with proper switching to other foraging areas or alternative prey. Because Sandwich Terns are single prey loaders, such shifts, if noticeable, will almost instantly be noticed in the diet of the chicks. Food provisioning to a tern colony is not only dictated by the energy requirements of the chicks (Klaassen *et al.* 1992), but as shown by various studies is also influenced by environmental conditions. Distinct diel and tidal rhythms in food transport to the colony have been described, and both food intake rate and growth of the chicks have been related to adverse weather conditions that influence fishing success of the parents (Pearson 1968; Dunn 1972, 1973; Veen 1977; Campredon 1978; Taylor 1983). However, nearly all these studies covered only a small part of the chick-rearing period. Only Veen (1977) compared the presence of different prey species in the chick diet over a period of 3 years. Our 7-year study on Sandwich Terns breeding on Griend, Dutch Wadden Sea, allows a detailed analysis of parameters affecting prey size and food delivery rate, and patterns in food transport will here be discussed in relation to changes in the availability of the prey fish.

STUDY AREA AND METHODS

The isle of Griend, The Netherlands (53°15'N, 5°15'W), is situated in the centre of the western Dutch Wadden Sea (Fig. 2.1). The small island (about 57 ha during normal high tide) is inhabited by several species of colonial nesting terns and gulls. The Sandwich Tern's feeding ecology was studied during the breeding season of 1992-98. During the study period the population of Sandwich Terns fluctuated between 5600 (1996) and 8300 (1994) pairs, consisting of several subcolonies. In each year part of a subcolony, containing 50-100 nests, was fenced (further referred to as 'enclosure') to prevent the chicks from walking away from the nest site.

Chicks hatched in the enclosures were ringed and aged immediately after hatching. Each year, about 20 chicks were colour-marked for individual recognition. Data on chicks' diet were collected from an elevated blind, placed at a few metres from the colony. Continuous observations on food provisioning were made from 4:30 a.m. to 10:30 p.m. In most years chicks were followed from hatching until fledging. Only in 1992, chicks were followed until 21 days and in 1995 the age of the chicks ranged from 15-26 days. Prey size was estimated in quarters of the parent's bill size (BL = 5.43 ± 0.25 cm, N = 679). Estimating prey size was calibrated per observer by holding fishes of

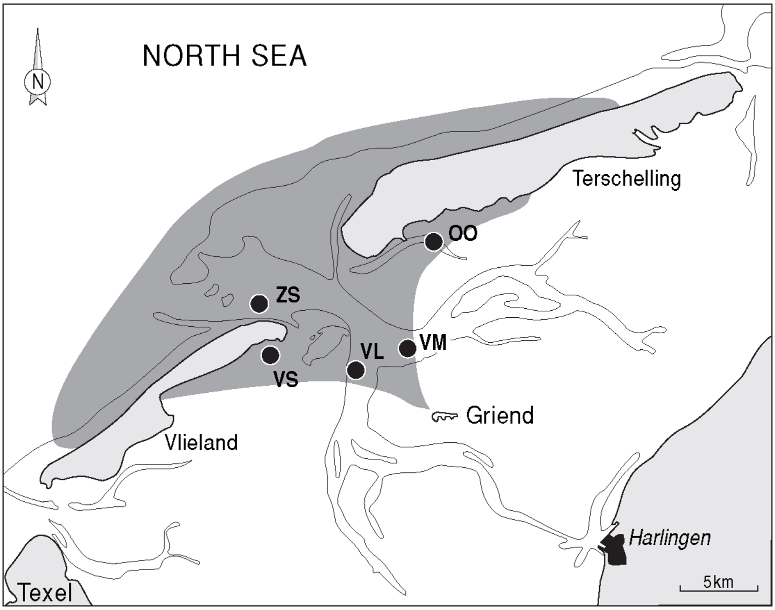

Figure 2.1. Map of the western Wadden Sea, indicating the location of Griend and the fish sampling points (dots). The grey area roughly indicates the foraging area of the Sandwich Terns breeding on Griend. ZS = Zuider Stortemelk, VS = Vliesloot, VL = Vliestroom, WM = West Meep and OO = Oosterom.

different species and various lengths in front of a stuffed tern's bill at distances comparable to the situation in the colony. Calibration greatly increased the accuracy of the estimates, and the largest error an experienced observer ultimately made was 0.25 BL. Both for *Clupeidae* and *Ammodytidae* an allometric equation relating fish length to fresh mass was obtained, using least square analysis on fish found in the colony and fish sampled in the Wadden Sea in 1993 and in 1994 (Fig. 2.2). We use the term 'delivery rate' when referring to the number of food items brought to the chicks and the term 'mass provisioning' when referring to the amount of mass brought to the chicks. Throughout the experimental work we recorded wind speed with a calibrated cup anemometer at standard meteorological level (10 m).

In 1995-98, a fish-sampling programme was performed at five locations in the foraging area of the terns (Vliestroom, Westmeep, Stortemelk, Vliesloot and Oosterom; Fig. 2.1). The locations covered an important part of the foraging area of the Sandwich Terns breeding on Griend. Fish sampling periods corresponded with the courtship period (end of April), the early chick stage (first week of June) and the late chick stage (end of June) of the terns. We used an Isaac's Kidd Midwater Trawl net (IKMT-net) with a mesh size of 6 mm that sampled only the upper 2 m of the water layer, in accordance with the diving depth of terns (Borodulina 1960; Dunn 1972). Each haul lasted approximately 30 minutes. The volume of water passed through the IKMT-net was measured by means of a flow meter mounted in the mouth of the net. Catches were converted to numbers per 10,000 m^3 water.

To avoid an unrealistic bias of observation duration, only when observations on fish brought to the chicks lasted more than 30 minutes (effects of time of day and wind speed) or more than 9 hours (age effects) were they used in the graphs. Unless otherwise indicated, for statistical tests all data were used, using protocol duration as offset

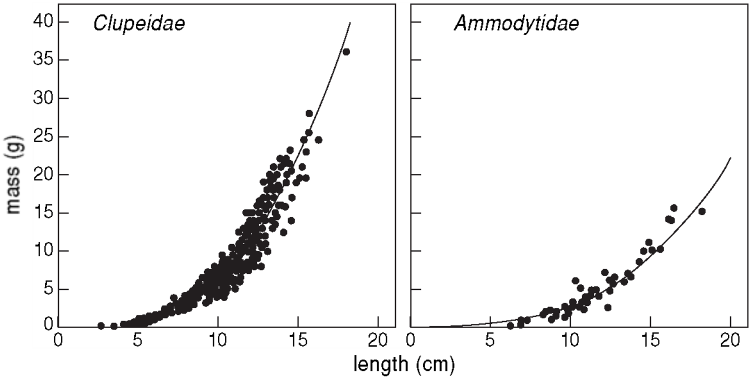

Figure 2.2. Length-mass relationship in herring and sandeel found in the colony in 1992-97 and sampled in the Wadden Sea in 1993-94. Herring: fresh weight=0.00682*length$^{2.996}$ (n = 825, r^2 = 94.0); sandeel: fresh weight=0.00296*length$^{2.982}$ (n = 73, r^2 = 97.4).

variable. For logistic regression analysis of the effects of hatching order, year, time of day, wind speed, age of the chicks and tide on delivery rate or mass provisioning rate data were separated into 1 hour periods (only periods lasting more than 30 minutes) using protocol duration as offset variable. Statistical tests were performed using the SPSS/PC+ 4.0 (Norusis 1990) and the Genstat statistical package (Genstat 5 Committee 1993).

RESULTS

Diet composition and prey size

In 1992-98, food brought to the colony mainly consisted of *Clupeidae* (herring *Clupea harengus* and sprat *Sprattus sprattus*) and *Ammodytidae* (sandeel *Ammodytes tobianus* and greater sandeel *Hyperoplus lanceolatus*). In total these prey species amounted to 99.3% of the diet (Table 2.1). Unless otherwise stated, we further use the term 'herring' when referring to *Clupeidae* and 'sandeel' when referring to *Ammodytidae*. Other prey species consisted of goby *Gobies* spp., cod *Gadus morhua*, whiting *Merlangius merlangus*, smelt *Osmerus eperlanus*, eelpout *Zoarces viviparus*, three-spined stickleback *Gasterosteus aculeatus*, pipefish *Sygnathus* spp., sea lamprey *Petromyzon marinus*, flounder *Platichthys flesus*, cephalopods *Sepia* spp. and brown shrimp *Crangon crangon*. Prey species other than herring and sandeel will only be included in this paper if relevant.

The size of the herring and sandeel provided to the chicks varied between 0.25 BL and 4.00 BL (Fig. 2.3), corresponding with 1.5-21.5 cm and 37 g as a maximum. On average sandeel were somewhat longer than herring (1.98 ± 0.42 BL and 1.59 ± 0.31 BL, respectively; two-directional Student's t-test, $t = 63.27$, $P < 0.001$), corresponding with 11 and 9 cm, respectively, and prey masses of 3.5 g and 4.5 g, respectively. Prey size significantly differed between years (Table 2.2), with relatively small herring brought to the colony in 1996 and 1998 and relatively small sandeel in 1993. Both herring and sandeel were relatively long in 1995, but this was partly an effect of the age of the chicks followed in that year. However, if effects of chick age and other effects influencing prey size were taken into account, year effects are still present (Table 2.3), but then sandeel appeared to be relatively small in 1995.

Table 2.1. The proportion of herring, sandeel and other prey species in the chicks' diet on Griend in 1992-98.

	1992	1993	1994	1995	1996	1997	1998
Herring	49.5	55.0	84.0	69.7	32.7	79.0	63.3
Sandeel	49.7	44.7	14.9	29.8	66.6	20.3	36.0
Other	0.8	0.3	1.1	0.5	0.7	0.7	0.8
Total number of fish	630	3469	3279	1290	3262	2579	2520

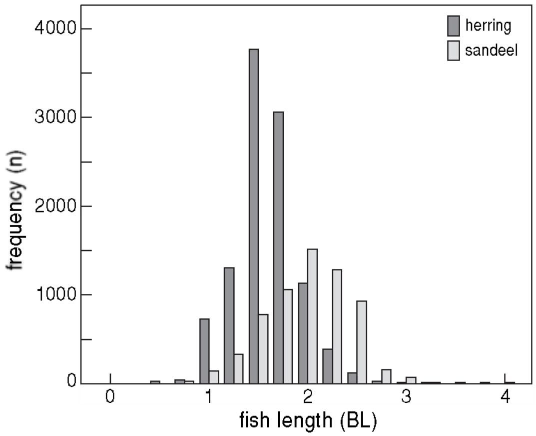

Figure 2.3. Length distribution of herring and sandeel brought to the chicks on Griend in 1992-98. BL = bill length of adult terns.

Table 2.2. Variation in prey size (BL) of Sandwich Tern chicks on Griend in 1992-98. Scheffé-test denotes significant differences ($P < 0.05$) with other years.

Year	Mean herring length± SD	Scheffé-test $F_{6,10373} = 171.39$	Mean sandeel length ± SD	Scheffé-test $F_{6,6263} = 71.66$
1992	1.63 ± 0.31	98,96	2.08 ± 0.34	93,98
1993	1.63 ± 0.30	98,96,94,97	1.83 ± 0.38	
1994	1.59 ± 0.29	98,96	2.17 ± 04.6	93
1995	1.86 ± 0.30	98,96,94,97,92,93	2.12 ± 0.32	93,98,96
1996	1.51 ± 0.30		2.02 ± 0.40	93
1997	1.59 ± 0.19	98,96	2.09 ± 0.40	93,98,96
1998	1.49 ± 0.41		1.96 ± 0.46	93

Fate of fish brought to the colony

Of all fish brought to the colony (n = 17,029) on average 69.8% were eaten by the chicks (Table 2.4). Most fish that were not eaten by the chicks was robbed by Black-headed Gulls *Larus ridibundus* (18.7%) or disappeared out of the observer's sight (7.9%). Some fish were robbed by neighbouring Sandwich Terns, but each year this was less than 2% of the total number of fish. Occasionally other species, mainly Common Gulls *L. canus* and Common Terns *S. hirundo*, succeeded in robbing fish of arriving Sandwich Terns. Some fish fell in the nest or was eaten by the parent (in total 2.9%). The latter could be divided into fish eaten by the parent under pressure of the robbing gulls (1.0%) and for

Table 2.3. *P*-values of multiple or logistic regression analyses examining the effects of hatching order (single chick, first hatchling, second hatchling), year (1992-98), time of day (hour 4-22), wind speed (in m s^{-1}), chick age (in days) and tide (hours before and after high tide) on the length of herring and sandeel (multiple regression, n = 9957 and 5901, respectively), the number of herring and sandeel and the total number of fish (poisson distributed logistic regression, n = 35983, 35004 and 35004, respectively) and mass (multiple regression, n = 35004) provisioned to Sandwich Tern chicks on Griend. For the analysis of the provisioning rate of herring and total prey hour 4 was omitted because of the deviate pattern (see text). Similarly hour 4-5 were omitted from the analysis examining the patterns in mass provisioning.

		Prey length		Number of prey			
Parameter	df	Herring	Sandeel	Herring	Sandeel	Total	Prey mass
Hatching order	2	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Year	6	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Time of day	1	< 0.001	< 0.001	NS	< 0.001	< 0.001	NS
Time of day2	1	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Wind speed	1	NS	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Wind speed2	1	< 0.001	< 0.001	< 0.01	< 0.001	< 0.001	< 0.001
Age	1	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Age2	1	< 0.001	< 0.001				
Tide	11	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Table 2.4. Fate (%) of fish brought to Griend by Sandwich Terns in 1992-98.

	1992	1993	1994	1995	1996	1997	1998
Eaten by chick	81.0	72.6	70.4	80.3	63.9	72.1	64.2
Robbed by Black-headed Gull	11.4	16.1	20.5	14.7	22.9	11.6	24.0
Robbed by Sandwich Tern	1.0[1]	1.6	0.8	0.2	0.5	0.1	0.1
Robbed by other species		0.1	0.2	0.0	0.1	0.1	0.0
Disappeared out of sight	5.1	6.9	5.4	4.1	11.5	8.6	9.4
Left in nest			0.4	0.1	0.2	0.6	0.4
Eaten by parent (gull pressure)	1.6[2]	2.7[2]	1.6	0.4	0.5	0.5	1.7
Eaten by parent (other reason)			0.7	0.2	0.6	6.4	0.2
Total number of fish	630	3469	3279	1290	3262	2579	2520

[1] no distinction made between 'robbed by Sandwich terns' and 'robbed by other species'

[2] no distinction made between 'eaten by parent under gull pressure' and 'eaten by parent because of other reasons'.

other reasons (1.6%). Prey size differed between the various categories of fate (Fig. 2.4). Fish robbed by Black-headed Gulls were significantly larger than fish eaten by the chicks, and fish lost from view were larger than fish eaten by the parents (Scheffé-test, herring and sandeel F = 66.6 and 84.7, respectively, $P < 0.05$).

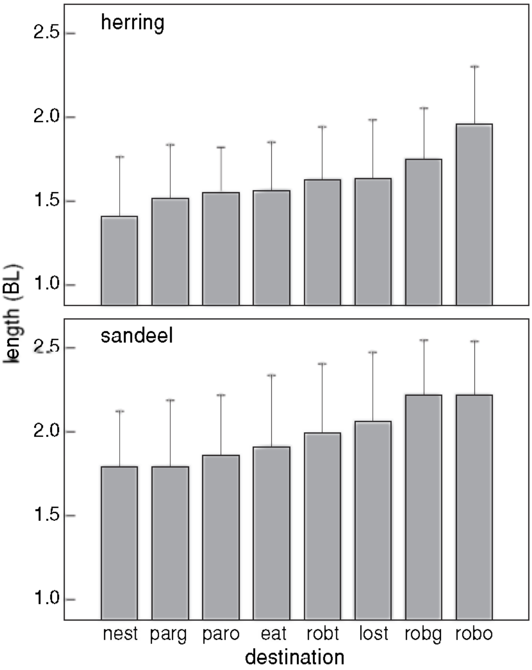

Figure 2.4. Length of herring and sandeel (mean ± SD) brought to the chicks on Griend in 1992-98 according to the fate of the fish. Nest = fallen in nest, parg = eaten by parent as a result of gull pressure, paro = eaten by parent for other reasons, eat = eaten by chick, robt = robbed by Sandwich Tern, lost = disappeared of the observer's sight, robg = robbed by Black-headed Gull and robo = robbed by other species.

Food provisioning in relation to the age of the chicks

In 1994 and 1996, prey delivery rate significantly increased towards the end of the chick-rearing period (Pearson regression, $r^2 = 0.03$, $P = 0.003$ and $r^2 = 0.45$, $P < 0.001$, respectively). In 1994, however, the increase was small. In all other years, there was no general trend or delivery rate slightly decreased (1998) with ongoing age of the chicks (Pearson regression, $r^2 = 0.05$, $P = 0.001$ in 1998). A logistic regression analysis also accounting for effects other than chick age showed a slight but significant increase in the delivery rate of herring, sandeel and total fish with age (Table 2.3). Instead of bringing in more fish, in all years parents brought in longer fishes to keep pace with the growing energy demands of their growing chicks (Fig. 2.5, Table 2.3). On average the daily prey mass brought to the colony amounted less than 15 g at hatching to about 55 g near fledging (Fig. 2.5). Prey other than herring and sandeel were mainly supplied during the first days after hatching, but on average never amounted more than 0.25 prey chick^{-1} day^{-1} (Fig. 2.5).

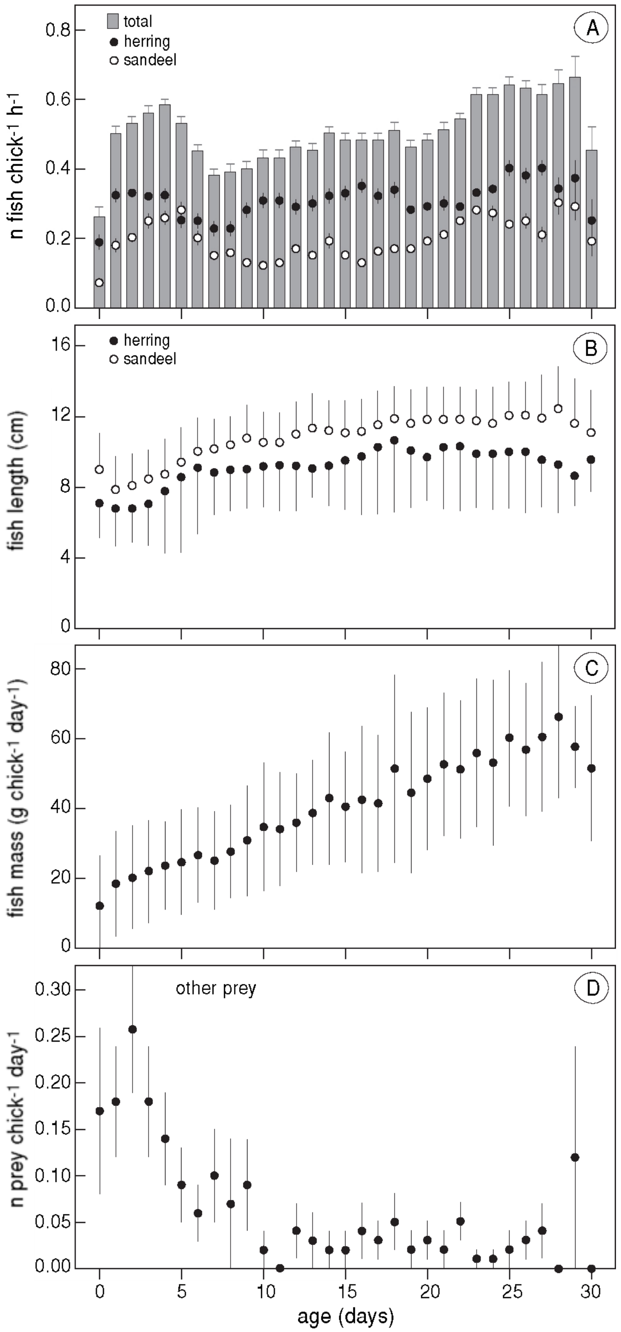

Figure 2.5. Effects of the age of Sandwich Tern chicks on Griend in 1992-98 on the provisioning rate of herring and sandeel (± SE, graph A), mean length of herring and sandeel (+/- SD, graph B), mean daily amount of mass (± SD, graph C) and mean provisioning rate of preys other than herring or sandeel (± SE, graph D).

Effects of hatching order

Hatching order had a large effect on the number of fish brought to the chicks (Table 2.3). The average daily number of fish offered to single chicks (9.56 ± 4.03, $n = 1789$) was slightly, but significantly lower than that offered to first hatched chicks in a brood of two (10.16 ± 5.22, $n = 207$). Since also the length of the herring significantly differed between those groups, there was no difference in mass provisioning rate (multiple regression, $t = 0.94$, $n = 35004$, n.s.). Second hatchlings were fed less than 3 fish per day (2.83 ± 2.80, $n = 155$) and although they were fed somewhat larger fish than their older sibling, there was still a large difference in mass provisioning rate between first and second hatchlings in a brood of two (multiple regression, $t = 11.40$, $n = 35004$, $P < 0.001$). The difference in prey length between first and second hatchling was only present in the first 12 days after hatching (Fig. 2.6). In this period, fish offered to second hatchlings was about the same size as that offered to their three days older sibling (the difference in hatching date is about 3 days, Veen 1977). In other words, parents seem to adjust prey size to the age of their first chick and as a consequence the second chick is fed with fish that is meant for its 3 days older sibling.

Food provisioning in relation to wind speed

The number of fish transported to the colony was particularly low at wind speeds less than 3 m s^{-1} and at wind speeds higher than 14 m s^{-1} (Fig. 2.7, Table 2.3). In between, food delivery to the colony was fairly stable at a rate of about 0.5 fish $chick^{-1}$ h^{-1}. Wind speed had also marked effects on the composition of the chicks' diet: the proportion of herring gradually decreased from about 65% when wind was weak to less than 50% at wind speed of 16 m s^{-1}. When wind was even stronger, the proportion of herring increased again. These changes were the result of different changes in the number of herring and sandeel brought to the colony with increasing wind speed (Fig. 2.7). The

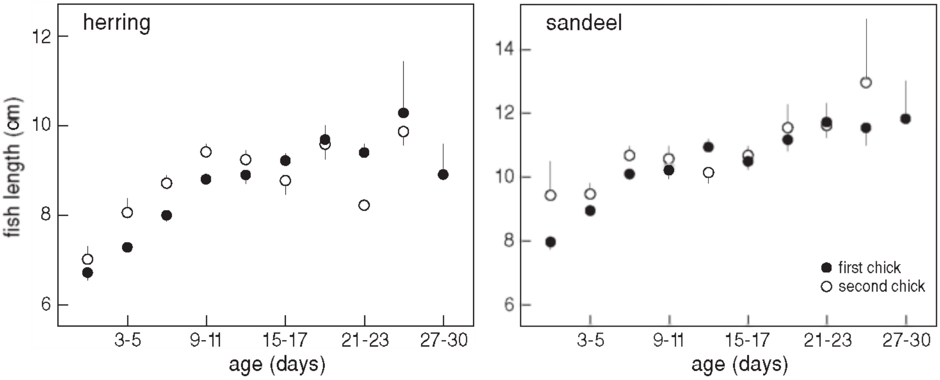

Figure 2.6. Differences in prey length in relation to hatching order and age of Sandwich Tern chicks on Griend in 1992-98. Means +/- SE are plotted.

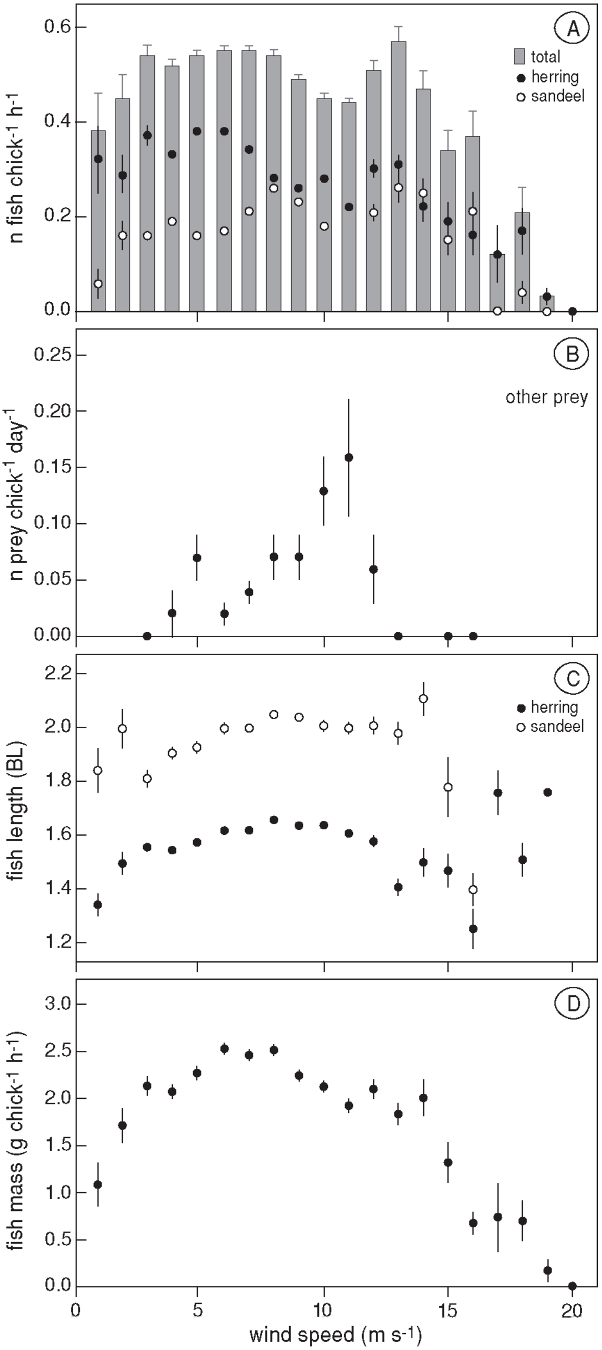

Figure 2.7. The effects of wind speed on the provisioning rate of herring and sandeel (A), other preys (B), prey length (C) and mass provisioning rate (D) of Sandwich Tern chicks on Griend (1992-98). Means ± SE are plotted.

delivery rate of herring gradually decreased, while that of sandeel initially increased with increasing wind speed. Small hatchlings were fed an increasing number of other preys with increasing wind speed, although this trend was broken when wind speed exceeded 11 m s^{-1} (Fig. 2.7). At intermediate wind speeds (5-12 m s^{-1}) significantly longer herring were brought to the chicks than at lower and higher wind speeds (Fig. 2.7). Wind had similar effects on sandeel length, but the slope of the effect did not significantly differ from zero (multiple regression, t = 0.13, n = 5901, n.s.). The amount of mass brought to the colony initially increased to 2.5 g h^{-1} at wind speeds of 6-8 m s^{-1}, but gradually decreased afterwards (Fig. 2.7).

Food provisioning in relation to the time of the day

No feeding was observed before 4:30 a.m. Almost no feeding occurred after 10:30 p.m. and it completely ceased before 11:00 p.m. The rate of food transport to the chicks was rather low in first hour of the day, but increased to high values directly afterwards (hour 5-6; Fig. 2.8). As the day progressed delivery rate gradually decreased and was more or less stable from 9 a.m. onwards. Note that in the first and last hour of the day delivery rate was actually lower than the extrapolated figures plotted in figure 2.8 because these periods lasted less than 60 minutes. Herring and sandeel peaked at different times of the day. If for a moment not considering the first hour of the day, when the transport of both prey types was low, transport of herring was high early in the morning and late in the evening, with less herring brought to the chicks in the intervening period (Fig. 2.8). The delivery rate of sandeel showed more or less the opposite pattern, with a particular high delivery rate just before noon and a gradual decrease towards dusk. The proportion of herring in the diet varied from more than 82% early in the morning and late in the evening to 50% just before noon. Distinct diurnal patterns were also found in the size of both prey species (Fig. 2.8, Table 2.3). Most obvious, were the small sandeel brought to the colony in the first few hours of the day. Combining delivery rate and prey length resulted in an increasing food mass in the early morning, followed by a decrease between 6 and 8 a.m. (Fig. 2.8). From 8 a.m. onwards the amount of mass brought to the colony was practically stable at a rate of about 2.2 g $chick^{-1}$ h^{-1}.

Food provisioning in relation to tide

The number of fish transported to the colony was relatively low at incoming tide, when delivery rates of both herring and sandeel were low (Fig. 2.9). Most sandeel was brought to the colony during high tide, while the delivery rate of herring was highest a few hours after high tide. In almost all years, an analogous tidal pattern in delivery rate was found. In 1997 and in 1998, however, a different pattern was found in the delivery rate of herring and in 1996 an additional peak in the delivery rate of sandeel was found around low tide. The proportion of herring in the diet varied between 53% at low tide to 78% at incoming tide. The length of the sandeel fluctuated during the tidal cycle, with relatively

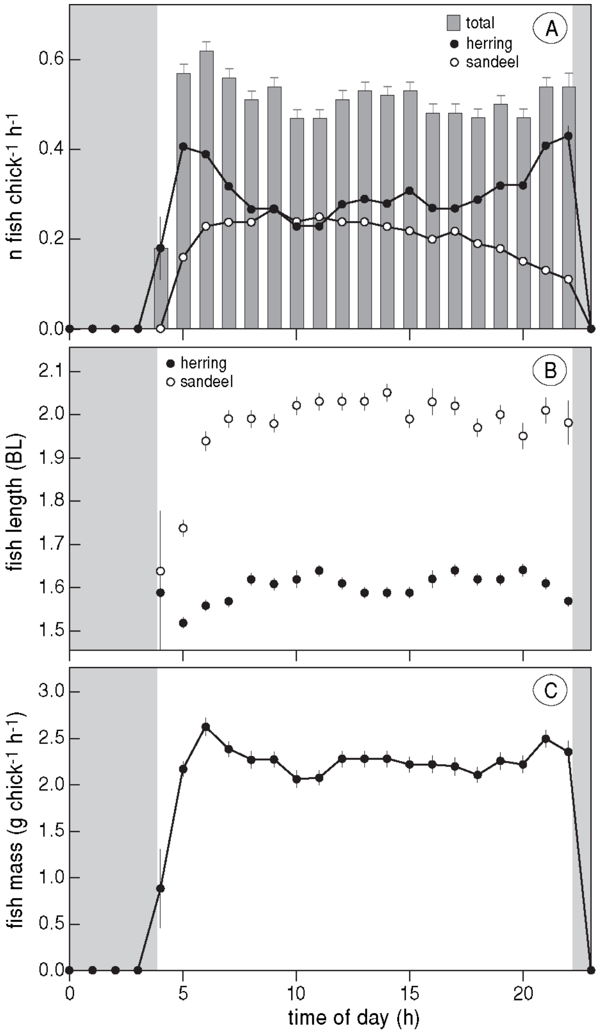

Figure 2.8. Diurnal patterns in provisioning rate of herring and sandeel (A), prey length (B) and mass provisioning rate (C) of Sandwich Tern chicks on Griend (1992-98). Means ± SE are plotted. It was assumed that no feeding occurred during the night (shaded areas).

large sandeel brought to the colony around high tide (Fig. 2.9, Table 2.3). Herring brought to the colony during incoming tide were slightly, but significantly larger than those supplied during other parts of the tidal cycle (Fig. 2.9, Table 2.3). Fish mass brought to the colony peaked around high tide and was relatively low a few hours after low tide (Fig. 2.9, Table 2.3).

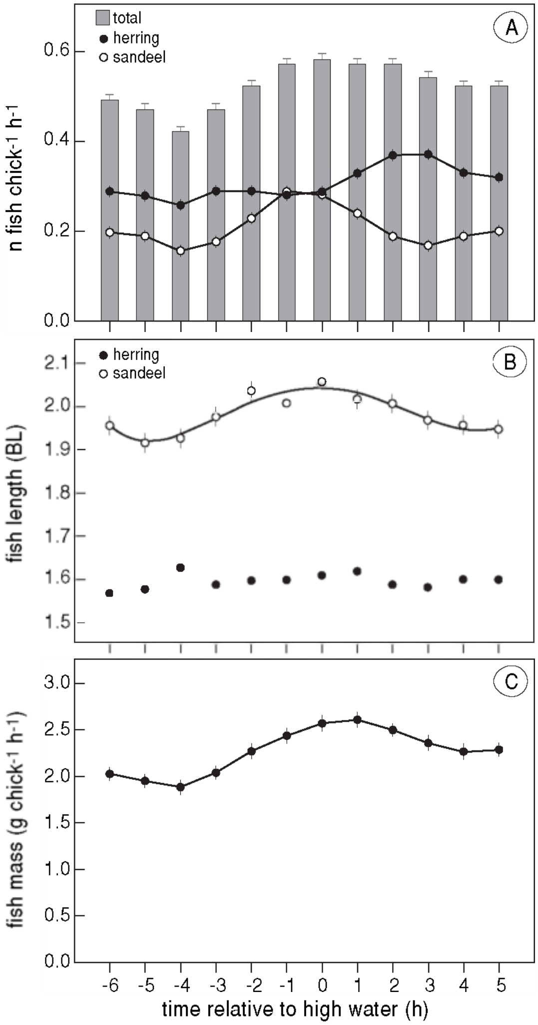

Figure 2.9. Tidal patterns in provisioning rate of herring and sandeel (A), prey length (B) and mass provisioning rate (C) of Sandwich Tern chicks on Griend (1992-98). Means ± SE are plotted.

Fish sampling

At all sampling locations fish abundance showed large standard deviations (Table 2.5), probably reflecting a combined effect of large variation in the occurrence of prey fish in the upper water layer, a patchy distribution of the prey and the small sample size. Especially herring had a patchy distribution and their occurrence at the surface seems very irregular. Most herring were caught in the coastal areas around Vlieland, whereas

Table 2.5. Differences in abundance and occurrence of herring and sandeel between 5 sampling locations in the foraging area of Sandwich Terns breeding on Griend, 1995-98. Fish were caught with an IKMT-net in the upper water layer. Catches were converted to number of fish per 10,000 m^3 water passed through the net.

Sampling Location	Catch per unit effort	% hauls with >10 fish	Number of hauls
Herring			
Vliestroom	0.9 ± 4.3	2.3	88
Westmeep	1.0 ± 4.5	2.2	92
Stortemelk	1181.6 ± 6896.8	11.1	81
Vliesloot	2832.4 ± 11966.5	53.0	83
Oosterom	30.6 ± 96.9	10.0	10
Sandeel			
Vliestroom	25.8. ± 98.2	17.0	88
Westmeep	18.4 ± 76.7	18.5	92
Stortemelk	32.2 ± 138.5	21.0	81
Vliesloot	66.7 ± 449.4	19.3	83
Oosterom	1.3 ± 2.6	0.0	10

the two sampling locations near Griend held relatively few herring. In the Vliesloot more than half of the hauls contained at least 10 herring, indicating a high predictability of the occurrence of this prey species. In the Stortemelk herring were relatively abundant, but occurred only in 11% of the hauls. Sandeel seem to have a more predictable distribution. Most sandeel were caught near Vlieland, but in contrast to herring they were also present in relatively high numbers at the two sampling locations near Griend. At all sampling locations they occurred in 17-21% of the hauls, except for the Oosterom, where almost no sandeel were caught.

Size distribution of the sandeel sampled with the IKMT-net closely matched that brought to the tern colony (Fig. 2.10). In contrast, the herring sampled in the IKMT-net was much smaller than those caught by the terns. It is, however, not clear whether this reflects selective feeding on large herring by the terns or poor sampling methods. Nevertheless some parallels can be seen between variation in herring length as found in the colony and variation in herring length as is reflected in the IKMT-samples (Fig. 2.11). For example the IKMT-catches indicate that the available herring were relatively small during the first week of June in 1998, and in the last week of June in 1996 and 1997. In these periods also herring brought to the colony was relatively small. The catches further indicate that the increase in prey length as observed in the colony was not always accompanied by an increase in length of the fish available. Unfortunately, the numbers of sandeel caught in June were not sufficient for proper comparative analysis.

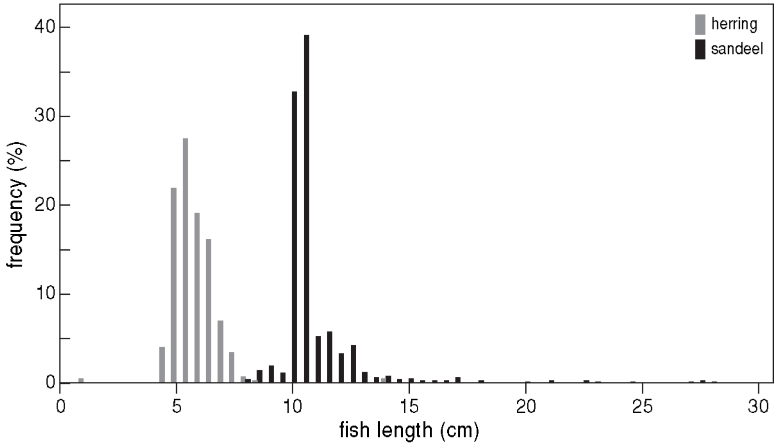

Figure 2.10. Length distribution of herring (n = 264,545) and sandeel (n = 1,625) sampled in the foraging area of Sandwich Terns breeding on Griend, 1995-98. The total length of each fish caught was measured in 0.5 cm classes.

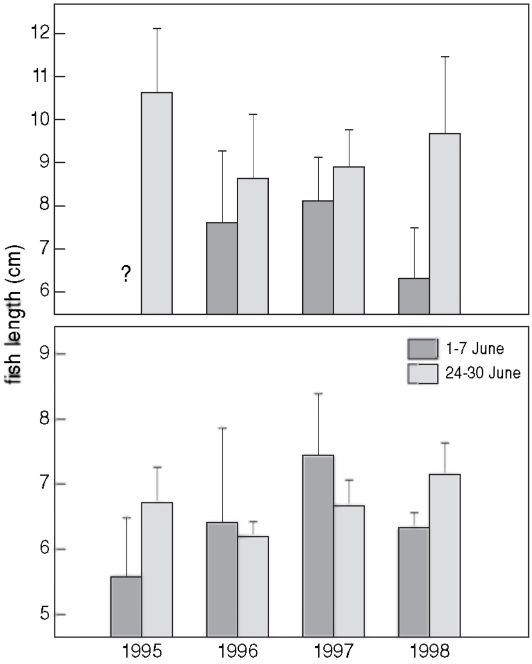

Figure 2.11. Mean length of herring (± SD) that Sandwich Tern parents brought to Griend (upper graph) compared to herring length as sampled in the foraging area of the terns (lower graph) in the first and last week of June, 1995-1998.

DISCUSSION

The diet composition of the Sandwich Terns on Griend reflects the highly specialised prey choice of this species. The observed range in fish size on Griend coincided closely with other studies conducted around the North Sea (Pearson 1968; Veen 1977; Garthe & Kubetzki 1998), although average prey length varies between sites and years. Part of the variation in prey length in our study arises from differences in age composition of the chicks observed, as parents adjusted prey length to meet the increasing energy demands of their growing offspring. Parents with two chicks seem to adjust prey size to the age of their oldest chick and fed too large fish to their second hatchling. However, when age differences and effects of hatching order, time of day, wind and tide were taken into account a year effect was still present (Table 2.3). If such variation in prey size indeed reflects fluctuations in food abundance, we would expect to find similar variations in the fish-sampling programme. However, great care must be taken in interpreting the sampling programme in terms of fluctuations in the food availability of the terns. In the first place the sampling programme only covered a part of the foraging areas of the terns. It was, for example, not possible to sample in the shallow coastal waters north of Vlieland and Terschelling where Sandwich Terns from Griend also frequently foraged. Also in the Wadden Sea only the deeper parts could be sampled, whereas the terns also foraged in shallow waters. In the second place by using a mesh size of 6 mm we selectively sampled for certain prey lengths. Moreover, fish abundance in the upper water layer appears to be highly variable, which requires enormous sample sizes to obtain accurate estimates of food abundance. With some care, one can conclude that large variation in food availability and prey length exists within the foraging area of the terns, and also between and within seasons. As expected, the largest variation was found in herring. The occurrence of suitable herring for Sandwich Terns breeding on Griend depends on a poorly understood system of influx of larvae into the Wadden Sea and migration of older herrings to the coastal areas (Corten & Van de Kamp 1976; Fonds 1978). The timing of these events seems crucial for the breeding performance of the terns as young chicks critically depend on small prey, whereas older chicks need to be fed with larger fish.

Small hatchlings are rather clumsy in handling the fish. After several trials parents sometimes give up feeding the fish to their chick, leaving the fish in the nest or eating it by themselves. When the chicks grow up, supplied fish that are not robbed, are almost instantly eaten by the chick and it practically never happens that a fish is left in the nest or is eaten by the parents. On Griend, the average chick age of fish that fell in the nest or was eaten by the parents, either with or without gull pressure was 4.7, 8.0 and 3.5 days, respectively; much lower than the overall age of chicks during the observations (15.2 days), thus probably largely explaining the smaller fish in these categories. The large size of the fish robbed by Black-headed Gulls and by species other than Sandwich Terns reflects a preference of these pirates for longer fishes. Several studies confirm that pirating Black-headed Gulls mainly take larger prey (e.g. Fuchs 1977; Veen 1977; Gorke 1990; Ratcliffe *et al.* 1997), and also when age differences of the chicks are taken into account robbed prey were significantly longer than other prey (this study). Similarly, pirating gulls may have contributed to the relatively large size of the fish categorised as 'lost out of sight'. In many occasions, a fish-carrying parent chased by a gull flew out of sight and subsequently returned to the colony without fish. Indeed in years when robbery was severe more prey were lost out of sight (Pearson regression, $r^2 = 0.30$, $P < 0.05$).

Effects of wind

Wind may have several effects on foraging terns. Firstly, terns hovering above a prey may have difficulties remaining stationary at low wind speeds (Dunn 1972), but also when wind is strong more vigorously hovering may be required to maintain stationary. Secondly, wind affects the sea surface itself and the turbidity of the water, with consequences for the terns' visibility of the fish and vice versa. Moreover, wind can influence the distribution and swimming activity of the prey fish (Corten & van de Kamp 1996; Bégout Anras & Lagardère 1998). Several studies investigating the influence of wind speed on fishing ability of terns found that fishing success (% of successful dives) and capture rate (number of fish caught per unit of time) in Sandwich Terns increase with increasing wind speed (Dunn 1972, 1973). Taylor (1983), however, found that capture rate in Sandwich Terns decreases with increasing wind speed. These contradicting results may be due to differences in diet composition or in characteristics of the foraging area, but the most plausible explanation is that they investigated a different range of wind speed. Dunn's (1972, 1973) studies covered wind speeds ranging from 0.5-7.0 m s^{-1}, while in Taylor's (1983) study wind speeds ranged from 3-16 m s^{-1}. In our study, food transport to the colony initially improved and gradually decreased with wind speeds higher than 8 m s^{-1}, but was only seriously affected when wind speed exceeded 14 m s^{-1}, thus far outside Dunn's (1972, 1973) range. This also explains why Dunn (1975) did not find any adverse effects of wind speed (0-9 m s^{-1}) on chick growth.

Analogous to our study, Frank (1992) found that Common Tern chicks on Minsener Oldeoog (German Wadden Sea) were fed fewer clupeids and more sandeel at high wind speeds. During bad weather, clupeids show a downward migration (Ehrenbaum 1936 in Frank 1992), while shoals break up (Birkhead 1976), as a result of which herring become less available to the foraging terns. Also the horizontal distribution of the prey fish provides a plausible explanation for the effects of wind on the diet composition of terns. Our IKMT-catches showed that herring was predominantly available in the coastal areas around Vlieland. These coastal waters also held relatively large amounts of sandeel, but in contrast to herring sandeel were also caught in relatively large numbers in the Wadden Sea directly north of Griend. Under stormy conditions dominated by northwesterly winds, the sea surface in the coastal areas is extremely rough. Under such conditions, the less exposed Wadden Sea probably provides better foraging conditions for terns than the coastal areas. Thus, if indeed terns switch to forage in the Wadden Sea with strong winds, one should expect an increasing proportion of sandeel. This would also explain the decrease in herring length with strong winds as the Wadden Sea typically holds small herring (Fonds 1978; Corten 1996)). Further observations on the distribution of foraging terns and more insight into the behaviour of their prey fish are, however, needed to effectively explain the observed changes.

When wind speed increased, chicks of less than 6 days old were fed an increasing number of prey other than herring and sandeel, predominantly small and energy low species, like Goby and Brown Shrimp. These alternate preys contribute to fulfil the energy demands of small chicks, but become unimportant when the chicks grow. Even under extremely rough foraging conditions when the provisioning of high energetic preys was severely affected, the parents of older chicks did not switch to less profitable prey species.

Diurnal rhythms

Several authors found diurnal rhythms in feeding activity in fish-eating birds (e.g. Cairns 1987; Hamer & Thompson 1997). In terns, peaks in feeding activity were found early in the morning and late in the evening (Dunn 1972; Hulsman 1977; Frank 1992). Dunn (1972) argued that such diurnal patterns could result from changing energy requirements of the chicks during the day, the peak in feeding activity at dawn would then result from the hunger state of adults and chicks after a night without food, while the peak at dusk follows the need for a final feeding bout before the night falls. A few studies have related the diel pattern in feeding activity in birds to vertical movements of their prey (Sjöberg 1985; Piersma *et al.* 1988; Richner 1995). Many fish show diurnal rhythmicity and move vertically in the water column as light or feeding conditions change (Thorpe 1978). *Clupea harengus* migrates upwards to the surface at dusk where they tend to disperse near the surface; they reform and move to deeper waters at dawn (Blaxter & Parrish 1965; Laevastu & Hayes 1981). Diving Sandwich Terns can reach a maximum depth of 2 m (Borodulina 1960; Dunn 1972), and thus are depending on fish present near the water surface. Furthermore, foraging Sandwich Terns utilise visual cues and therefore do not feed during darkness (Smith 1975), when herring is most available in the upper water column. Thus parallel to the pattern in herring transport to Griend, *Clupea harengus* is typically available for foraging terns during the early morning hours and before the night falls. *Ammodytes tobianus*, like other *Ammodytes* spp. (Thorpe 1978; Yamashita *et al.* 1985), are buried in the sediment at night and swim near the surface during daylight (Macer 1966; Reay 1970). So, the patterns of vertical migration in *Clupea harengus* and *Ammodytes* perfectly match the patterns found in the colony. Unfortunately, we do not know of any publications on vertical movements in *Sprattus sprattus* and *Hyperoplus lanceolatus*, but it is likely that they resemble the migration patterns of *Clupea harengus* and *Ammodytes tobianus*. This strongly suggests that the observed diel patterns in food transport to the ternery are related to the vertical movements of the tern's prey fish. Although this pleads against Dunn's (1972) hypothesis that these patterns arise from changing energy requirements of the chicks, his view can not be excluded. In this respect, it would be interesting to investigate how Sandwich Terns organise their activities during the day in colonies where only sandeel is available.

Interestingly, in the first two hours of the light period relatively small sandeel were brought to the colony. This suggests that these small prey were found closer to the colony and as a consequence parents returned to the colony sooner. In this way some parents could partly satisfy the hunger of their chicks, but the low rate of food transport in the first hour of the day suggests that most parents did not chose for this option.

Tidal rhythms

Several studies on terns report variation in food transport to the colony throughout the tidal cycle (Dunn 1972; Hulsmann 1977; Frank 1992). Combining observations in the colony with radio-tracking results, Becker *et al.* (1993) showed that Common Terns visited specific foraging areas in the Wadden Sea and North Sea depending on the tide. Sandeel were mainly caught by these terns at the North Sea during incoming tide, while herring were mainly caught in the Wadden Sea at high tide. Aerial counts of foraging Sandwich Terns performed in 1994 indicate that terns breeding on Griend also use different foraging areas during a tidal cycle (Essen *et al.* 1998). During low tide, foraging terns concentrated around the gullies in the Wadden Sea and North Sea. Observations in the colony showed that fishing success was low during this part of the tidal cycle. Just before high tide terns were mainly seen foraging in the deep waters between Vlieland and Terschelling. Colony observations showed that herring and sandeel could be caught here in equal numbers and that relatively long sandeel were available here. During receding tide, relatively high numbers of herring were brought to Griend and according to the aerial counts in 1994 during his stage of the tidal cycle the terns mainly foraged around the west point of Terschelling. Surprisingly, the waters around the east point of Vlieland, where IKMT-catches indicate a high abundance of herring, were largely avoided during receding tide. We have no explanation for this than herring being only available around Vlieland during other parts of the tidal cycle, since the fish-sampling project did not account for differences during the tidal cycle. Many species of fish, however, have synchronised their activities with the tidal cycle or show horizontal movements oscillating with the tide (Gibson 1978; Aprahamian *et al.* 1998). It was beyond the scope of this study, but it would be challenging to further extend the sampling programme and to pay more attention to the distribution of the foraging terns during the entire tidal cycle.

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Chapter 3

Living with gulls: the consequences for Sandwich Terns of breeding in association with Black-headed Gulls

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ASTRACT

We studied the feeding ecology of Sandwich Terns (*Sterna sandvicensis*) in the presence of kleptoparasitising Black-headed Gulls (*Larus ridibundus*) on the Isle of Griend, The Netherlands, between 1992 and 1998. About 30% of all of the food parents transported to the colony were lost, mainly through intervention of Black-headed Gulls. The gulls mainly took the larger fish, but showed no preference for the energetically more profitable herring. Apparently the gulls selected for prey length or visibility of the prey, rather than for energy content of the fish. The proportion of food robbed by the gulls increased with the age of the tern chicks and paralleled the increase in prey length Sandwich Tern parents brought to the colony. Kleptoparasitism showed a clear pattern with time of the day, tide and wind speed. During the first few hours of the day, almost no kleptoparasitism occurred, while robbery was high around 09.00 and at dusk. This bimodal pattern in kleptoparasitism might be related to the foraging activity of the gulls. A tidal effect on food loss was less pronounced, although kleptoparasitism was significantly higher during high tide, when foraging activity of gulls for other foods was low and the number of potential pirates in the tern colony was high. Wind strength had significant negative effects on the amount of food transported to the colony, while kleptoparasitism increased. Therefore, wind speed severely affected energy intake of the tern chicks and had strong negative effects on chick growth. During the first two weeks post-hatching kleptoparasitism was relatively low and had only small effects on chick growth, even under unfavourable weather conditions. From then on, however, the negative effects of kleptoparasitism on growth became considerable. Especially with strong winds, chick growth was severely affected. Sandwich Terns show several behavioral strategies in order to reduce the rate of food loss by the gulls and to minimise the effects on chick growth and survival.

INTRODUCTION

Kleptoparasitism or food piracy, the stealing of already procured food by individuals of one species from individuals of another species, is widely spread among birds (Brockmann and Barnard 1979). This is especially common in seabirds, which generally breed in dense colonies and often form aggregations when feeding (Furness 1987). In contrast to most other seabirds, nesting Sandwich Terns (*Sterna sandvicensis*) intentionally seek the proximity of potential kleptoparasites. In The Netherlands, most Sandwich Tern colonies are situated in the vicinity of or are surrounded by nesting Black-headed Gulls (*Larus ridibundus*; Veen 1977). In this way, the non-aggressive Sandwich Terns benefit from the anti-predator behavior of the gulls. By seeking the proximity of the gulls, predation on eggs and freshly hatched chicks is greatly reduced (Lind 1963; Veen 1977). However, soon after hatching of the tern chicks, some nearby breeding gulls develop into specialised kleptoparasites, resulting in serious losses of food that the tern parents bring for their offspring. With the growing of the chicks, the terns become less susceptible to predation, thus the advantages of associative nesting with Black-headed Gulls become less important. At the same time, the disadvantage from food robbery strongly increases (this study). Stienen and Brenninkmeijer (1999) showed by experiment that the current rate of food parasitism in the Sandwich Tern colony on the Isle of Griend, The Netherlands, has negative effects on chick growth and body condition at fledging. In this study, we give a detailed analysis of various factors influencing food parasitism by gulls. A simple model is presented that shows the combined effects of kleptoparasitism and wind speed on the growth of the tern chicks on Griend. Wind speed and sea surface conditions influence the fishing ability of adult Sandwich Terns (Dunn 1973; Taylor 1983). In accordance with this, Stienen *et al.* (2000) found strong effects of wind speed on diet composition and the amount of food transported to Sandwich Tern chicks on Griend. As wind speed also influences the rate of food loss to kleptoparasitising gulls, adverse effects on chick growth are expected, although Dunn (1975) did not find an effect of wind speed on the weight increase of Sandwich Tern chicks.

METHODS

Study Area

The study was conducted on the Isle of Griend, situated in the Dutch Wadden Sea (53°15'N, 5°15'E). Griend (about 57 ha at normal high tide) consists of a low salt marsh area, partly surrounded by a somewhat higher dune ridge. The isle supports several species of colonial nesting terns and gulls. During the study period (1992-1998) 5,600-8,300 pairs of Sandwich Terns and 16,000-28,500 pairs of Black-headed Gulls nested on the island. Each year, the Sandwich Terns formed several subcolonies, which were separated from each other either in space or time. Each year, a subcolony of Sandwich Terns in which hatching fell around the first of June was chosen for study of the food transported to the nest and also kleptoparasitism. Just before hatching, 50-100 nests within the subcolony were enclosed to prevent the chicks from moving from the study site. The enclosures were made of 50 cm high wire netting of which the lower 20 cm was covered with plastic, to avoid injuries to the chick's head and bill.

Wind speed at 10 m was recorded every 5 minutes with a calibrated cup-anemometer in the vicinity of the colony. For most statistical analyses we used the average hourly wind speed. However, to analyse the effects of wind speed on the daily energy intake of the chicks we used the average wind speed during the daylight period.

Chick Observations

Within the enclosures, all chicks were banded within three days of hatching. At banding, the chicks were aged using the size of yolk sac, the length of the bill to head and feather characteristics. Each year, chicks from about 20 nests were dyed with picric acid or ink for individual recognition. The chicks were followed daily from hatching until fledging. Except in 1992 and 1995, only chicks younger than 21 days and older than 15 days, respectively, were followed. Each day, observations lasted from approximately 04.30 to 22.30. If possible, the same chicks were observed each day, but when a chick died a new chick of known age was studied. Observations were performed from an elevated blind placed at about 2 m from the enclosure. During the observations we registered prey species, prey length and the fate of the prey (for more details see Stienen *et al.* 2000). Prey size was estimated in quarters of the parent's bill size (bill length = 5.43 ± 0.25 cm, N = 679). Observations were stored in data loggers with a time resolution of 1 sec. Food transported to the colony and food intake rate of the chicks were transformed into energy values according to the allometric relationships given by Stienen and Brenninkmeijer (2002).

Growth and Condition of Chicks

When weather conditions allowed it, chicks were weighed at intervals of three days to the nearest g using an electronic balance. The length of the total head (head + bill, ± 0.1 mm) was measured with a vernier calliper. When intervals between two measurements lasted less than five days, in between body mass was calculated assuming linear growth.

For each age, the expected body mass (M_{exp}, g) was computed by taking the average body mass of all study chicks which survived to fledging (*i.e.* > 24 days old). An index for chick condition (CI) was obtained by calculating the deviation in body mass (M, g) from the expected body mass for that age:

$$CI = \frac{M - M_{exp}}{M_{exp}} \times 100\%$$

Data Analysis and Statistics

Data analyses were performed using SPSS/PC+ 4.0 statistical package (Norusis 1990). All statistical tests were performed using the Genstat statistical package (Genstat 5 Committee 1993). In all logistic regression analyses, the statistical parameters of prey species, tide and year were treated as factor-variables. Depending on the parameter, the factor-variables were subdivided into 2-12 categories or levels. To analyse the effects prey length (in bill length), prey energy content (in kJ), prey species (2 types, namely herring *Clupea harengus/Sprattus sprattus* or sandeel *Ammodytes tobianus/Hyperoplus lanceolatus*), wind speed (in m s^{-1}), time of day (in h), tide (12 classes, relative to high water) and year (7 categories, 1992-98), respectively. The fate of the prey brought to the colony we analysed using a stepwise logistic regression approach. In all cases, the variables were entered into a logistic model in the order given above. Prey species, other than Clupeidae (in future called herring) and Ammodytidae (in future called sandeels), were omitted from all analyses since they amounted less than 1.1% of all food items supplied to the chicks (Stienen *et al.* 2000).

RESULTS

Of all herring and sandeels brought to the colony (n = 16,650) 70.7% were eaten by the Sandwich Tern chicks. Food items not eaten by the chicks could be classified as follows:

1. robbed by Black-headed Gulls (18.0%),
2. eaten by the tern parent under pressure of robbing gulls (1.4%),
3. lost by the adult when out of the observer's view and parent then returned without fish (7.7%),
4. robbed by species other than Black-headed Gulls, mainly Sandwich Terns, but also some Common Terns (*Sterna hirundo*) and Common Gulls (*Larus canus*; 0.7%), and
5. other losses, such as prey that fell to the ground or that were eaten by the parent without intervention of gulls (1.5%).

Thus, just over 66% of the food losses could be directly linked to robbing activities of gulls (robbed by gulls or eaten by the parent under pressure of gulls). The most common event was prey robbed by a gull when a parent tern either attempted to land next to its chick or presented a fish to its chick. Loss of prey when out of the observer’s view often happened when gulls chased an arriving parent tern away from the colony and the tern subsequently returned to the colony without a fish. However, losing prey when out of view also occurred when a chick refused food and the fish-carrying parent left the colony or when the parent was chased away from the colony by “pirates” other than Black-headed Gulls. These cases occurred rarely, thus the main reason for the loss of fish was because of intervention by gulls.

The length of the fish brought to the colony varied between 0.25 and 4.0 bill length. However, prey smaller than 0.75 bill length (0.2% of all prey) exclusively consisted of broken pieces of fish. The proportion of prey robbed by Black-headed Gulls or other species and the proportion lost when out of view significantly increased with prey length, while the proportion of food eaten by the parent and other losses decreased with

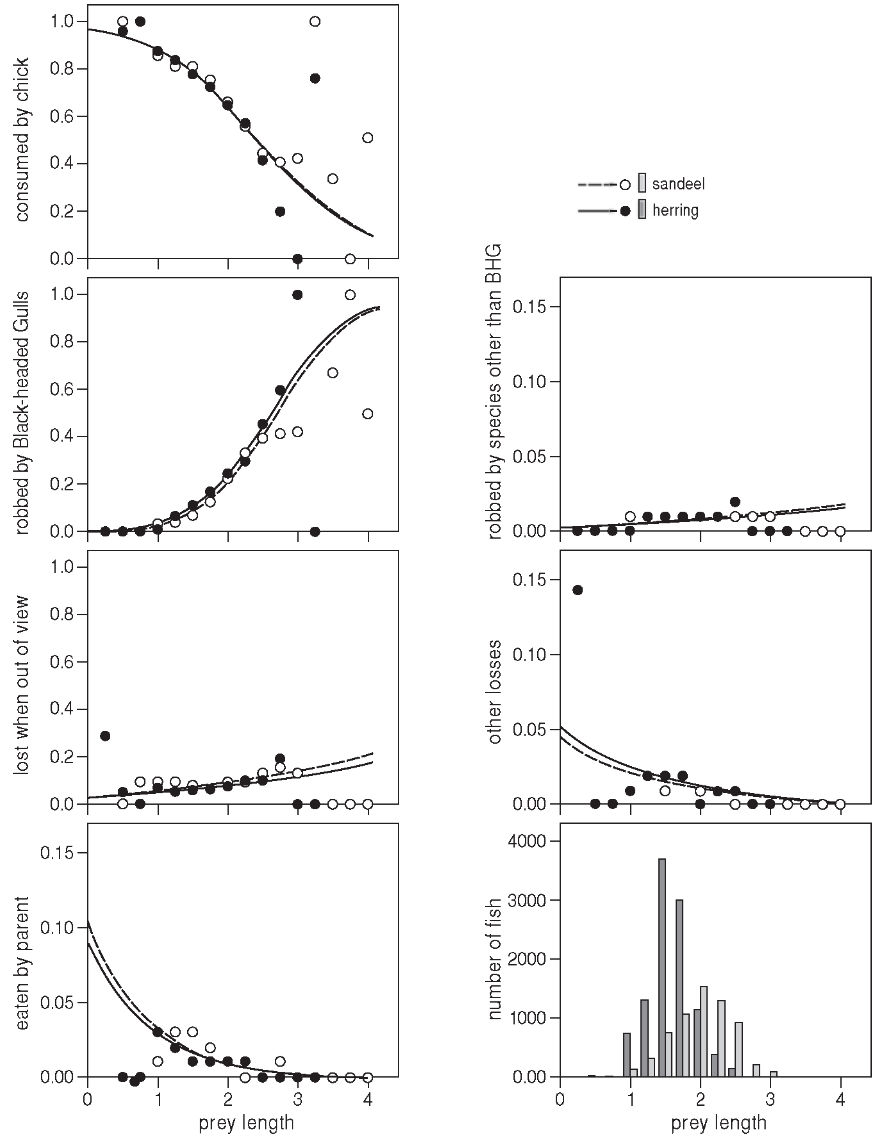

Figure 3.1. Fate of fish brought to Sandwich Tern chicks on Griend in 1992-98 in relation to prey length. The lines represent the regression equations given in Table 3.1. The lower right graph shows the number of fish considered.

prey length (Fig. 3.1, Table 3.1). Since the proportion of food robbed by Black-headed Gulls and lost out of view were by far the most important causes of food loss, the probability of consuming prey sharply decreased with prey size. If the prey species was included in the logistic regression model after prey length, it had significant effects when it concerned prey taken by Black-headed Gulls and prey lost when out of view (Table 3.1).

Table 3.1. Logistic regression analyses examining the effect of prey length and prey species on the occurrence of various fates of fish (*n* = 16,650) brought to Sandwich Tern chicks on Griend in 1992-98. Prey length in adult bill length units.

Variable	Change in deviance	df	P-value	Estimates of coefficients ± SE
Proportion eaten				
Constant				3.33 ± 0.095
Prey length	989.8	1	< 0.001	-1.38 ± 0.055
Species	0.8	1	n.s.	0.036 ± 0.044 for sandeels
Proportion robbed by Black-headed Gulls				
Constant				-4.85 ± 0.10
Prey length	1171.8	1	< 0.001	1.87 ± 0.059
Species	17.4	1	< 0.001	-0.207 ± 0.047 for sandeels
Proportion lost when out of view				
Constant				-3.37 ± 0.10
Prey length	65.3	1	< 0.001	0.443 ± 0.059
Species	10.1	1	< 0.01	0.215 ± 0.049 for sandeels
Proportion eaten by parent				
Constant				-2.41 ± 0.11
Prey length	40.2	1	< 0.001	-1.156 ± 0.071
Species	0.6	1	n.s.	0.120 ± 0.058 for sandeels
Proportion robbed by other species				
Constant				-5.64 ± 0.12
Prey length	4.5	1	< 0.05	0.393 ± 0.073
Species	0.3	1	n.s.	0.119 ± 0.061 for sandeels
Proportion rest				
Constant				-2.91 ± 0.11
Prey length (BL)	23.8	1	< 0.001	-0.714 ± 0.072
Species	1.1	1	n.s.	-0.155 ± 0.060 for sandeels

Compared with herring, sandeels were less often robbed by Black-headed Gulls, but more often lost while out of view. These effects annul each other, so that no significant effect was found between prey species and the probability of consuming the prey. Further, adding prey energy content to the model had no significant effects on the probability of consumption of prey (logistic regression: change in deviance = 0.2, df = 1, n.s.). If the prey energy content was entered into the model first, it had a significant effect on the consumption probability of a prey (logistic regression: change in deviance = 500, df = 1, P < 0.001), but removed only 2.5% of the variance, while another 2.4% was removed by then entering prey length. If the order of inclusion was reversed, prey length removed 4.9%, while only 0.002% of the variance was removed by prey energy content. So, food consumption by the tern chicks depends on the size of the fish offered rather than on its energy content.

Age of the Chicks

During the first five days post-hatching, food loss was relatively high (Fig. 3.2). Freshly hatched chicks were rather clumsy and it took them a relatively long time to handle prey. This resulted in a high proportion of the food robbed by either neighbouring terns or Sandwich Terns visiting the colony, but probably having no chicks of their own. Furthermore, freshly hatched chicks sometimes refused food. The fish was then left in the nest, consumed by the parent or the parent left the colony still carrying the fish.

Kleptoparasitism by Black-headed Gulls gradually increased from hatching until day 15 and remained more or less constant thereafter (Fig. 3.2). This parallels the increase in the length of the prey brought to the colony from day 0-15 (Stienen *et al.* 2000). During the entire chick period, prey consumed by chicks were, on average, smaller than prey robbed by gulls (Fig. 3.3). The average size of the prey taken by the gulls increased with the age of the tern chicks. Prey of relatively small size, which were sometimes robbed from freshly hatched chicks, were never taken from older chicks. This suggests that gulls selected the largest prey available at that moment, rather than showing a fixed threshold of prey size, above which they made attempts to steal a fish.

Adding the age of the chicks into a logistic regression model after inclusion of prey size and species had significant effects on the probability of prey consumption (Appendix 3.1). In Figure 3.2, the difference between the expected probability of prey consumption (obtained when average prey length for a specific age is entered into the logistic curve shown in Fig. 3.1) and observed prey consumption is plotted against the age of the chicks. It shows that, during the first few days after hatching, consumption probabilities of both prey species were lower than expected, reflecting the high food losses to causes other than kleptoparasitism by Black-headed Gulls. From day 5-15 sandeels were consumed more often than expected, while consumption probabilities of herring fit the expected pattern. From day 15 onwards, sandeels were consumed less often, while herring was consumed more often than expected on the basis of average prey length. We do not know what mechanism underlies these patterns, but it might have something to do with either a learning process by the gulls, variation in food composition, or both.

Energy provisioning to each chick increased from 62 kJ chick^{-1} day^{-1} at hatching to about 300 kJ chick^{-1} day^{-1} near fledging (Fig. 3.2). During the first five days after hatching, about 74% of the energy which parents brought to the colony was consumed by the chicks, decreasing to about 55% near fledging. In the last week before fledging, maximum energy intake amounted to 195 kJ chick^{-1} day^{-1}.

Effects of Wind

The proportion of food consumed by the chicks decreased from about 74% at low wind speed ($\leq$ 5 m s^{-1}) to about 68% at high wind speeds (> 11 m s^{-1}; Fig. 3.4). This was mainly due to an increase in the proportion of food robbed by Black-headed Gulls, while the proportion of food lost out of view significantly decreased with increasing wind speed (Appendix 3.1). The decreasing proportion of food consumed by chicks with increasing wind speed is remarkable considering the decrease in prey length brought to

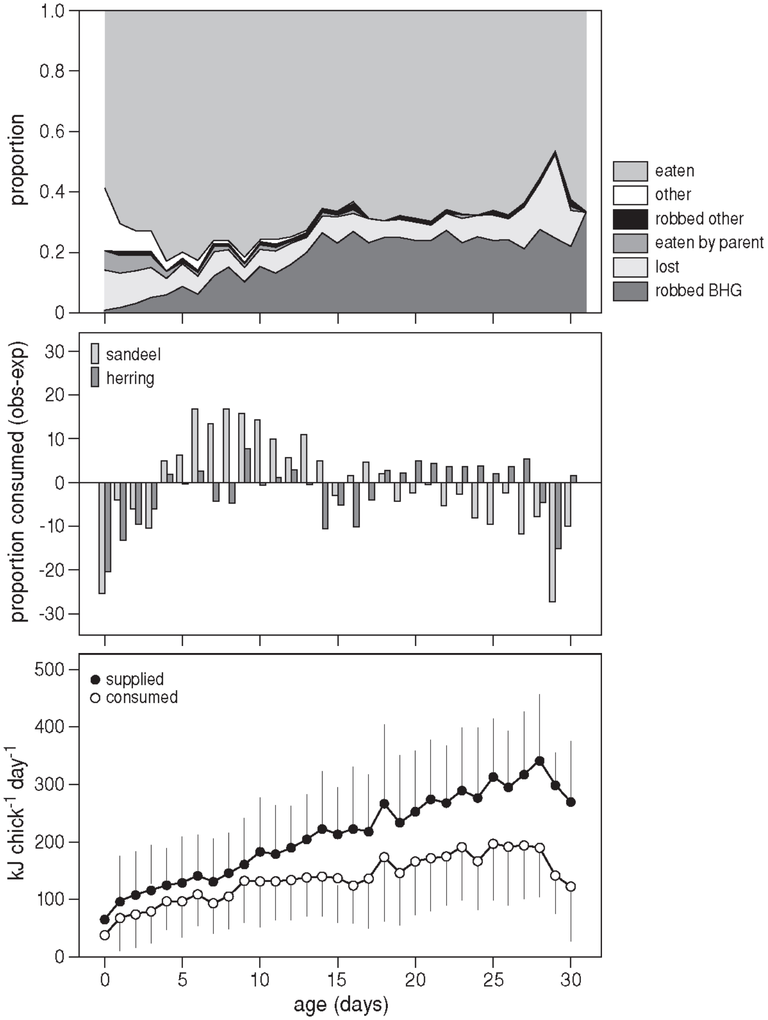

Figure 3.2. Top graph: fate of prey brought to the colony in relation to the age of the Sandwich Tern chicks on Griend in 1992-98. Middle graph: deviation from the expected pattern in prey consumption probabilities (*i.e.* observed prey consumption – consumption probability as expected from the observed prey length, see text) during the chick period. Bottom graph: the daily amount of energy brought to the colony and consumed by the tern chicks (mean ± SE) in relation to the age of the chicks. Robbed BHG = robbed by Black-headed Gulls, lost = lost when out of the observer's view, eaten parent = consumed by the Sandwich Tern parent, robbed other = robbed by species other than Black-headed Gulls, other = other losses, eaten = consumed by chick.

the chicks (Stienen *et al.* 2000). The effect of wind speed on the consumption probability of a prey is even more pronounced after correcting for prey length (Fig. 3.4). At high wind speeds, the consumption of sandeels was much lower than expected, while this effect was less pronounced in herring (Fig. 3.4).

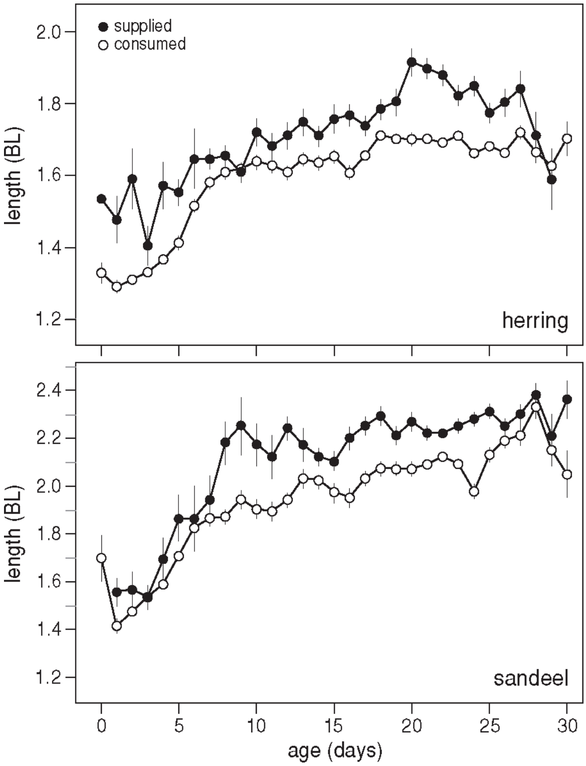

Figure 3.3. The length of the prey (mean ± SE) consumed by Sandwich Tern chicks on Griend in 1992-98 compared with the length of the prey (mean ± SE) lost to kleptoparasitising Black-headed Gulls in relation to the age of the chicks. BL = bill length of parent.

Wind speed had a strong effect on the amount of energy supplied to the chicks. Highest inputs were found with wind speed around 7 m s^{-1}, while energy supply strongly decreased at speeds higher than 8 m s^{-1} (Fig. 3.4). At high wind speeds, the low transport rate coincided with high food losses, thus the energy intake rate of the chicks was severely affected.

Diel Pattern in Kleptoparasitism

During the first few hours of the day, almost all food brought to the colony was eaten by the chicks (Fig. 3.5). At that time, the gulls showed almost no interest in the fish brought to the colony. Until 09.00, robbing activity of the gulls increased, resulting in an increasing proportion of the food being robbed by the gulls and of the proportion of the food lost when out of view, and a decreasing proportion of the food being consumed by the chicks (Appendix 3.1). The highest losses were found around 09.00 and at the end of the day. This typical bimodal pattern was found in all years, although the exact timing

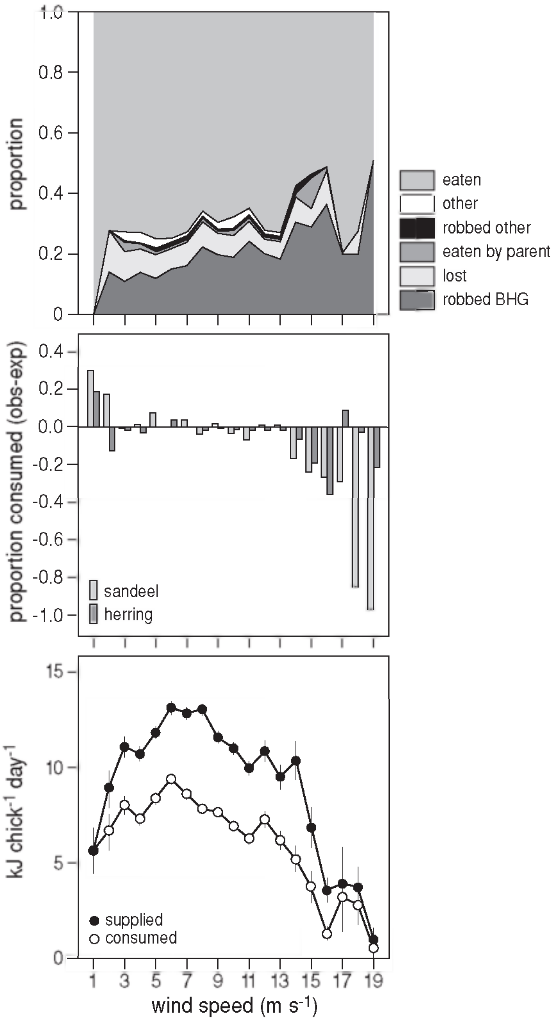

Figure 3.4. Top graph: the effect of wind speed on the fate of food brought to Sandwich Tern chicks on Griend in 1992-98. Middle graph: the deviation from the expected pattern in prey consumption probabilities (*i.e.* observed prey consumption – consumption probability as expected from the observed prey length, see text) in relation to wind speed. Bottom graph: the amount of energy brought to the colony and consumed by the chicks (mean ± SE) in relation to wind speed. Robbed BHG = robbed by Black-headed Gulls, lost = lost when out of the observer's view, eaten parent = consumed by the Sandwich Tern parent, robbed other = robbed by species other than Black-headed Gulls, other = other losses, eaten = consumed by chick.

varied somewhat from year to year. Since prey length did not vary much during the day (Stienen *et al.* 2000), a correction for prey length gave almost identical results (Fig. 3.5).

Energy transport rate to the colony peaked around 06.00 (Fig. 3.5). At that time, food loss to robbing gulls was still low, resulting in high energy intake rates by the chicks. In

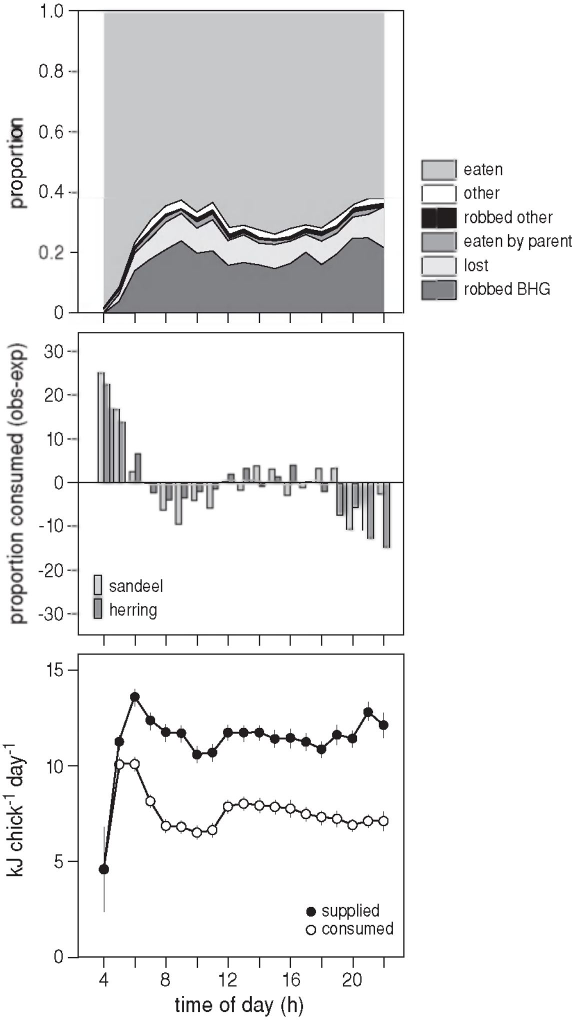

Figure 3.5. Top graph: variation in the fate of the prey brought to the colony during the course of the day. Middle graph: the deviation from the expected diel pattern in prey consumption probabilities (*i.e.* observed prey consumption – consumption probability as expected from the observed prey length, see text). Bottom graph: fluctuations in the amount of energy brought to the colony and consumed by the tern chicks (mean ± SE) during the day. Robbed BHG = robbed by Black-headed Gulls, lost = lost when out of the observer's view, eaten parent = consumed by the Sandwich Tern parent, robbed other = robbed by species other than Black-headed Gulls, other = other losses, eaten = consumed by chick.

contrast, the peak in energy transport at the end of the day coincided with high proportions of food loss, so that no peak in energy intake rate was found at the end of the day. Energy intake rate of chicks was lowest around 09.00, when low rates of food transport coincided with high proportions of food loss.

Tidal Effects

Tidal influences on the probability of food consumption were significant (Appendix 3.1), but the effect was much smaller than the effect of chick age, wind speed and time of day. Relatively high proportions of food loss were found around high water (Fig. 3.6). At that time, sandeels brought to the colony were relatively long (Stienen *et al.* 2000), which to some extent might explain the high rates of kleptoparasitism. When prey length was taken into account, food loss of both sandeels and herring was somewhat higher than expected at high tide (Fig. 3.6). The high rate of food loss around high tide coincided with a peak in energy transport to the colony, so that energy intake rate of the chicks showed only small fluctuations during the tidal cycle (Fig. 3.6).

Effects on Chick Growth

In this paragraph, we will analyse to what extent food losses influence body mass growth of the chicks. Also, the effects of wind speed are included in the analyses, as wind speed has strong effects on both the amount of food brought to chicks and the proportion of food actually consumed by chicks. In all years, most of the fluctuations in chick condition closely followed the fluctuations in wind speed (Fig. 3.7). With strong winds, the average condition of the chicks rapidly decreased, but when weather conditions improved, body condition of surviving chicks increased again.

To investigate to what extent the loss of food to Black-headed Gulls affected growth of the tern chicks, a curve was fitted describing body mass growth in relation to the age of the chicks and daily gross energy intake:

$$GR = 8.07 \pm 0.59 - 0.32 \pm 0.09 * age - 0.0040 \pm 0.0030 * age^2 + 0.024 \pm 0.0020 * GEI$$
$(n = 1{,}093$ chick measurements, $r^2 = 0.28$, $F_{3,1090} = 152.1$, $P < 0.001)$,

where GR is the daily growth of a chick (g day^{-1}), age is the age of the chick in days and GEI is the daily gross energy intake rate (kJ day^{-1}).
Subsequently, the effects of wind speed on energy transport to the colony and energy intake rate of the chicks were computed:

$$GET = 66.3 \pm 20.1 + 7.42 \pm 0.28 * age + 16.36 \pm 5.04 * wind\ speed - 1.30 \pm 0.30 * wind\ speed^2$$ $(n = 1{,}583$, $r^2 = 0.33$, $F_{3,1579} = 287.5$, $P < 0.001)$

$$GEI = 88.5 \pm 16.5 + 4.01 \pm 0.22 * age + 5.24 \pm 4.16 * wind\ speed - 0.70 \pm 0.25 * wind\ speed^2$$ $(n = 1{,}583$, $r^2 = 0.19$, $F_{3,1579} = 124.8$, $P < 0.001)$,

where GET is the daily amount of energy transported to a chick (kJ day^{-1}), GEI is the daily amount of energy consumed by a chick (kJ day^{-1}), age is the age of the chick in days and wind speed is the average daily wind speed (m s^{-1}).

Using these formulae, we computed two measurements of chick growth, namely:

1. Assuming that all food transported to the chick was actually eaten by the chick, and

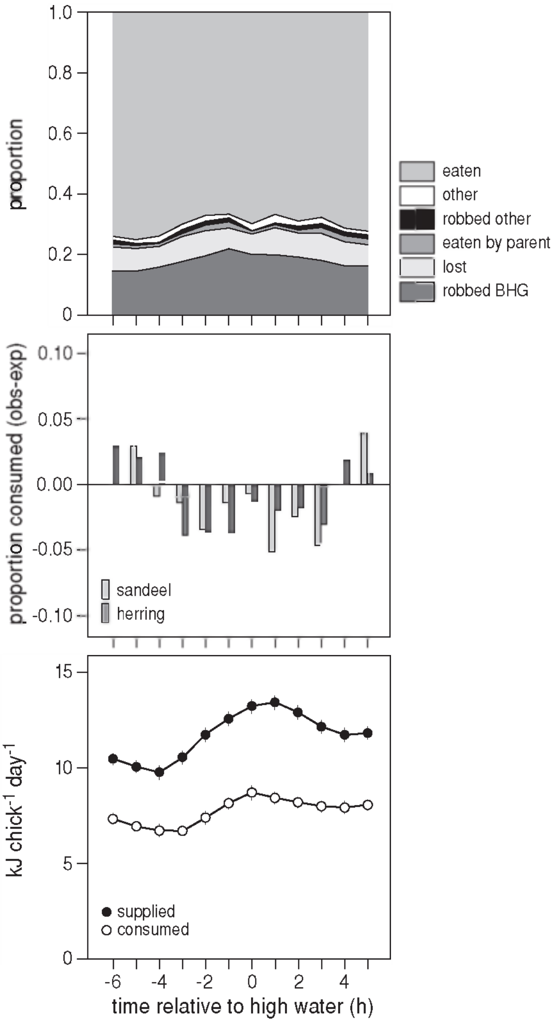

Figure 3.6. Upper graph: tidal effects on the fate of the prey supplied to the colony. Middle graph: the deviation from the expected pattern in prey consumption probability (*i.e.* observed prey consumption – consumption probability as expected from the observed prey length, see text) during a tidal cycle. Lower graph: tidal influence on the amount of energy brought to the colony and consumed by the chicks (mean ± SE). Robbed BHG = robbed by Black-headed Gulls, lost = lost when out of the observer's view, eaten parent = consumed by the Sandwich Tern parent, robbed other = robbed by species other than Black-headed Gulls, other = other losses, eaten = consumed by chick.

2. When food loss (*i.e.* all food that is not consumed by the chick) is taken into account. Furthermore, we modelled growth in calm and in stormy weather situations (wind speed 5 m s^{-1} and 15 m s^{-1}, respectively). Second hatched chicks were omitted from this exercise and maximum body mass growth was set at 13 g day^{-1} (*i.e.* maximum growth rate

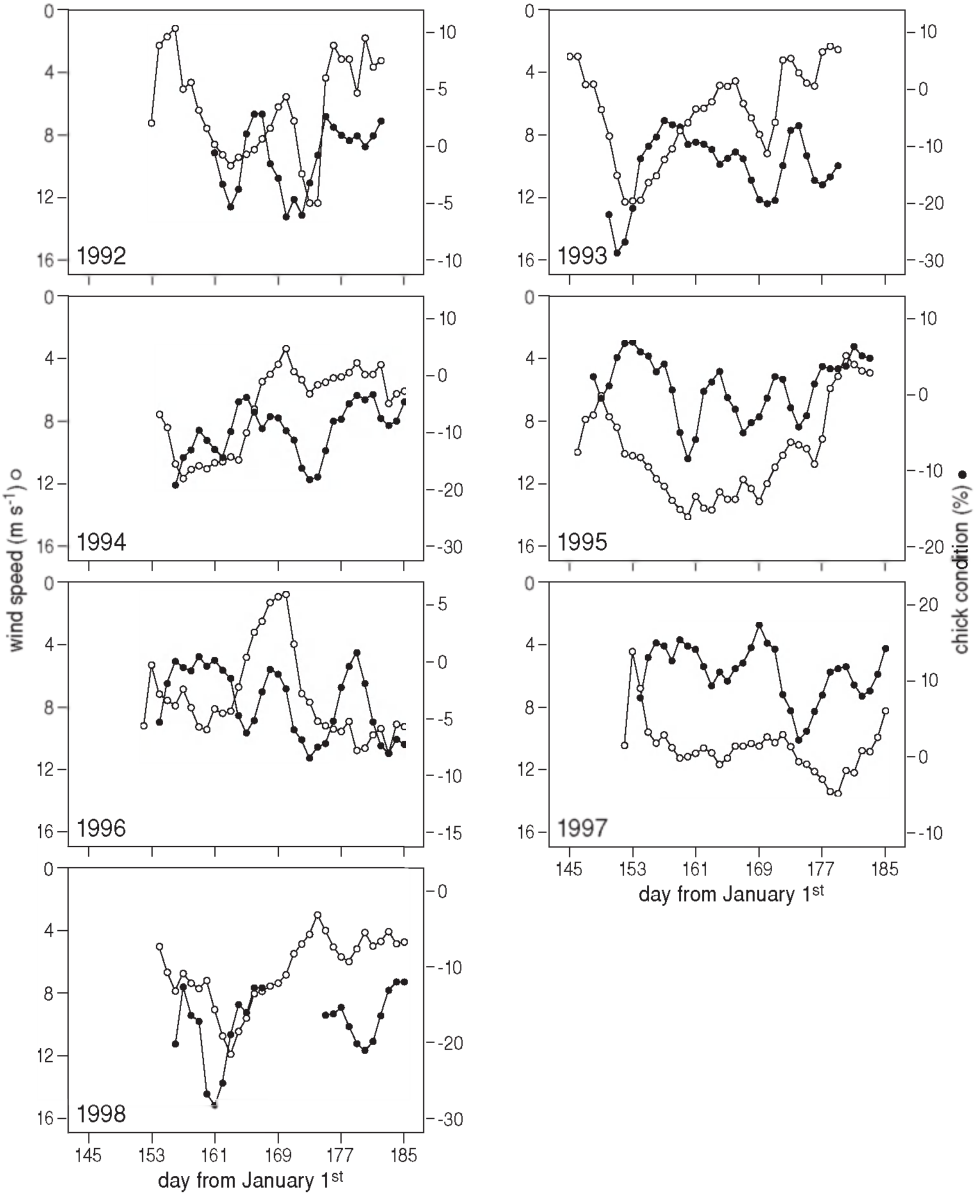

Figure 3.7. Development of the condition of Sandwich Tern chicks (dots, right axis) on Griend in 1992-98 in relation to wind speed (circles, left axis).

recorded in the laboratory; Klaassen *et al.* 1992). The results are shown in Figure 3.8. Under favourable weather conditions and in the absence of Black-headed Gulls, the chicks would theoretically reach a maximum body mass of 256 g at day 36. If, however, food loss is taken into account, maximum body mass would be reached when the chicks

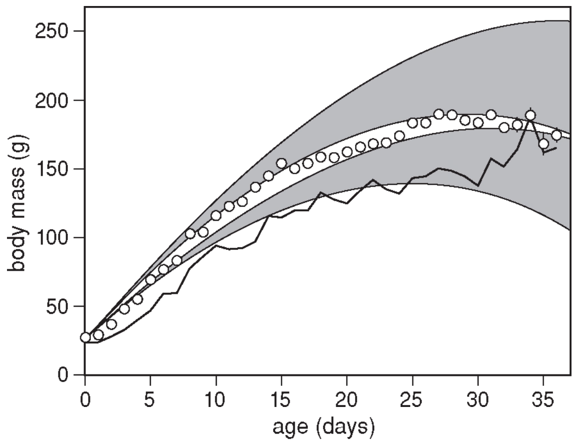

Figure 3.8. Body mass growth (circles, mean ± SE) of first-hatched and single Sandwich Tern chicks on Griend in 1992-98. The line represents the average of the five lowest measurements of body mass of surviving chicks (*i.e.* chicks which reached an age of at least 25 days). The two shaded areas show a model of body mass growth that incorporates effects of kleptoparasitism and wind speed (see text). The upper shaded area encloses the maximum body mass growth (*i.e.* assuming that all food brought to the colony is actually consumed by the chicks) and normal body mass growth (*i.e.* accounting for prey losses) under favourable weather conditions (*i.e.* wind speed 5 m s^{-1}); the lower shaded area encloses the maximum and minimum body mass growth of the chicks under stormy weather conditions (i.e. wind speed 15 m s^{-1}).

are 29 days old, but maximum body mass would be 186 g, a decrease of 27% compared with the situation without food loss. The prediction of growth under these conditions (wind speed = 5 m s^{-1} and accounting for food loss) closely follows the observed growth of the chicks (Fig. 3.8). This is not surprising, since during our study the wind speed averaged 7.7 ± 2.4 m s^{-1}, close to 5 m s^{-1} used in the model. Under persistent windy conditions (wind speed 15 m s^{-1}) maximum body mass would be 179 g at day 31, assuming that all food brought to the colony is actually consumed by the chicks. However, since kleptoparasitism is high under stormy conditions, growth would stagnate at day 25. At that time, maximum body mass would amount to only 139 g, which is below the body mass of the four slowest growing chicks Klaassen *et al.* (1992) raised in the laboratory under a restricted food regime. Also, it is close to the minimum body mass of surviving chicks on Griend (Fig. 8). The model further predicts that chicks older than 25 days would quickly lose weight under stormy conditions and would fall behind the minimum body mass recorded on Griend. Adverse wind conditions do affect chick growth during the first two weeks post-hatching, but the effects are not disastrous for the average chick. Even when strong winds blow for a long period, most first hatchlings would survive the first two weeks after hatching. For chicks older than 25 days, however, such conditions would seriously affect growth and the chicks would starve to death.

DISCUSSION

In the first two weeks after hatching, food loss to Black-headed Gulls was low and had no major effects on the growth of Sandwich Tern chicks. From two weeks old, the length of the prey brought to the tern chicks was at a maximum and kleptoparasitism was high. At this time, the effects of kleptoparasitism on the growth of Sandwich Tern chicks can be considerably. Still, chick mortality can be very high in the first week after hatching (Langham 1974; chapter 7). This reflects a high mortality of second hatched chicks, as they receive almost no food from their parents (Stienen *et al.* 2000). Mortality of first hatchlings between day 20-24 as observed on Griend (chapter 7) probably is a combined effect of peak energy demands being reached (Klaassen *et al.* 1992) and high rates of kleptoparasitism. At that time, some subcolonies of Sandwich Terns on Griend become almost totally deserted, as parents lure their chicks to other sites on the island. Stienen and Brenninkmeijer (1999) argued that leaving the colony site could be an evasive behavior to avoid high prey losses to the gulls and to improve the chicks' survival chances. Leaving the colony site to avoid kleptoparasitism by the neighbouring gulls becomes even more important during periods of windy weather, when food transport to the colony is low. If under such conditions, the terns can not avoid the kleptoparasitising gulls (in the current study because the chicks were enclosed or in natural situations because the subcolony is surrounded by thick vegetation), growth is severely curtailed and can even become negative. Nevertheless, tern chicks have wide margins within which they can survive (Klaassen *et al.* 1992; chapter 7) and only when a long lasting period of windy weather occurred was large-scale chick mortality observed (Veen 1977). Dunn (1975) did not find any effects of wind speed on the body mass growth of Sandwich Tern chicks. However, Dunn's study (1975) covered wind speeds ranging from 0-9 $m.s^{-1}$, while the adverse effect of wind on the energy intake of chicks only become obvious at higher wind speeds. Also, the number of Black-headed Gulls nesting on Coquet Island, where Dunn (1975) did his study, was much lower than on Griend, and kleptoparasitism might have been accordingly low.

Economics of Black-headed Gulls

In the present study, we found that the loss of food positively correlated with the length of the prey supplied to the chicks. As the gross energy content of fish exponentially increases with its length, larger fish are far more profitable for the gulls than small ones. Several studies show that both the chance of being attacked by pirating gulls and the probability of losing a fish to them increases with the length of the fish (Hopkins and Wiley 1972; Hulsman 1976; Ratcliffe *et al.* 1997), although very large fish are sometimes avoided by kleptoparasites (Dunn 1972). Such increase would be expected if the pirates prefer larger and therefore more profitable prey or if larger prey simply are more conspicuous to kleptoparasites. However, in contrast to what we might expect from economic reasoning, prey length was a better predictor of the rate of prey loss than the energy content of the prey. Herring of a specific size were robbed as often as sandeels of the same length, whereas herring has a much higher energy content (Stienen and Brenninkmeijer 2002). Assuming that robbing success does not depend on prey length (but see Dunn 1972), this finding suggests that Black-headed Gulls selected for prey length or visibility of the prey rather than for energy content of the prey. Similar results were found in a Sandwich Tern colony at the Sands of Forvie (Scotland), where Black-headed Gulls selected terns carrying large sandeels, but almost ignored birds carrying shorter, but more profitable gadoids or clupeids (Fuchs 1977).

Patterns in Kleptoparasitism

Dunn (1973) showed that the robbing intensity of Roseate Terns *Sterna dougallii* increases with the number of hosts present at a certain moment. In contrast, in interactions between Sandwich Terns and Black-headed Gulls, there seems to be no relationship between the number of host terns and the rate of kleptoparasitism. In the early morning, the pirating gulls, although present, showed no interest in the potential food resource provided by the terns. Furthermore, food supply peaked around 06.00, while the rate of food loss was highest three hours later. Moreover, the variation in diet composition during the day did not provide an explanation for the observed diel pattern in kleptoparasitism. The proportion of herring in the diet is high during the crepuscular hours and relatively low around 12.00 (Stienen *et al.* 2000). Since relatively short herring are subjected less to kleptoparasitism, one would expect food piracy to be highest just before noon and then gradually decreasing towards dusk, which was not the case. Light conditions can be excluded as a factor determining the diel pattern in kleptoparasitism, because although the incidence of robbery was low in the early morning, it was relatively high at dusk. Apparently other factors are important. From an energetic point of view, it might be expected that kleptoparasitism is especially high during the first hours after sunrise. After a night without food the hunger of the gull chicks would urge the parents to get sufficient food and thus one may expect an increased intensity of food piracy in the early morning. On the other hand, if gull parents start to search for food at sea, kleptoparasitism would be particular low in the early morning. There are, however, specialists and occasional pirates among the gulls (Veen 1977; Gorke 1990). The number of specialised pirates is relatively low and their activity tends to be constant during the course of the day (Veen 1977). The number of occasional pirates, however, greatly outnumbers the specialists and their presence in the colony can greatly vary during the day (Veen 1977). Only when occasional pirates cannot find sufficient food elsewhere, they visit the ternery to pirate the terns (Veen 1977; Monaghan *et al.* 1989; Oro 1996). The diurnal pattern in foraging activity of Black-headed Gulls shows a bimodal pattern, with most activity in the early morning and in the late afternoon (Glutz von Blotzheim and Bauer 1982), which might explain the typical pattern in kleptoparasitism. Veen (1977) also found that the number of fish-stealing Black-headed Gulls present in the tern colony varied with the state of the tide. During high tide, when the main feeding grounds of the gulls are out of reach and foraging activity of the gulls is low (Gorke 1990), the number of pirating gulls present in the colony is relatively high (Veen 1977). As a result, we found a high rate of kleptoparasitism around high tide. Kleptoparasitism decreased towards low tide, when the gulls resume feeding at the tidal flats. Weather conditions may influence the robbing behavior of the gulls in the same way. With strong winds the mud flats are less exposed during low tide and moreover, the gulls may have difficulties while searching for food in flight. So the high rates of food loss with strong winds probably result from high numbers of occasional pirates present in the tern colony.

Adaptive Strategies against Kleptoparasites

Birds that are victims of kleptoparasites have adopted several behavioral strategies to reduce food loss. Barnard (1984) distinguishes three forms of behavioral strategies against kleptoparasites, namely retaliation, evasion and increased effort. Probably the most obvious thing to do when suffering from high rates of kleptoparasitism is to simply avoid the pirates. As mentioned, Sandwich Terns appear to lure their chicks away from the robbing gulls. In this way, the terns can improve food intake, resulting in faster growth and improved survival of the chicks (Stienen and Brenninkmeijer 1999). When Sandwich Terns are not able to escape from the gulls, the birds have other strategies to reduce the impact of pirating gulls. A common strategy is for a parent to mask a feeding event by forming a shield around the chick with its wings, while the partner feeds the youngster. Some tern parents have developed an uncommon strategy to diminish the chance of robbery and, unlike most Sandwich Terns, they hold the fish longitudinally in the bill, almost invisible to the gulls. Also retaliation is sometimes practiced by Sandwich Terns, but the effectiveness of this behavior is low. Another way to diminish kleptoparasitism would be to shift towards a herring dominated diet, as this prey species is less vulnerable to kleptoparasitism than sandeels. However, in most years, parents did not supply more herring with increasing age of the chicks (Stienen and Brenninkmeijer 2002), suggesting that the availability of this prey species is limited. Instead, the parents compensated for the prey losses by increasing their foraging effort. So by adopting a wide range of behavioral strategies Sandwich Terns are usually able to live with the kleptoparasitising gulls, from which anti-predator behavior they benefit during the egg and early chick stage.

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Appendix 3.1. Estimates of coefficients (± SE) of a logistic regression analysis examining the effects of prey length (in adult bill length units), prey species (2 levels), chick age, wind speed, time of day, tide (12 levels) and year of observation (7 levels) on the fate of the fish brought to the tern chicks on Griend (*n* = 16,650). Estimates are printed bold if the added effect of a variable resulted in a significant change in deviance ($P < 0.05$). In cases of significant factor-variables (prey species, tide and year) estimates are printed bold for all levels. Robbed other sp. = robbed by species other than Black-headed Gulls, age^2 = quadratic function of age, wind speed^2 = quadratic function of wind speed etc.

Variable	Fate of the fish					
	Eaten by chick (R^2=0.08)	Robbed BHG (R^2=0.14)	Lost out of view (R^2=0.04)	Eaten parent (R^2=0.16)	Robbed other sp. (R^2=0.08)	Rest (R^2=0.37)
Constant	16.4 ± 1.03	-21.1 ± 1.13	-9.40 ± 1.17	-16.05 ± 1.45	-8.32 ± 1.28	-15.85 ± 2.95
Prey length	**-1.60 ± 0.068**	**1.41 ± 0.068**	**0.85 ± 0.071**	**0.88 ± 0.081**	**1.08 ± 0.079**	**1.48 ± 0.083**
Prey species *for sandeels*	0.19 ± 0.052	**-0.11 ± 0.055**	**-0.067 ± 0.058**	-0.56 ± 0.061	-0.14 ± 0.066	-0.083 ± 0.060
Age	**0.065 ± 0.011**	**0.22 ± 0.014**	**-0.140 ± 0.012**	**-0.36 ± 0.014**	**-0.17 ± 0.014**	**-0.32 ± 0.017**
Age^2	**-0.0020 ± 0.0004**	**-0.0055 ± 0.00042**	**0.0043 ± 0.00039**	**0.0080 ± 0.00052**	0.0044 ± 0.00046	**0.0018 ± 0.00084**
Wind speed	**-0.0045 ± 0.034**	**-0.0094 ± 0.037**	**-0.034 ± 0.039**	0.028± 0.039	0.26 ± 0.047	**-0.14 ± 0.045**
Wind speed^2	**-0.00264 ± 0.00205**	**0.0058 ± 0.0022**	0.00060 ± 0.0024	-0.0047 ± 0.0023	-0.012 ± 0.0027	0.0072 ± 0.0029
Time of day	**-3.99 ± 0.36**	**4.88 ± 0.39**	**1.72 ± 0.40**	**3.75 ± 0.49**	0.55 ± 0.45	1.59 ± 0.43
Time of day^2	0.45 ± 0.044	-0.58 ± 0.048	-0.16 ± 0.050	-0.45 ± 0.061	-0.073 ± 0.057	-0.20 ± 0.055
Time of day^3	**-0.021 ± 0.0023**	**0.028 ± 0.0025**	**0.0056 ± 0.0026**	0.023 ± 0.0032	0.0038 ± 0.0030	**0.0098 ± 0.0029**
Time of day^4	**0.00035 ± 0.00004**	**-0.00048 ± 0.000045**	-0.00006 ± 0.00005	**-0.00042 ± 0.00006**	-0.00007 ± 0.00005	-0.00017 ± 0.00005

Variable	Fate of the fish					
	Eaten by chick (R^2=0.08)	Robbed BHG (R^2=0.14)	Lost out of view (R^2=0.04)	Eaten parent (R^2=0.16)	Robbed other sp. (R^2=0.08)	Rest (R^2=0.37)
Tide						
for tidal hour –5	0.071 ± 0.10	0.000 ± 0.11	-0.22 ± 0.11	-0.19 ± 0.13	0.48 ± 0.13	-0.12 ± 0.12
for tidal hour –4	0.015 ± 0.10	0.049 ± 0.11	-0.11 ± 0.11	-0.19 ± 0.14	-0.43 ± 0.17	0.017 ± 0.12
for tidal hour –3	-0.15 ± 0.10	0.21 ± 0.10	-0.095 ± 0.11	-0.16 ± 0.14	0.43 ± 0.13	0.14 ± 0.11
for tidal hour –2	-0.25 ± 0.10	0.31 ± 0.10	-0.071 ± 0.11	0.23 ± 0.12	0.50 ± 0.13	0.20 ± 0.12
for tidal hour –1	-0.22 ± 0.093	0.39 ± 0.10	-0.25 ± 0.11	0.33 ± 0.12	-0.050 ± 0.14	-0.12 ± 0.12
for tidal hour 0	-0.16 ± 0.094	0.30 ± 0.10	-0.20 ± 0.10	-0.044 ± 0.13	-0.52 ± 0.16	0.44 ± 0.11
for tidal hour 1	-0.32 ± 0.094	0.37 ± 0.10	0.041 ± 0.10	-0.039 ± 0.13	0.26 ± 0.13	0.50 ± 0.12
for tidal hour 2	-0.29 ± 0.10	0.40 ± 0.10	-0.023 ± 0.11	-0.35 ± 0.13	0.33 ± 0.13	0.62 ± 0.12
for tidal hour 3	-0.36 ± 0.10	0.38 ± 0.10	0.16 ± 0.10	0.18 ± 0.12	0.11 ± 0.14	0.84 ± 0.11
for tidal hour 4	-0.14 ± 0.10	0.19 ± 0.10	-0.033 ± 0.11	0.35 ± 0.12	0.21 ± 0.14	0.22 ± 0.12
for tidal hour 5	-0.019 ± 0.10	0.11 ± 0.10	-0.18 ± 0.11	0.33 ± 0.12	-0.21 ± 0.15	0.15 ± 0.12
Year						
for 1993	-0.65 ± 0.13	0.28 ± 0.13	0.37 ± 0.16	2.75 ± 0.34	0.83 ± 0.15	0.48 ± 2.86
for 1994	-0.77 ± 0.13	0.60 ± 0.13	0.12 ± 0.16	2.19 ± 0.34	0.29 ± 0.16	7.50 ± 2.70
for 1995	0.17 ± 0.15	-0.50 ± 0.15	-0.19 ± 0.18	1.95 ± 0.38	-1.55 ± 0.25	8.75 ± 2.70
for 1996	-0.87 ± 0.13	0.58 ± 0.13	0.71 ± 0.15	0.98 ± 0.35	-0.40 ± 0.17	7.06 ± 2.70
for 1997	-0.66 ± 0.13	-0.062 ± 0.14	0.52 ± 0.16	0.24 ± 0.36	-1.37 ± 0.19	8.76 ± 2.70
for 1998	-0.79 ± 0.14	0.69 ± 0.14	0.49 ± 0.16	1.88 ± 0.35	-1.80 ± 0.22	5.97 ± 2.70

Chapter 4

Foraging decisions of Sandwich Terns in the presence of kleptoparasitising gulls

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ASTRACT

We studied prey selection of Sandwich Terns (*Sterna sandvicensis*) in the presence of kleptoparasitising Black-headed Gulls (*Larus ridibundus*) on Griend, Dutch Wadden Sea, from 1992 to 1998. Of the two major prey items, gulls robbed the larger sandeel more often than herring. Therefore, if the chicks would be exclusively feed on sandeel energy intake would be too low for the chicks to survive, provided that one parent attends the chick. By provisioning an increasing proportion of herring, parent terns could theoretically overcome an imminent food shortage when the chicks grow older. However, in most years the proportion of herring did not increase with the age of the chicks. Instead, parents increased their foraging effort with the growth of their offspring. In years with high proportions of food loss, parents left their chicks unattended at the nest more often. In this way parents were largely able to counterbalance food shortage of their offspring. In 1992 and 1996, when diet composition was unfavourable and food losses were high, parents left their chicks unattended at the nest for about 80% of the daylight period. It is argued that the present working level of parents might be higher than in the 1960s.

INTRODUCTION

A central theme in animal ecology is how animals organise their foraging activities in order to maximise the rate of energy intake (*e.g.* Schoener 1971; Krebs 1973; Charnov 1976). Orians and Pearson (1979) developed a foraging model that incorporates the special problems of travel restrictions encountered by animals returning to a central place after each foraging trip (see also Lessels and Stephens 1983). More complex models incorporate additional costs, like competition and predation risk (review in Stephens and Krebs 1986). In this paper, we will discuss some of the foraging decisions that Sandwich Terns (*Sterna sandvicensis*) must make in order to maximise food intake rate of their chicks in the presence of kleptoparasites. Sandwich Terns are almost strictly piscivorous birds and their food choice is highly specialised. Chicks are almost exclusively fed with high energetic prey species (*e.g.* Pearson 1968; Campredon 1978). On Griend, Dutch Wadden Sea, the diet of the chicks mainly consists of Clupeidae (herring (*Clupea harengus*) and sprat (*Sprattus sprattus*)) and Ammodytidae (mainly sandeel (*Ammodytes tobianus*)) (Veen 1977; Stienen *et al.* 2000). The specialised food choice of Sandwich Terns makes them extremely vulnerable for changes in the availability of one of their prey species. It therefore seems likely that the large between-year variation in diet composition on Griend (Veen 1977; this study) reflects strong fluctuations in food availability. This study examines the effects of changes in food composition on growth and survival of the chicks, and the parental ability to buffer imminent food shortage by increasing their foraging effort.

Sandwich Tern colonies are characterised by a high degree of coloniality, as is reflected in extremely synchronised breeding and very high nest densities (*e.g.* Veen 1977). After foraging the parents return to the colony with one prey held in full view in the bill. Under these conditions kleptoparasitism is likely to evolve (Brockmann and Barnard 1979). In fact, prey-carrying Sandwich Terns arriving in the colony are often heavily parasitised by neighbouring gulls and terns (*e.g.* Fuchs 1977; Veen 1977; Gorke 1990; Ratcliffe *et al.* 1997). On Griend, the current rate of kleptoparasitism by Black-headed Gulls (*Larus ridibundus*) has serious consequences for growth and survival of the tern chicks (Stienen and Brenninkmeijer 1999). In some subcolonies parents are able to escape from the high losses inflicted by the gulls by guiding their chicks away from the gulls. However, not all subcolonies provide suitable escape routes; some are surrounded by dense vegetation. In this study, we simulated this non-escape situation by keeping chicks in enclosures. This made it possible to study how parent terns faced with kleptoparasitism organise their feeding activities in order to maximise energy intake of their chicks. Only recently, a few studies have addressed to prey selection in the presence of kleptoparasites. Since kleptoparasites often select specific prey items it may be economical for hosts to avoid these prey items, as for example has been observed in American Oystercatcher (*Haematopus palliatus*), Golden Plover (*Pluvialis apricaria*) and Lapwing (*Vanellus vanellus*) (Thompson and Barnard 1984; Tuckwell and Nol 1997). In this paper, several behavioural strategies employed by Sandwich Terns to avoid or compensate for the losses inflicted by kleptoparasitising Black-headed Gulls will be discussed.

STUDY AREA AND METHODS

Study area

Sandwich Terns were studied on the Isle of Griend (ca. 57 ha during high tide), The Netherlands (53°15'N, 5°15'E), from April to August 1992-98. Apart from Sandwich Terns, three other species of gulls and terns nested on Griend in large numbers during the study period: Black-headed Gulls (16,000-28,500 pairs), Common Terns (*S. hirundo*; 1,500-3,300 pairs) and Arctic Terns (*S. paradisaea*; 800-1,250 pairs). During the study period, the population of Sandwich Terns fluctuated between 5000 (1997) and 8300 (1994) pairs, consisting of 8-14 subcolonies.

Observations of chicks and parents

Each year a part of a subcolony containing 50-150 nests was fenced to prevent the chicks from walking away from the nest site (see Stienen and Brenninkmeijer 1999). Within the enclosures all chicks were ringed, as soon as possible after hatching, so that their age could be determined accurately. In addition, each year about 20 chicks were colour-marked to enhance individual recognition. In 1992-98, observations on diet composition, prey length and parental nest attendance were made from an elevated hide placed at ca. 3 metres from the fenced colony. In general, observations were made continuously from 4:30 am to 10:30 pm. Prey size was estimated in quarters of the adult's bill length. Estimating prey size was calibrated per observer by holding fishes of different species and length in front of a stuffed tern's bill at a distance comparable to the field situation. Calibration greatly increased the accuracy of the estimates, and the largest error an experienced observer made was 0.25 bill lengths. Bill length (BL) of 697 adults trapped on their nests varied between 47.60 and 62.80 mm, corresponding with a deviation from the mean (54.31 ± 2.54 mm) of -0.12 to 0.16 BL. Three prey types were distinguished: Clupeidae (Herring *Clupea harengus* and Sprat *Sprattus sprattus*; further referred to as herring), Ammodytidae (Sandeel *Ammodytes tobianus* and Greater Sandeel *Hyperoplus lanceolatus*; further referred to as sandeel) and other prey. The category 'other prey' can largely be ignored since it amounted to less than 1% of all prey items (Stienen *et al.* 2000). The fate of the food was categorised as eaten by the chick, robbed by Black-headed Gulls, or lost otherwise (*e.g.* through intervention of other gulls and terns, fallen on the ground or lost out of the observer's sight).

In 1993-96, parents of 6, 6, 1 and 1 nests, respectively, were individually followed to obtain information on round trip travel time. Parents of each nest were distinguished from each other by characteristics of head moult, the presence of a ring or the yellowish colour of feathers we had dyed with picric acid. Mean trip duration was computed when more than 4 measurements for a specific prey length were obtained. Foraging trips lasting more than 180 min were excluded from the analysis as there was reason to believe that these parents either spent considerable time roosting or had already returned to the colony earlier but lost their fish out of the observer's sight and subsequently returned to forage before being observed by us.

Growth rate

When weather conditions allowed it, the chicks were weighed to the nearest gram every third day. For days in between, body mass was interpolated assuming linear growth. If a chick was measured at least 4 times until day 21 (day 0 = day of hatching), its average growth rate between age 3 and age 21 (phase of linear mass growth) was computed. Individual growth rates varied between 0.0 and 10.6 g.day^{-1} and averaged 6.25 ± 2.01 g.day^{-1} ($n = 181$). Growth rate of surviving chicks was significantly higher than that of non-survivors (7.03 ± 1.19, $n = 131$ and 4.22 ± 2.28, $n = 50$, respectively, Student's t–test, $T = 8.29$, $P < 0.001$).

Energy intake

For both herring and sandeel an allometric equation relating fish length to mass was obtained, using least square analysis on fish found in the colony and fish sampled in the Wadden Sea (Stienen *et al.* 2000). Water content measured for 10 herring and 12 sandeel ranging in length from 4.6 to 18.4 cm amounted to 74.51 ± 1.12% and 75.05 ± 2.43%, respectively. Energy density of the fish was measured by bomb calorimetry and amounted to 20.54 ± 1.50 kJ.g^{-1} and 20.30 ± 1.81 kJ.g^{-1} dry matter for herring and sandeel, respectively. From this the following equations relating fish length (L in cm) to energy content (E in kJ) can be computed:

Equation 1: $E = 0.03571 * L^{2.996}$ for herring
Equation 2: $E = 0.01499 * L^{2.982}$ for sandeel

In this paper, length-specific roundtrip travel time combined with energy content of the fish is used to predict energy provisioning to the chicks for each prey length and species, assuming a daylight period of 18 h. Further incorporation of length-specific consumption rates yields a prediction of daily energy intake of the chicks, assuming all prey provisioned to the chicks are of the same species and length. These predictions are then used to compute predictive foraging effort of the parents, which will be compared with observed foraging effort.

Energy requirements of the chicks

Klaassen *et al.* (1992) raised Sandwich Tern chicks in the laboratory under two feeding regimes. Four chicks, which were fed *ad libitum* herring and sandeel, achieved an average growth rate of 12.8 g.day^{-1}, while restricted food intake in four other chicks resulted in an average growth rate of 5.0 g.day^{-1}. These growth rates are close to the limits measured in the field, where minimum and maximum growth rates of surviving chicks amounted to 3.3 and 9.8 g.day^{-1}, respectively. We therefore used daily gross energy intake of the two groups of laboratory raised chicks as upper and lower boundaries for our calculations. Daily gross energy intake of the slow growing chicks must therefore be reached in order to survive and daily gross energy intake of the fast growing chicks can be regarded as the maximum amount of energy chicks can assimilate effectively. Figure 4.1

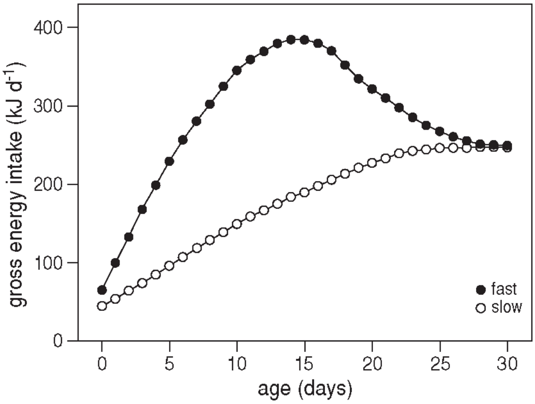

Figure 4.1. Gross energy requirements of growing Sandwich Tern chicks. Redrawn from Klaassen *et al.* (1992), lines are fitted by eye. Slow (circles) = chicks growing at 5 g.day^{-1}; Fast (dots) = chicks growing at 12 g.day^{-1}.

shows that energy intake of slow growing chicks gradually increased from 45 kJ.day^{-1} at hatching to 247 kJ.day^{-1} near fledging, while daily energy intake of the fast growing chicks was generally higher and reached a maximum of 385 kJ.day^{-1} when the chicks were two weeks old.

Data analysis and statistics

Data analyses were performed using SPSS/PC+ 4.0 statistical package (Norusis 1990). All statistical tests were performed using the Genstat statistical package (Genstat 5 Committee 1993). For logistic regression analyses, logit-transformed estimates of coefficients are presented in the tables. Linear terms were included in logistic regression analyses irrespective of the significance level if the quadratic term proved significant.

Although clutch size averaged 1.6 eggs per nest during the study period, Sandwich Terns hardly ever raise two chicks to fledging. Second hatched chicks receive almost nothing of the food parents bring to the nest (Stienen *et al.* 2000). During this study, 34% of the second hatched chicks died within ten days from hatching and only 0.7% of all pairs raised two chicks to fledging. The computations in this study referring to optimal prey size, diet selection and biparental foraging time therefore assume that only one chick is present in the nest.

RESULTS

Foraging yield

Round trip travel time was highly variable and ranged from 2 to 178 min. The duration of a foraging trip significantly increased with prey length (Fig. 4.2B, analysis of covariance, $F_{1,487} = 21.56$, $P < 0.001$). Foraging trips for herring generally lasted longer than for sandeel, and the added effect of prey species was almost significant ($F_{1,487} = 3.64$, $P = 0.06$). For that reason, we used separate regression equations for herring and sandeel (Fig. 4.2B) to compute daily foraging yield for each prey length, using the allometric relationships given in equations 1 and 2, and assuming a daylight period of 18 hours. Energy provisioning to the chicks can be greatly improved by feeding on large prey items (Fig. 4.2C). Maximum prey length observed in the field was 4 BL, corresponding with a foraging yield of 1089 and 2892 kJ.day^{-1} for sandeel and herring, respectively. This would be far more than the energy needed for maximal growth. However, such large prey was only exceptionally brought to colony. Average prey length as observed in the colony (2.0 and 1.6 BL for sandeel and herring, respectively) corresponds with a foraging yield of 270 and 359 kJ.day^{-1}, respectively, less than energy demands for maximal growth, but well above minimum energy requirements.

However, not all food brought to the colony was actually eaten by the chicks. Prey were sometimes lost to kleptoparasitising Black-headed Gulls, robbed by other species, fell to the ground, eaten by the tern parent or lost by the adult when out of the observer's view. In 1992-98, 64-81% of all food items were ultimately ingested by the chicks (Stienen *et al.* 2000). Food loss to the gulls and other losses significantly increased with prey length (Table 4.1). Adding the effect of prey species to that of prey size significantly improved the models, but had opposite effects on the probability of losing a prey to the gulls and to other causes. Taking prey length into account, sandeels were robbed less often than herring, while they were more often lost to other causes. Therefore, adding prey species after inclusion of prey size had no significant effects on the probability of prey consumption. Because of the high losses of long prey items (Fig. 4.2D), the prediction for the most profitable prey drastically changes (Fig. 4.2E). Now, herring of 2.9 BL and sandeel of 2.7 BL become the most profitable prey items, corresponding with maximum intake rates of 525 and 214 kJ.day^{-1}, respectively.

Diet selection

The preceding paragraph shows that Sandwich Tern chicks can achieve a maximum intake rate of 525 kJ.day^{-1} by exclusively feeding on herring of 2.9 BL. Provided that these large herring are available in sufficient quantities, adverse effects on chick growth are not to be expected because the maximum energy requirements of fast growing chicks amount to 385 kJ.day^{-1} (see methods). But when exclusively feeding on sandeel, chick growth will fall behind the maximum rate already within 5 days from hatching (Fig. 4.3). At day five, fast growing chicks need 230 kJ per day, while even by foraging on optimal sized sandeel of 2.7 BL energy intake is only 214 kJ.day^{-1}. When entirely feeding on sandeel, within 18 days from hatching energy intake would be insufficient even for minimum growth requirements (Fig. 4.3).

If we now compare average prey length as observed in the colony (dots in Fig. 4.3) with prey length needed for maximum and minimum growth, it shows that in the first 6 days after hatching parents increased the length of the supplied herring sufficiently to meet maximum growth requirements of their offspring. However, between age 7 and 17

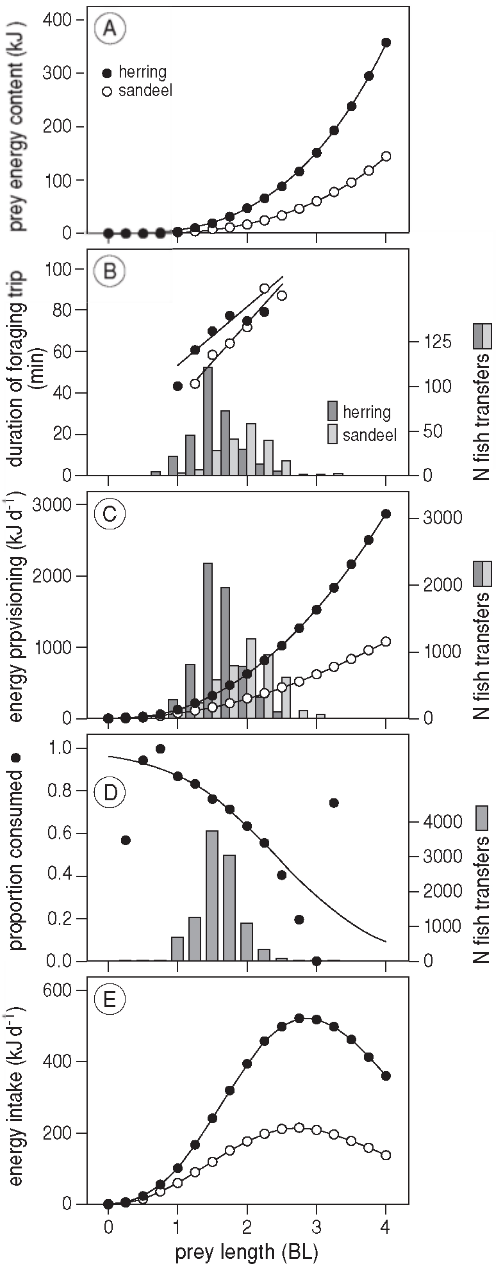

Figure 4.2. Relations between prey length (BL = adult bill length) and species, and energy content of the prey (A), round trip travel time (B), daily foraging yield (C), consumption probability (D) and daily energy intake (E) of Sandwich Tern chicks on Griend in 1993-96. (A) Drawn lines are allometric relationships given in equation 1 and 2. (B) Drawn lines are results of linear regressions examining the effect of prey size (BL) on the duration of the foraging trip (DF) (herring: $DF = 26.37+17.16*BL$, $n = 301$, $r^2 = 0.04$, $P = 0.006$; sandeel: $DF = 3.27+35.22*BL$, $n = 189$, $r^2 = 0.07$, $P = 0.004$). (C) Predictive daily energy provisioning (dots) to Sandwich Tern chicks on Griend if all food brought to the colony would be eaten by the chicks. The calculations are based on round trip duration and energy content for each prey species and prey length. Frequency distribution of prey delivered to the colony (bars) is shown on the right axis. (D) The drawn line shows the regression equation from Table 4.1. Bars indicate the observed number of fish transfers. (E) Energy intake was calculated by deducting length-specific consumption rates (Fig. 4.2D) from predictive daily energy provisioning to the chicks (Fig. 4.2C).

parents failed to increase prey length sufficiently for maximal development of their chicks, although minimum growth requirements were reached. For sandeel the prospects would be even worse, since already from day 2 onwards maximum growth requirements are not met. From day 14 onwards the sandeel transported to the colony were on average even too small for minimum growth of the chicks.

Table 4.1. Logistic regression analysis examining the effects of prey length and species (n = 10,976) on the fate of the prey brought to Sandwich Tern chicks on Griend in 1993-96. Food losses other than robbed by Black-headed Gulls consisted of food robbed by other species, fallen to the ground, eaten by the tern parent or lost by the adult when out of the observer's view.

Parameter	Estimate ± SE	Deviance change	df	*P*
Proportion robbed by Black-headed Gulls				
Constant	-4.311±0.126			
Prey length	1.597±0.071	587.8	1	< 0.001
Prey species	-0.158±0.055 if sandeel	7.6	1	< 0.01
Proportion lost otherwise				
Constant	-3.156±0.123			
Prey length	0.408±0.071	42.5	1	< 0.001
Prey species	0.233±0.058 if sandeel	9.5	1	< 0.01
Proportion eaten by the tern chicks				
Constant	3.180±0.118			
Prey length	-1.279±0.068	560.9	1	< 0.001
Prey species	0.004±0.052 if sandeel	0.01	1	NS

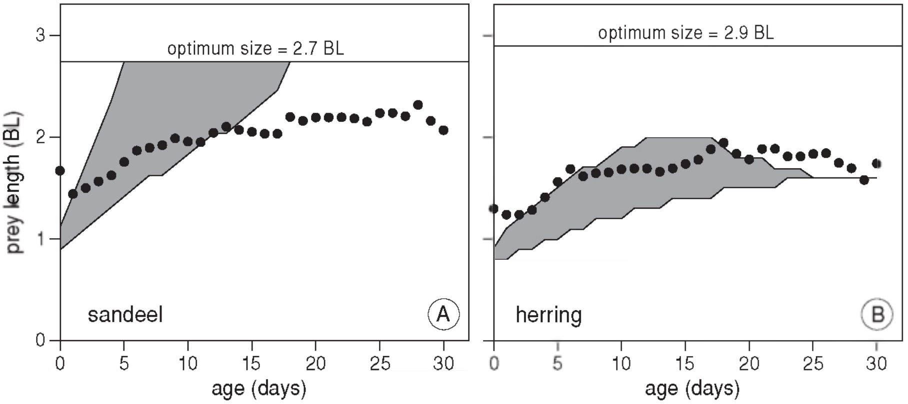

Figure 4.3. Age-specific prey size (means, BL = adult bill length) of Sandwich Tern chicks as observed in the colony (dots). Shaded areas enclose theoretical prey size needed for minimum and maximum growth. Optimum size = prey length required for maximum energy intake rates. When Sandwich Terns exclusively feed on sandeel (Fig. 4.3A) growth will fall behind maximum growth at day 5. At this point provisioning of even larger sandeel would not lead to increased energy intake by the chicks as a result of the high incidence of loss of large prey. At day 18 energy intake would become too low for minimum growth, even if the terns would exclusively catch optimum-sized sandeel. When feeding exclusively on herring (Fig. 4.3B) maximal growth can be achieved.

Concluding, in the first two weeks after hatching sandeel would be suffice for minimum growth. However, sandeel should be largely avoided when the chicks grow older or if parents strive for maximal growth of their chicks already during the early chick stage. One might, therefore, expect that as the chicks grow the diet would comprise more herring, with peak inputs of herring between ages 15 and 30, depending on the growth rate of the chicks. Although in all years diet composition varied significantly with the age of the chicks (Table 4.2), no general pattern was found. Only in 1996 and 1998, but not in other years, the highest proportion of herring was found between age 15 and age 30.

Effects of diet composition on energy intake, growth and survival of the chicks

The yearly average proportion of herring in the diet of Sandwich Tern chicks on Griend ranged from 33% in 1996 to 85% in 1994. From the above paragraphs, one would expect that these large differences in diet composition would have effects on the rate of food loss and energy intake of the chicks, and thus on chick growth and survival. Indeed, the average yearly rate of food loss significantly increased with higher proportions of sandeel

Table 4.2. Logistic regression examining the relationship between diet composition (proportion herring) and the age of Sandwich Tern chicks on Griend in 1992-98. Degrees of freedom (df) refer to the number of chick days.

Year	Parameter	Estimate ± SE	df	Deviance	P-value
1992	Constant	-1.181 ± 0.415	177		
	Age	0.2315 ± 0.0898		8.0	< 0.01
	Age^2	-0.00912 ± 0.00433		7.4	< 0.01
1993	Constant	0.060 ± 0.166	420		
	Age	0.0339 ± 0.0252		0.8	NS
	Age^2	-0.001296 ± 0.00084		4.3	< 0.05
1994	Constant	0.544 ± 0.199	393		
	Age	0.2569 ± 0.0337		1.7	NS
	Age^2	-0.00899 ± 0.00112		103.1	< 0.001
1995	Constant	-1.38 ± 5.86	146		
	Age	0.271 ± 0.567		4.7	< 0.05
	Age^2	-0.0078 ± 0.0136		0.7	NS
1996	Constant	-0.437 ± 0.176	335		
	Age	-0.1560 ± 0.0303		80.2	< 0.001
	Age^2	0.006296 ± 0.00098		77.3	< 0.001
1997	Constant	1.606 ± 0.165	328		
	Age	0.0193 ± 0.0331		28.6	< 0.001
	Age^2	-0.00192 ± 0.00125		4.1	< 0.05
1998	Constant	1.136 ± 0.112	303		
	Age	-0.1742 ± 0.0243		0.1	NS
	Age^2	0.006647 ± 0.00090		55.7	< 0.001

(Pearson regression, $n = 7$, $r^2 = 0.57$, $P = 0.05$). Although energy intake was relatively low in years when sandeel dominated the chicks' diet (Fig. 4.4), the relationship was not significant ($r^2 = 0.25$, $P = 0.25$). However, energy intake was positively correlated with the yearly proportion of fish eaten by the chicks (Fig. 4.4, $r^2 = 0.63$, $P = 0.03$). The average yearly growth rate of surviving chicks varied between 6.0 and 7.5 $g.day^{-1}$ and showed no relationship with the proportion of herring or food consumption probability (Fig. 4.4, $r^2 = 0.18$, $P = 0.34$ and $r^2 = 0.39$, $P = 0.13$). Also fledging success showed no relationship with either diet composition or food consumption probability (Fig. 4.4, $r^2 = 0.01$, $P = 0.88$ and $r^2 = 0.12$, $P = 0.45$, respectively). Fledging success within the enclosures was lowest in 1992, when 46% of all first hatchlings survived until fledging, and highest in 1995, when 75% survived.

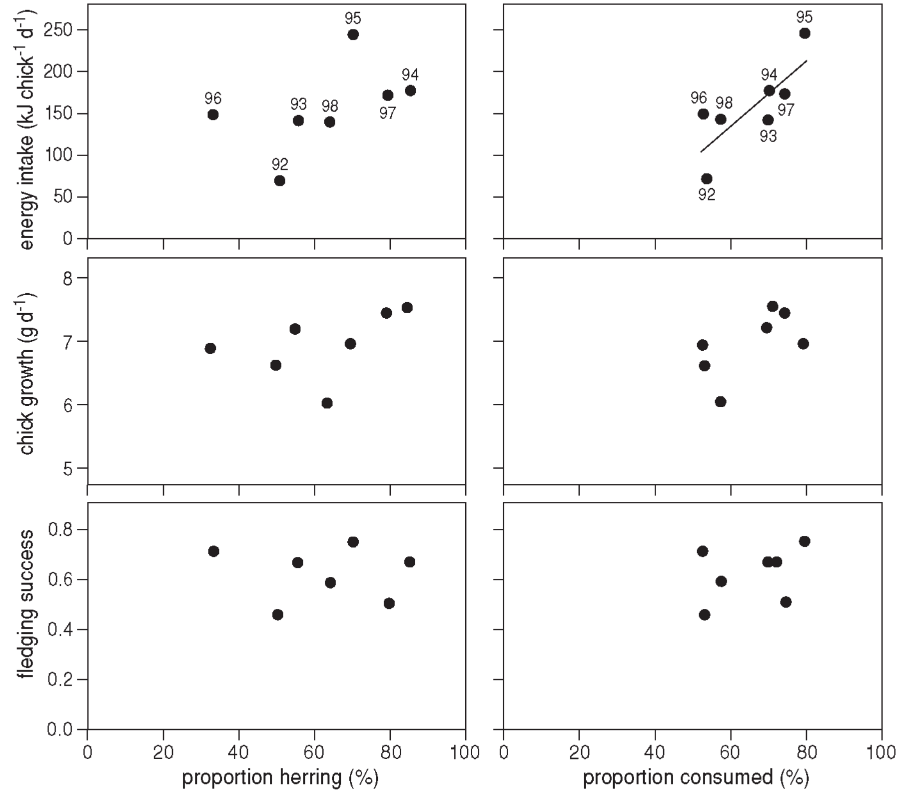

Figure 4.4. Effects of yearly average diet composition and food consumption probability on average yearly daily energy intake (upper graphs), chick growth (middle graphs) and fledging success (lower graphs) of Sandwich Tern chicks on Griend, 1992-98. To largely exclude effects of age, food consumption probabilities and energy intake rates were computed for chicks older than 15 days. A chick was assumed to have fledged when it had reached the age of 25 days. Average yearly growth was computed for first hatchlings that survived until fledging. Results of linear regression analyses are shown at the top of each figure. Lines represent significant relationships.

Parental foraging effort

One of the assumptions used so far is that the other parent stays with the chick when the partner goes out foraging. In fact, this assumption is not supported by observations in the field. Not only did parents spend some time together at the nest, but even more important they sometimes left their offspring unattended at the nest. The time that both parents were present at the nest can be neglected since on Griend it was on average less than 1% of the daylight period. The time that both parents were absent averaged 16.5% of the daylight period and showed considerable variation with chick age and between years (Fig. 4.5). Because small hatchlings cannot do without brooding (Klaassen *et al.*

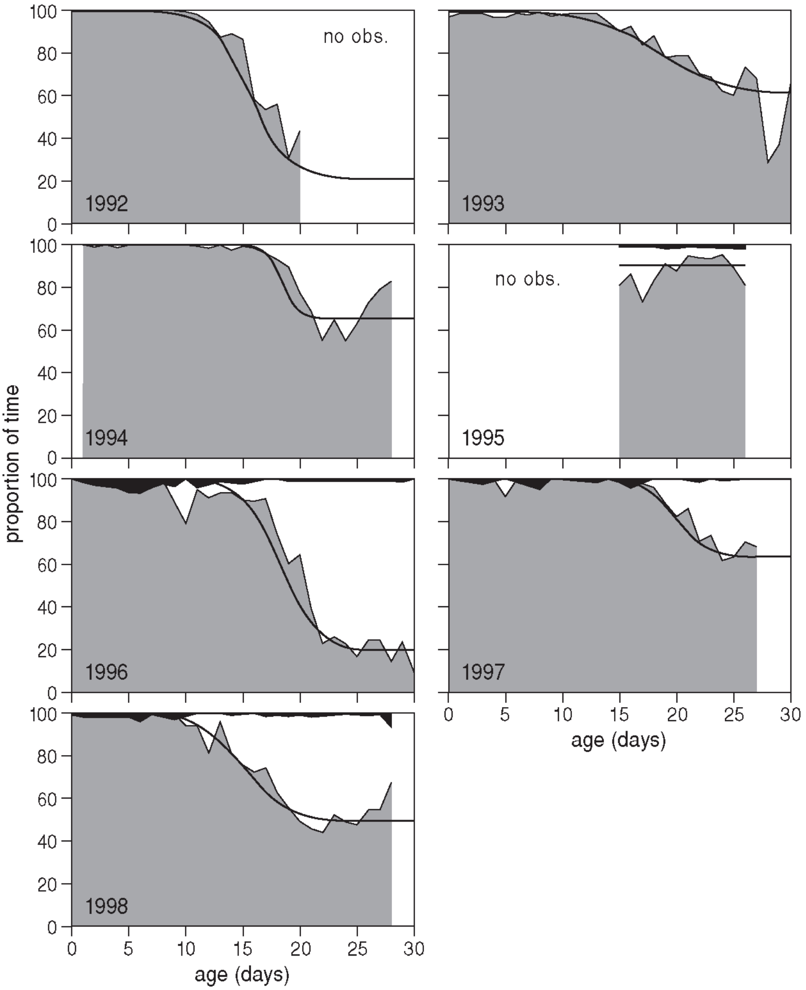

Figure 4.5. Development of parental nest attendance with the age of Sandwich Tern chicks on Griend in 1992-98 (grey shaded areas: 1 parent present at the nest, black areas: 2 parents present, white areas: no parents at nest). Drawn lines are the results of least square analysis of the proportion of time the chicks were attended by at least one parent.

1994) and because they have low energy needs, these chicks were almost never left alone at the nest. When the chicks grew older they were left alone more often, and especially in 1992, 1996 and 1998, when the proportion of herring in the chicks' diet was less than 50% (Fig. 4.4), chicks were left unattended relatively often (Fig. 4.5). In order to describe the relationship between chick age and the proportion of time the chicks were left unattended at the nest, for each year a logistic curve was fitted (Fig. 4.5). Asymptotic values of the logistic equations were used as a measurement of parental effort. Only for 1995, when observations were restricted to relatively old chicks, the mean value of biparental foraging time in this year was used. Average yearly parental effort significantly decreased with higher proportions of herring in the diet (Fig. 4.6, r^2 = 0.57, P = 0.05) and strongly correlated with the average yearly proportion of food eaten by the chicks (r^2 = 0.91, $P < 0.001$).

Increasing parental effort seems to be an important mechanism for buffering against fluctuations in food availability or kleptoparasitism. This is further illustrated in figure 4.7, where parental effort in Sandwich Terns is predicted from diet composition and growth rate of the chicks. If the diet consists totally of herring, minimum growth requirements of the chicks can be met without biparental foraging, whereas if the food would contain only sandeel parents have to leave their chicks unattended for 40% of the daylight period (drawn lines in Fig. 4.7). If parents strive for maximum growth, they have to leave the chick unattended for 43% of the daylight period if the diet would totally consist of herring. If the diet consists entirely of sandeel, maximum growth requirements can not be met, even if the parents leave their chicks unattended for the entire daylight period. Except for 1995, observed parental effort (dots in Fig. 4.7) was higher than predicted from average yearly diet composition and growth rate of the chicks (circles in Fig. 4.7). In 1992, 1996 and 1998 predictions of parental effort were much lower than observed parental effort.

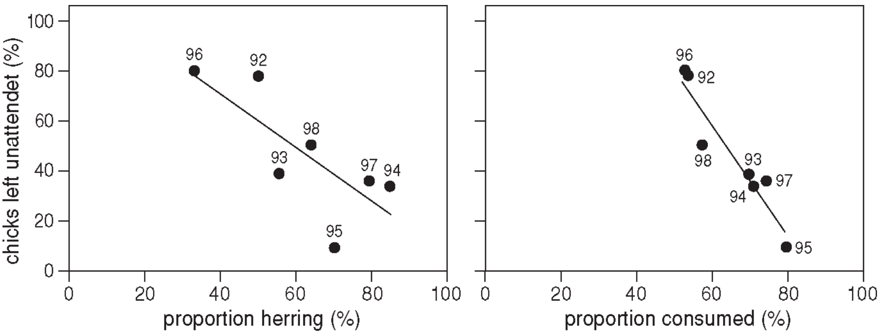

Figure 4.6. Parental nest attendance (asymptotic values of the proportion of time parents left the chicks unattended at the nest, Fig 4.5) in relation to diet composition (left graph: Pearson regression, $r^2 = 0.55$, $n = 7$, $P = 0.06$) and food consumption probability (right graph; Pearson regression, $r^2 = 0.84$, $n = 7$, $P = 0.004$), Griend, 1992-98.

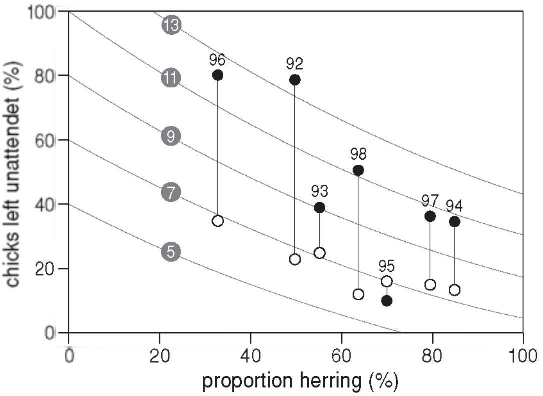

Figure 4.7. The proportion of time a Sandwich Tern chick must be left unattended in order to achieve peak energy intake rates at different growth rates of the chick in relation to diet composition (drawn lines) and assuming that only one chick is present in the nest. Numbers above lines indicate growth rate. Peak energy requirements of the chicks are computed using the relationship between growth rate and maximum gross energy intake (GEI_{MAX}) from figure 5 in Klaassen *et al.* (1992): $GEI_{MAX} = 157 + 17.8 * growth$. Energy intake rate of the chicks (GEI) was computed assuming that only average observed sized prey was fed to the chicks (1.6 and 2.0 BL, respectively, in herring and sandeel, corresponding with daily intake rates of 272 kJ and 176 kJ): $GEI = (1 + \%CU/100) * (PH/100*272+(1-PH/100)*176)$, where %CU = proportion of time the chick is left unattended at the nest and PH = proportion of herring. Dots = the average observed yearly proportion of time the chicks were left unattended. Circles = prediction of the proportion of time the chicks are left unattended, given the average observed growth rate and diet composition.

DISCUSSION

Buffering against fluctuating environmental conditions

Prey-stealing by Black-headed Gulls plays a crucial role for the foraging decisions that Sandwich Terns on Griend have to make. Energy intake of Sandwich Tern chicks may be limited to a critical level as a result of high robbing pressure on large prey. Due to the higher energy content of herring, smaller fish can be taken to obtain the same amount of energy. These smaller fish are less likely to be stolen by gulls, making herring a much more profitable prey species for the terns. If parent terns would exclusively forage on sandeel energy intake would be too low for the chicks to survive. By supplying the chicks also a sufficient amount of the more advantageous herring, energy intake, and thus growth and survival of the chicks, can be improved. Our calculations suggest that already during the first week after hatching, when both the energy demand of the chicks and the rate of kleptoparasitism are still relatively low (own observations), diet composition will have large effects on chick growth provided that one parent stays at the nest. As the season progresses, herring becomes increasingly important. But even when exclusively feeding on herring of observed prey length, maximum growth of the chicks can not be reached without simultaneously foraging of the parents. Parents do not seem to have much leeway in their choice of prey species as in most years the chicks' diet did not show the expected shift towards more herring with increasing age of the chicks. This suggests a limited availability of the more profitable herring, so that a shift towards a less vulnerable diet could not be realised. Instead, parents tried to compensate for an imminent food shortage by increasing their foraging effort, leaving the chicks unattended at the nest more often in years when food losses were high. Since food consumption probabilities were closely related to diet composition, parental effort also tended to increase with higher proportions of sandeel. In years when diet composition suggested a short supply of herring (1992, 1996), parents had to work hard. In these years, older chicks were left alone at the nest for more than 50% of the daylight period. In 1994, 1995 and 1997, however, the diet of the chicks was dominated by herring, suggesting a relatively high availability of this prey species. As a consequence simultaneous parental foraging occurred at a low level, while chick growth was among the highest recorded in this study.

On Griend, average annual growth rates varied between 6.0 and 7.5 g.day^{-1}, thus most chicks in our study grew at a rate well below that of chicks fed *ad libitum* (12.8 g.day^{-1}; Klaassen *et al.* 1992). So also in favourable years, chicks grew at a rather slow rate, while parents could theoretically have increased their foraging effort to achieve faster growth. Fast growth, however, results in relatively high energy demands of the chicks (Klaassen *et al.* 1994). On the other hand, fast growth might improve the survival chances of a chick, but in Sandwich Terns chick survival was almost not affected above a growth rate of 7 g.day^{-1} (unpubl. data). Thus, increased foraging efforts would probably not lead to a large increase of reproductive output, unless some parents might have been able to raise two chicks, which now occurred only very rarely. The predictions shown in figure 4.7 suggest that even when the diet contains only herring it would be impossible for an average parent to raise two chicks growing more than 7 g.day^{-1} to fledging. This is in accordance with the very few pairs (0.7%) that fledged two chicks during the study period. Other fitness costs might be that unattended chicks are more vulnerable to predation, as is frequently observed in seabird colonies (*e.g.* Hamer *et al.* 1991; Bukacinski *et al.* 1998), although in the Sandwich Tern chick predation is relatively low towards the end of chick-rearing (Veen 1977). Moreover, unattended tern chicks provoke serious attacks of neighbouring gulls and terns, which sometimes results in the death of a chick (own observations). Nevertheless, fledging success in our study was not correlated with parental nest attendance (Pearson regression, $r^2 = 0.18$, $P = 0.34$). On the other hand, increased parental foraging might involve fitness costs for the parents. Effects of parental effort on subsequent fecundity have been demonstrated in a wide variety of bird species (*e.g.* Røskaft 1985; Smith *et al.* 1987; Gustafsson and Sutherland 1988; Verhulst 1995; Wernham and Bryant 1998). An effect of increased parental effort on subsequent survival is more difficult to demonstrate, but evidence is growing that such effects occur (Daan *et al.* 1996; Golet *et al.* 1998). Life history theory predicts that individuals should strive for maximisation of lifetime reproductive success. Long-lived species like

Sandwich Terns should, therefore, reduce their current breeding effort rather than jeopardise their residual reproductive value (Drent and Daan 1980). In Herring Gulls (*L. argentatus;* Pons and Migot 1995) and Puffins (*Fratercula arctica*; Wernham and Bryant 1998), variation in food availability indeed affects clutch size and reproductive output, but not adult (local) survival. In the Kittiwake (*Rissa tridactyla*), however, reproductive costs do affect survival (Golet *et al.* 1998), thus also in long-lived species parents sometimes trade their own survival for that of their offspring.

Energy intake of the chicks is a product of food delivery rate to the colony, length distribution and consumption probability of the food. Prey delivery rate can be adapted by simultaneously foraging of the parents to fit energy demands of the chicks and to counteract variation in food availability and consumption rates caused by factors other than prey length (*e.g.* wind speed, Veen 1977). In this study, the average yearly proportion of time the chicks were left unattended correlated very well with the average yearly energy intake per parent (Pearson regression, $n = 7$, $r^2 = 0.86$, $P = 0.003$). Apparently in most years parental buffering was sufficient to keep actual energy intake of the chicks above 140 kj.day^{-1} and to avoid negative effects on chick growth and survival (Fig. 4.4). The model presented in figure 4.7 depicts that only in most unfavourable years, when no herring is available, parents would not be able to fully compensate for the high losses inflicted by the gulls. In order to achieve a growth rate of 7 g.day^{-1}, which was the average growth rate of surviving chicks in this study (see methods), we expected biparental foraging to occur between 10 and 36% of the time, given the average annual proportions of herring observed. However, the proportion of time the chicks were left unattended varied between 10 and 80% of the time. Except for 1995, our computations yielded a conservative prediction (Fig. 4.7), which might have several reasons. In the first place, energy requirements of the chicks were measured under laboratory conditions. In the field chicks have higher costs for thermoregulation and activity, so that gross energy requirements will be somewhat higher than shown in figure 4.1. In the second place, some parents had to feed two chicks during the last week before fledging, while the predictions assume that only one chick is present. Also, the predictions are based on length-specific food transport rates and food consumption rates mainly measured in relatively favourable years (1993 and 1994). However, the magnitude of the deviation differs from year to year, with relatively high parental effort measured in 1992, 1996 and 1998 and low effort in 1995. This variation is due to yearly differences in energy intake rate caused by differences in provisioning rate, prey length and robbing intensity. In 1992, only 129kJ.day^{-1} was provided to the chicks per parent (Table 4.3). In combination with low proportions of herring and high prey losses, this resulted in low energy intakes per parent, even when considering that in this year chicks were only followed until 21 days old. In 1996 and 1998, at least one of the two prey items was relatively short compared to other years (Stienen *et al.* 2000). Still, robbery was high resulting in low rates of energy intake per parent. In contrast in 1995, provisioning rates were high and food losses exceptionally low, resulting in high intake rates per parent and accordingly low parental effort.

Table 4.3. Daily energy provisioning per parent (kJ.chick^{-1}.day^{-1}.parent^{-1}) and daily energy intake rate per parent (kJ.chick^{-1}.day^{-1}.parent^{-1}) of Sandwich Tern chicks older than 15 days on Griend in 1992-98. Daily energy provisioning to the chicks (DEP, kJ.chick^{-1}.day^{-1}) and daily energy intake rate (DEI, kJ.chick^{-1}.day^{-1}) were corrected for the proportion of time the chicks were left unattended (%CU) as follows: DEP^{cor}=100%*DEP/(100+%CU) and DEI^{cor}=100%*DEI/(100+%CU).

Year	Energy provisioned (mean ± SE)	Energy intake (mean ± SE)	Number of Chick days
1992	128.7 ± 14.3	58.7 ± 8.0	32
1993	181.6 ± 6.7	115.2 ± 4.9	207
1994	221.2 ± 6.8	147.7 ± 5.6	212
1995	299.6 ± 8.4	225.5 ± 7.4	143
1996	177.2 ± 4.6	88.4 ± 3.7	163
1997	213.5 ± 5.6	147.0 ± 4.7	152
1998	190.6 ± 6.6	101.0 ± 4.4	172

There are indications that food availability around Griend was much better in the past than in the 1990s. In 1966, under normal weather conditions, individual chicks were fed 15 fish per day and already at age 5 they were fed 38 g fish per day (Veen 1977), corresponding with an energy intake of 192-199 kJ.day^{-1}. In the 1990s, however, chicks at this age were fed only 7.1 ± 4.2 fish.day^{-1} (n = 91), corresponding with an energy intake of 97.7 ± 63.9 kJ.day^{-1}. Chick mortality was, however, almost equal in the two periods (unpubl. data). It thus seems likely that chicks grew faster and parental nest attendance was higher than in the 1990s, but unfortunately no data on growth and parental effort are available for 1966. A low availability of herring might explain why the population on Griend only partly recovered from the collapse in the 1960s caused by poisoning of the Dutch coastal waters with pesticides (Koeman and Van Genderen 1966; Brenninkmeijer and Stienen 1992). The current population size on Griend (on average about 7000 pairs in the 1990s) is less than half the size prior to the collapse, which is not compensated for by an increase in other parts in The Netherlands (Brenninkmeijer and Stienen 1992). The pesticide incident was followed by an extremely low stock size and recruitment rate of North Sea herring in the 1970s (Corten 1990). So following the collapse in the 1960s there probably was a period with highly unfavourable food composition, resulting in maximum working levels of parents. This might have affected reproductive output and the number of pairs that actually started breeding on Griend, but no studies are available that can support this. However, many studies found that changes in bird numbers are related to changes in food supplies (Newton 1998). Also in terns it has often been suggested that food availability directly influences the number of pairs that attempt to breed (Monaghan & Zonfrillo 1986; Crawford & Dyer 1995; Phillips *et al.*

1996). Such might also be the case in Sandwich Terns. Indeed, we found a strong positive correlation between the number of pairs nesting on Griend in the period 1992-1996 and the proportion of herring in the chicks' diet (Pearson regression, $n = 5$, $r^2 = 0.88$, $P = 0.02$). Until 1997, Griend supported all Sandwich Terns nesting in the Dutch Wadden Sea. From 1997 onwards, other large colonies were established in the area and the correlation between the number of pairs nesting on Griend and diet composition was no longer valid. Nevertheless, the fewer breeding attempts in poor years might have indirectly improved breeding success if mainly 'high quality' individuals started breeding. These individuals might be able to spend more time on foraging and counterbalance the expected negative effects on growth and survival of their offspring.

Foraging decisions

The optimal foraging theory predicts a selective prey choice depending on the encounter rate of the prey (Stephens and Krebs 1986). When a tern encounters a small prey it can choose between catching the prey or continue searching for a larger prey. The theory of central place foraging predicts that the acceptance of a prey depends on the availability of higher-ranked prey. If insufficient numbers of highly ranked prey are available, the diet will be broadened through inclusion of lesser-ranked prey. There is growing evidence that birds incorporate additional constraints, like kleptoparasitism, in their consideration of which prey to catch (Thompson and Barnard 1984; Tuckwell and Nol 1997). Taking kleptoparasitism into account, herring would by far be the most profitable prey species for Sandwich Terns on Griend. However, the encounter rate of the most profitable size seems low, as the majority of all herring brought to the ternery were much smaller than the most profitable size (2.9 BL). The main foraging area of Sandwich Terns nesting on Griend is situated between the isles of Vlieland and Terschelling, 10-12 km northwest of Griend (Veen 1977). These waters support mainly small herring (Fonds 1978; Corten 1996), thus narrowing the food choice of Sandwich Terns on Griend.

The advantage of a herring dominated diet for Sandwich Terns breeding on Griend can not be translated to other areas and might even be restricted to the research period as it totally depends on the length-specific encounter rate and consumption probability. In fact, on the Farne Islands in the early 1960s the prey of Sandwich Terns consisted for 74% of sandeel, while chick growth was much higher than in our study (Pearson 1968). However, sandeel provided to the chicks were smaller (on average about 2.5 g) and fishing trips lasted shorter (1.03 h) than in our study (3.5 g and 1.2 h). Sandeel availability around the Farne islands might have been higher or sandeel was found closer to the colony. Also the rate of kleptoparasitism on the Farne Islands was probably extremely low, as at that time the Farne Islands held only a few pairs of Black-headed Gulls (1-2 pairs). So diet composition cannot be generally used as an indicator for reproductive success. Parental effort on the other hand seems a good candidate to serve as a general indicator of energy intake in Sandwich Terns.

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Chapter 5

Keep the chicks moving: how Sandwich Terns can minimize kleptoparasitism by Black-headed Gulls

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Animal Behaviour 57: 1135-1144 (1999)

ASTRACT

Sandwich Terns *Sterna sandvicensis* often nest in association with Black-headed Gulls *Larus ridibundus*. The gulls provide protection against predators, but can also adversely affect the terns' reproductive success through predation and piracy of fish. To test whether leading the chicks away from the nest site is an evasive strategy used by the parents to reduce the incidence of robbery by the gulls, we kept one group of Sandwich Tern chicks at their original breeding site, while, with a wire-netting enclosure, we moved another group away from the gulls. The rate of kleptoparasitism was greatly reduced when the tern chicks are led away from the original nest site, resulting in faster growth and an earlier fledging. The rate of food parasitism and chick condition were affected only during the first 5 days of the experiment. After that, the rate of kleptoparasitism no longer differed between chicks that we moved away and those remaining in the colony. A second shift of the chicks again led to less kleptoparasitism and better chick condition. In line with these findings, the condition of free-living chicks that were lured away from their nesting site by their parents also improved. In particular chicks initially in poor condition that apparently suffered from high rates of kleptoparasitism left the colony site. Free-living chicks are often lured away from the robbing gulls. However, not all subcolonies provided suitable escape routes and subsequently chicks in such subcolonies suffered from high mortality rates.

INTRODUCTION

Kleptoparasitism, the stealing of already procured food by other conspecific or heterospecific individuals, is widespread among birds (Brockmann & Barnard 1979). It often occurs among seabirds as they are generally colonial nesters and also highly aggregated when foraging (Furness 1987). Terns are especially vulnerable to kleptoparasitism. In contrast to many gulls, the majority of the tern species does not swallow the fish after catching it, but hold it visible in the bill when transporting it to the colony. Many studies report that terns are victims of kleptoparasitic behaviour of gulls or other terns (*e.g.* Hopkins & Wiley 1972; Hatch 1975; Hulsman 1976; Taylor 1979). Birds have adopted several behavioural strategies to reduce food loss through kleptoparasitism (Barnard 1984), such as retaliation or evasion. They may also tolerate losses or compensate for them by increasing their foraging effort. Evasion, the avoidance of attacks, is probably the most frequent strategy adopted and includes faster handling of prey, shifting the diet, synchronizing feeding activities and increasing the distance from the pirates (Amat 1990). To our knowledge these behavioural strategies have not yet been reported for terns.

Sandwich Terns *Sterna sandvicensis* almost exclusively breed together with other tern species or close to gulls (*e.g.* Ansingh *et al.* 1960; Langham 1974; Fasola & Canova 1992; Gorke 1990; Yorio & Quintana 1997). In The Netherlands, they always breed in association with Black-headed Gulls *Larus ridibundus* (review in Veen 1977). By seeking the proximity of the gulls, the terns benefit from the aggressive antipredator behaviour of their neighbours. Gulls actively chase away avian predators and act as a buffer against ground predators (Veen 1977). However, breeding together with Black-headed Gulls also involves disadvantages for the terns. The gulls themselves are important predators of tern eggs and chicks, and steal fish the parents bring to their chicks (Lind 1963; Fuchs 1977a, b; Veen 1977; Gorke 1990; Ratcliffe *et al.* 1997). It is generally assumed that the advantages of associative nesting outweigh the disadvantages (Lind 1963; Veen 1977). This assumption, however, is based mainly on findings during incubation and the onset of the chick-rearing period, whereas the advantages of associative nesting become less important with increasing age of the chicks. The main chick predators (Black-headed Gull, Herring Gull *L. argentatus*, and Lesser and Great Black-backed Gull *L. fuscus* and *L. marinus*) prefer chicks of up to 2 weeks old, whereas larger chicks are much less subject to predation (Veen 1977). Thus with increasing size of the chicks there is less need to stay within the protection of the Black-headed Gulls. In fact, it is known that Sandwich Tern parents often lead their chicks away from the nesting site (Cullen 1958; Chestney 1970; Veen 1977), which is often interpreted as a result of human disturbance (Chestney 1970; Campredon 1978) or as a mechanism to avoid infectious diseases (Cullen 1958). However, it could also be a mechanism to avoid piracy by the neighbouring gulls. Kleptoparasitism can remove a considerable part of the food brought to the chicks and therefore can therefore have serious consequences for their daily food intake. Kleptoparasitism may thus impair the chicks' growth rate and survival. We hypothesize that leading the chicks away from the gull colonies reduces kleptoparasitism, resulting in increased growth and survival of the tern chicks. To test this hypothesis, we kept one group of Sandwich tern chicks at their original breeding site, while another group was moved away from the colony. We then compared the growth rate of these groups and free-living chicks.

METHODS

Study Area, Colony Structure and Meteorological Measurements

We conducted the study on the Isle of Griend, The Netherlands (53°15'N, 5°15'W) in the Dutch Wadden Sea. Griend harbours the largest colony of nesting Sandwich Terns (8200 and 5600 breeding pairs in 1995 and 1996 respectively) in Europe. In 1995 and 1996, the breeding population at Griend consisted of a number of subcolonies, varying in size between 140 and 1590 breeding pairs. Subcolonies were separated from each other by 25-200 m. Within a subcolony the onset of laying was highly synchronised, although some pairs settled in the colony at a later stage. Subcolonies of terns were at least partly surrounded by nesting black-headed gulls and some gulls even nested within the tern colony.

Throughout the experimental work we recorded wind speed with a calibrated cup anemometer placed within 500 m of the colony at standard meteorological level (10 m). We also recorded air temperature and rainfall, but only wind speed is considered here since this parameter is known to influence the rate of kleptoparasitism (Veen 1977).

Enclosures

In 1995 and 1996, we enclosed a small part of a colony, containing ca. 100 clutches, using wire netting 50 cm high. The lower 20 cm of the wire netting was covered with black plastic, to avoid injuries to the chick's bills. In 1995, about 2 weeks after they hatched we transported nine chicks from the initial enclosure (from now on called the permanent enclosure) to an enclosure placed at 50 m from the original colony site (from now on called the moved enclosure). The remaining chicks were held in the permanent enclosure. At first, some parents had difficulties finding their chicks again in the moved enclosure, but within a few hours all but three pairs had found their chick. The three lost chicks were replaced on their original site, leaving six chicks in the moved enclosure. In 1996, the enclosure was moved stepwise to resemble more closely the natural situation in which chicks may constantly be lured away to new sites on the island. As an added advantage, it was easier for the parents to find the displaced chicks. At first the enclosure was placed 15 m from the original colony. This time all 15 pairs found their chick within a few hours. Seven days later the moved enclosure was moved 25 m farther away. The direction in which the chicks were moved corresponded with the main direction in which free-living chicks moved. This was always away from the black-headed gull colony.

Observation on Food Supply and Kleptoparasitism

Observations on food supply were made by the unaided eye or with binoculars (up to 10x magnification) from a hide several meters from the enclosure. The observations were restricted to the hours around high tide. To facilitate individual recognition within the permanent enclosures, we colour marked 19 chicks in 1995, and 20 chicks in 1996, using picrinic acid and ink. Within the moved enclosures chick recognition was possible by individual differences in size or plumage characteristics and by location within the enclosure. We classified the fate of fish brought to the chicks as 'eaten by the chick', 'robbed by black-headed gulls' and 'other causes of loss' (such as lost out of the observer's sight, rejected by the chick, left in the nest or eaten by the parent). Whenever possible, we noted the time between the arrival of a parent in the colony and the feeding of the fish. In 1996, we recorded the numbers of black-headed gulls participating in a robbery incident.

Growth

All chicks within the enclosures were banded within 3 days of hatching. We estimated the age at ringing from the size of the yolk sac, the size of the head and plumage characteristics. Every third day (when weather conditions permitted) the chicks were weighed to the nearest gram, and total head size (head + bill, ± 0.1 mm) and stretched wing chord (± 1 mm) were measured. Body mass on days between two measurements was computed assuming linear growth. We obtained a condition index (CI, %) by calculating the deviation of the measured body mass (M, g) from the expected body mass (M_{exp}, g) for that age (based on the mean body mass of all chicks of known age, both within and outside the enclosures, measured in 1995 and 1996; Fig. 5.1) (Eq. 1):

$$CI = \frac{M - M_{exp}}{M_{exp}} \times 100\%$$

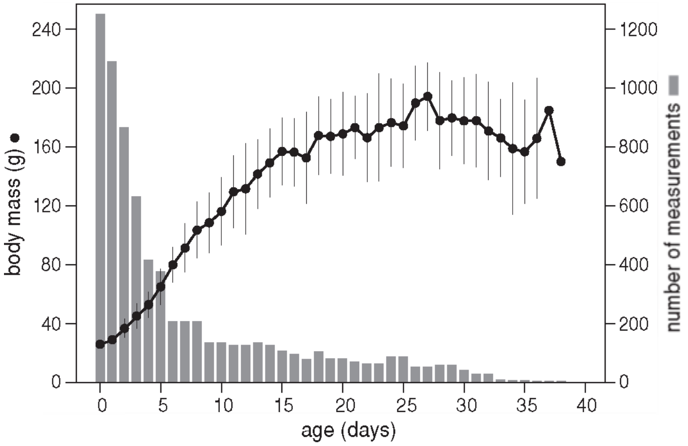

Figure 5.1. Increase in body mass ($\bar{X}$ ± SD) of tern chicks in 1995-1996.

The age of nonenclosed chicks was often unknown, which made it impossible to compute their condition index from equation (1). Therefore, we calculated an alternative condition index (CI^h), using the mean body mass at a certain head size (instead of age) for expected body mass (M_{exp}, g). Although deviations between these two measurements of condition index were sometimes large, there is a reasonable relationship between them (Pearson regression, $n = 289$, $r^2 = 0.537$, $P < 0.001$). CIh was computed for chicks with heads larger than 60 mm (*i.e.* approximately 11 days old) as kleptoparasitism only becomes obvious when chicks are older than 10 days (unpublished data).

To calculate age at fledging, we used data collected in 1992-1996 at Griend on flight capacity of chicks in relation to wing length (Fig. 5.2). Fledging was defined as being able to stay in the air for at least 50 m. For convenience, we defined fledging age as the first day when wing length exceeded 200 mm, and we calculated it assuming linear growth between the last two measurements. When wing length at the last measurement did not exceed 200 mm, the last recorded growth rate was extrapolated until wing length exceeded 200 mm ($n = 50$ chicks). The latter was only done when wing length already exceeded 175 mm. With these restrictions, fledging age of one chick in the moved enclosure in 1996 could not be estimated.

Data Analysis and Statistics

Data analysis and all statistical tests, except for multiple and logistic regression analysis, were performed using the SPSS/PC+ 4.0 statistical package (Norusis 1990). Multiple and logistic regression analyses were performed using the Genstat statistical package (Genstat 5 Committee 1993). Daily wind speed was defined as the average wind speed during the daylight period (0400-2200 hours). Each observation bout lasted approximately 3 h during which food supply (number of fish/chick per h) was calculated. Sample sizes in this respect refer to the number of chicks. Unless stated otherwise, means are shown ± SD.

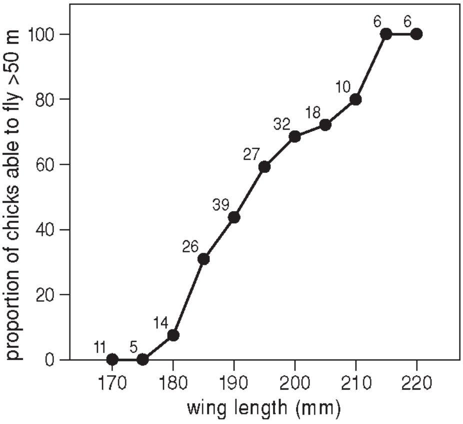

Figure 5.2. Relationship between wing length and flight ability of the tern chicks. The number of chicks processed is shown for each point.

Ethical Note

All manipulations were conducted under permission of the Dutch Ministry of Agriculture, Nature Conservation and Fisheries in The Netherlands. The chicks under study were handled carefully and their condition monitored every third day. None of the moved chicks, including those returned to the permanent enclosure was deserted by its parents.

RESULTS

We recorded the fate of 1701 fish brought to the colony. Of these fish 64.4% were eaten by the chicks, 25.8% were robbed by black-headed gulls and 9.8% were lost in other ways. In 1995, the number of fish supplied to the chicks did not differ from that in 1996 (0.60 ± 0.29 fish $\text{chick}^{-1}\ \text{h}^{-1}$, $n = 167$ and 0.61 ± 0.29 fish $\text{chick}^{-1}\ \text{h}^{-1}$, $n = 325$ respectively; Student's t test, $t_{490}=0.83$, n.s.). In 1995, both in the permanent and in the moved enclosure 67-100% of the supplied fish were eaten by the chicks (Fig. 5.3). In 1996, these figures were much lower and ranged from 44 to 73% in the permanent enclosure and from 30 to 100% in the moved enclosure.

To examine the effect of enclosure type on the probability that a fish was eaten, robbed or lost, we first controlled for possible effects of year (two levels), age, wind speed and any interactions between these parameters, before entering enclosure type (two levels) into a logistic regression model. In 1996, the probability that a fish was eaten by the chick was lower than in 1995 and decreased with increasing wind speed (Table 5.1). Neither age nor any of the interaction terms proved to have significant effects. Adding enclosure type to the model resulted in a significant change in deviance. So, controlling for the effects of year and wind, the proportion of fish eaten by the chicks was higher in the moved enclosure than in the permanent enclosure, and the proportion of fish robbed was higher in the permanent enclosure than in the moved enclosure. Controlling for the effects of year and age of the chicks, the proportion of fish lost otherwise was also lower in the moved enclosure than in the permanent enclosure. The latter can be explained because the category 'lost otherwise' also partly depended on the robbing behaviour of the gulls. This category is predominantly formed by fish lost out the observer's sight (unpublished data), which happened mainly when a gull chased a fish-carrying parent away from the colony after which the tern returned without the fish. In conclusion, the incidence of robbery and losing a fish decreased when the chicks were led away from their original nest site, resulting in the chicks consuming more of the food.

The number of gulls participating in kleptoparasitism had large effects on the proportion of food eaten by the tern chicks (Fig. 5.4, logistic regression, $r^2 = 0.272$, $\text{deviance}_{1,220} = 82.72$, $P < 0.001$). In the permanent enclosure, the chicks ate all the fish when no gull attempted to rob, but none when 10 gulls participated in robbing actions. Significantly more black-headed gulls tried to rob a fish from the arriving parents in the permanent enclosure (3.18 ± 1.95 and 1.30 ± 1.51 gulls, respectively; loglinear regression:

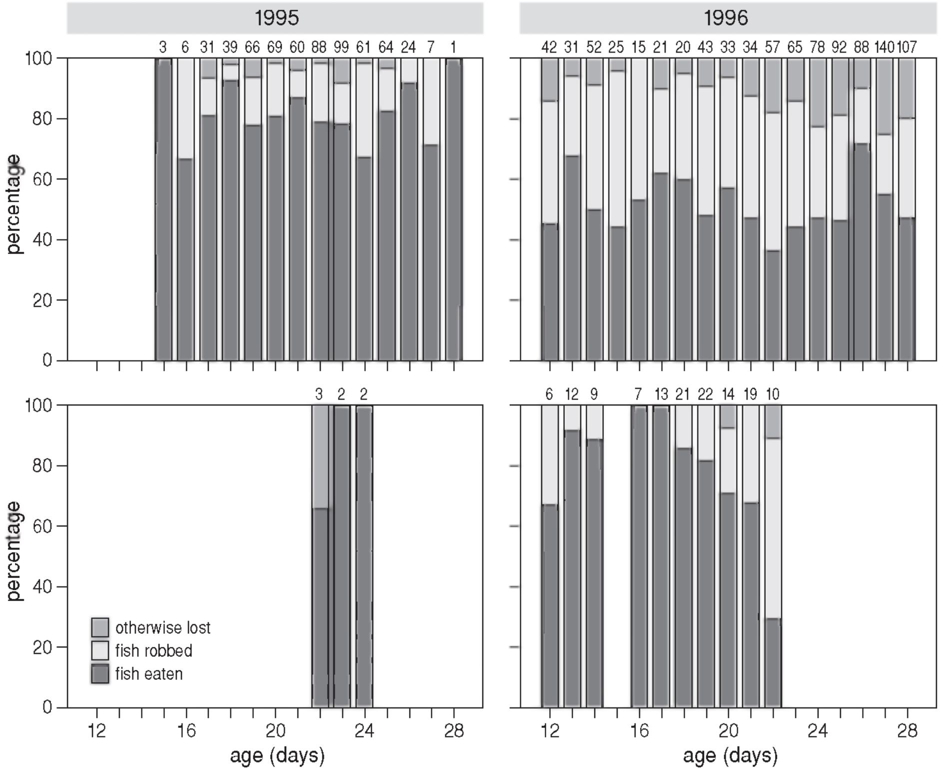

Figure 5.3. Fate of fish delivered to tern chicks of various age in the permanent enclosure in 1995 and 1996 (upper graphs) and in the enclosures moved away from the original colony in 1995 and 1996 (lower graphs). The number of fish observed is shown above the bars.

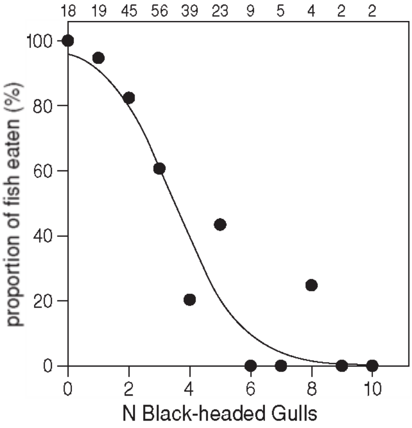

Figure 5.4. The percentage of food eaten by tern chicks in the permanent enclosure in relation to the number of black-headed gulls participating in robbing. The number of observations is shown.

$\text{deviance}_{1,325} = 103.58$, $P < 0.001$). The average number of robbing gulls in the moved enclosure ranged from 0.4 to 2.3. This coincides with consumption rates of 75.2-94.5%, close to the figures presented in Table 5.2.

When a parent arrived in the colony with a fish, it usually made several loops before landing next to its chick. The time a parent spent flying above the colony before successfully delivering the fish was highly variable and ranged from 0-26 minutes. Unsuccessful deliveries lasted 0-35 minutes. Delivery time depended on the number of black-headed gulls trying to rob the fish. When no gulls were present, it took a parent approximately 2 min to deliver the fish to its chick, increasing to more than 6 min when five gulls were present. When even more gulls were present a parent unsuccessfully tried to feed its chick after 6-7 min of flying above the colony. There was no difference in delivery time between successful and unsuccessful deliveries (multiple regression: $t_1 = 0.86$, $P = 0.39$).

Examining the proportion of fish consumed by the chicks for the days on which simultaneous observations were available (Table 5.2), suggests that during the first 5 days after the onset of the experiment, consumption rate in the moved enclosure was about 30% higher than in the permanent enclosure. After day 5 the difference dropped markedly and from day 7 onwards it no longer existed. Owing to strong wind on the first day after the second move, consumption rates were relatively low in both enclosure types. Nevertheless, the second move again resulted in a more than 30% higher consumption rate compared with that of the chicks in the permanent enclosure, although the difference was not significant at the level of 0.05 owing to the large variation. The same pattern can be seen in the difference in the number of robbing gulls between the two enclosure types (Table 5.2). In 1996, during the first 5 days of the experiment, a parent arriving in the permanent enclosure was on average attacked by 2.4-3.2 black-headed gulls, while in the moved enclosure only 0.4-0.5 gulls participated in kleptoparasitism. On day 7, the difference in the number of robbing gulls was almost zero. The second move again resulted in a difference of 2.8 gulls between the two enclosures.

Effects on Growth and Survival

At the start of the experiment, age and condition index of the chicks did not differ significantly between the two enclosure types (Student's t test: age: 1995: $t_{23} = 1.35$; 1996: $t_{35} = 0.54$; condition: 1995: $t_{23} = 0.73$; 1996: $t_{35} = 0.44$; n.s. in all cases), although in both years chick condition was on average lower in the moved enclosure than in the permanent enclosure. In line with the findings that consumption rates improved during the first 5 days after the shift, chick condition in the moved enclosure greatly improved in this period (Fig 5.5). All steps resulted in a considerable increase in Δ condition (*i.e.* the difference in chick condition between the moved and permanent enclosure) during the first 5 days after moving. In all cases the change in chick condition during the first 5 days of the experiment differed significantly between the two enclosure types (Table 5.3). After this period, Δ condition either stabilized or decreased. The decrease in Δ condition in 1995 can be explained to a large extent by the majority of the chicks in the moved enclosure being close to the theoretical maximum body mass, thus further improvement

Table 5.1. Logistic regression analysis of the proportion of food eaten by the tern chicks, robbed by black-headed gulls and lost in other ways.

Variable	Change in deviance	df	*P*	Estimates of coefficients±SE
Proportion eaten				
Constant		488		2.538 ± 0.320
Year	112.8	1	< 0.001	-1.443 ± 0.153 for 1996
Wind speed	15.4	1	< 0.001	-0.139 ± 0.035
Enclosure type*	45.7	1	< 0.001	1.370 ± (0.274) for moved enclosure
Proportion robbed				
Constant		488		-2.936 ± 0.326
Year	50.5	1	< 0.001	1.075 ± 0.154 for 1996
Wind speed	21.2	1	< 0.001	0.1562 ± 0.036
Enclosure type*	17.4	1	< 0.001	-0.896 ± 0.268 for moved enclosure
Proportion lost otherwise				
Constant		488		-4.851 ± 0.475
Year	48.2	1	< 0.001	1.434 ± 0.222 for 1996
Age	24.1	1	< 0.001	0.073 ± 0.019
Enclosure type*	13.1	1	< 0.001	-1.692 ± 0.544 for moved enclosure

Only significant parameters are shown.
*Chicks were kept in enclosures either in the colony or moved away from the colony.

Table 5.2. Logistic regression analysis of the percentage of the fish eaten ($\bar{X}$ ± SD) by the chicks in the permanent and moved enclosures.

Year	Days after	Δ gull	Percentage of fish consumed		Deviance	*P*
			Permanent	Moved		
1995	8		78.4 ± 10.3	80.0 ± 19.9	0.70	NS
1996	4	2.0	67.5 ± 8.8	94.1 ± 5.9	11.3	< 0.001
	5	2.6	53.6 ± 12.3	88.2 ± 6.8	6.45	< 0.02
	7	0.6	65.7 ± 8.0	63.5 ± 10.2	0.01	NS
	1*	2.8	32.1 ± 11.3	63.9 ± 10.5	3.2	0.06

Days after start: days after the moved enclosure was placed around the chicks; Δ gull: difference in the number of robbing gulls between the two enclosure types.
*One day after the enclosure was moved a second time. See text for details.

of their condition was not possible. At the same time chick condition in the permanent increased as a result of improved weather, thus reducing Δ condition. After day 13, the first chicks flew out of the enclosures, sometimes resulting in considerable changes in average chick condition.

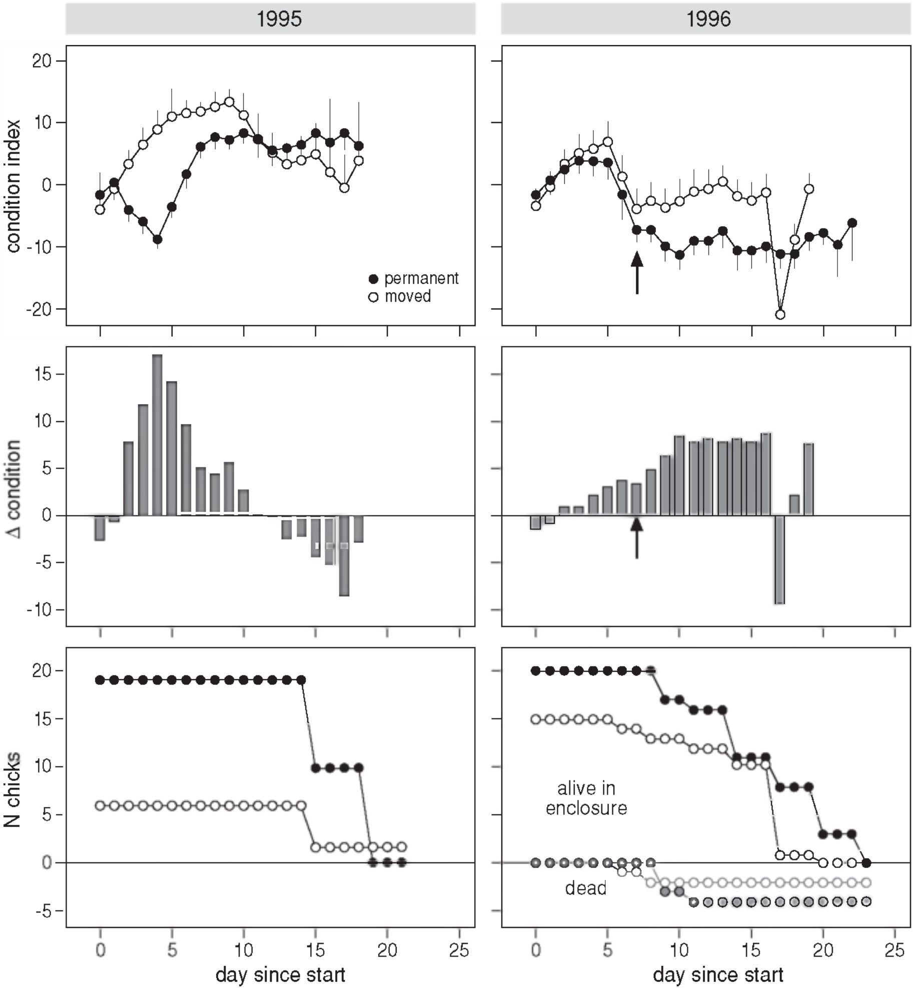

Figure 5.5. (upper graphs) Variation in chick condition ($\bar{X}$ ± SD) for the permanent and moved enclosures throughout the experiment in 1995 and 1996. (middle graphs) Difference in average condition index between the two enclosure types. Positive values indicate that the chicks in the moved enclosure were in better condition than those in the permanent enclosure. The arrow indicates when the enclosure was moved 25 m further away. (lower graphs) Number of chicks alive in the enclosure and number of chicks found dead.

To analyse the daily changes in chick condition, we carried out a multiple regression analysis separately for the permanent and the moved enclosure with independent variables condition index at first measurement ('CI^1'), average wind speed on the day before the measurement ('wind'), year of observation ('year' two levels) and time after onset of the experiment ('time' two levels: 1-5 days and > 5 days). In the permanent enclosures, daily change in chick condition depended on CI^1, wind speed and year of observation

Table 5.3. The mean of each chick's change in condition ± SE over the first 5 days of the experiment.

Experiment	Permanent	Moved	T*	*P*
1995 step 1	-2.05 ± 1.38	14.72 ± 3.29	5.50	< 0.001
1996 step 1	5.21 ± 1.57	9.64 ± 2.21	1.68	0.05
1996 step 2	-5.53 ± 1.46	0.67 ± 2.64	2.18	0.02

Chicks were kept in enclosures either in the colony or moved away from the colony in one (1995) or two (1996) steps. *One-tailed Student's t test.

Table 5.4. Multiple regression analyses examining the effect of previous condition (CI^1), wind speed, year and time after onset of the experiment on the daily change in chick condition

Variable	Estimate ± SE	Variance ratio	F-probability
Permanent enclosure			
Constant	5.02 ± 0.84		
CI^1	-0.10 ± 0.02	16.11	< 0.001
Wind speed	-0.49 ± 0.09	21.47	< 0.001
Year	-1.75 ± 0.36 for 1996	22.84	< 0.001
Time after onset	-0.63 ± 0.37 for > 5 days	2.93	NS
Walking enclosure			
Constant	6.59 ± 1.26		
CI^1	-0.10 ± 0.02	16.19	< 0.001
Wind speed	-0.38 ± 0.13	1.28	NS
Year	-2.47 ± 0.56 for 1996	6.14	0.01
Time after onset	-3.34 ± 0.51 for > 5 days	43.64	< 0.001

(Table 5.4). In the moved enclosures, CI^1 and year had significant effects on the change in condition. Controlling for these variables and in contrast to the findings in the permanent enclosure, the time after onset of the experiment had a significant effect on the change in chick condition, showing that chick condition improved during the first 5 days after the shift.

In 1995, all chicks in the permanent and in the moved enclosure survived until fledging. In 1996, in the permanent enclosure 16 chicks fledged (80%), while in the moved enclosure 13 chicks survived (87%). The difference is, however, not significant (Fisher exact test, n.s.). The age at fledging was related to both year and enclosure type, and differed by 4 days between the earliest and latest group (Table 5.5). Chicks in the moved enclosure fledged 1-2 days sooner than the chicks in the permanent enclosure.

Condition of Free Living Chicks

In accordance with our findings in the enclosure experiments, the condition of free living chicks was significantly higher in 1995 (6.14 ± 12.89, n = 362) than in 1996 (-0.87 ± 16.84, n = 589; ANOVA, $F_{1,949} = 45.44$, $P < 0.001$). Furthermore, the condition of chicks recaptured outside their colony of birth (2.15 ± 13.42, n = 194) did not differ from the condition of chicks that did not leave the colony site (1.73 ± 16.40, n = 737; ANOVA, $F_{1,949} = 0.26$, n.s.), which seems to contradict our results found in the experiments. The discrepancy can be explained if chicks in especially poor condition leave the colony site. Thus, when they are recaptured outside the colony area their condition, although probably improved, is still low. We therefore selected chicks that were captured inside the colony of birth and recaptured within 4 days outside the colony site. Only 11 chicks met these conditions (Table 5.6). Their condition index at first capture was indeed lower than the condition of chicks that did not leave the colony site (one-tailed t test, $t_{146} = 1.93$, $P < 0.05$). At recapture, the condition index of the moved chicks was improved by 0.11, while that of chicks captured twice within the same colony improved by only 0.01 (one-tailed t test, $t_{146} = 2.63$, $P < 0.01$). Of the chicks that left the colony site, 81.8% were in better condition when recaptured, while an improvement was measured for only 46.7% of the chicks captured twice in the same colony ($\chi^2_1 = 5.02$, $P < 0.05$).

Table 5.5. Age at fledging ± SD in the permanent and moved enclosure in 1995 and in 1996.

Year	Enclosure type	Age at fledging	Number of chicks
1995	permanent	29.63 ± 1.38	19
	moved	28.67 ± 0.82	6
1996	permanent	32.81 ± 3.31	16
	moved	30.50 ± 2.97	12

Multiple regression analysis revealed a significant effect of year ($F_{1,49} = 12.73$, $P < 0.001$) and enclosure type ($F_{1,49} = 5.91$, $P < 0.05$).

Table 5.6. Average condition indexes (CI ± SE) of chicks that stayed in their natal colony or those that walked away from the colony.

Recapture site	CI at capture	CI at recapture	Change	No. of chicks	No. improved*
No	2.54 ± 1.23	3.31 ± 1.44	0.77 ± 1.05	137	64
Yes	-6.06 ± 3.85	4.84 ± 3.21	10.90 ± 3.48	11	9

Chicks were recaptured within 4 days. *Number of chicks whose condition improved.

DISCUSSION

Leading young Sandwich Terns away from the original colony site reduced the incidence of food piracy by Black-headed Gulls. By avoiding the robbing gulls, the chicks lost 30% less food. Moreover, as delivery time of the fish decreased when the gulls were avoided, parents could achieve a 5% higher delivery rate. Thus parents that adopt such evasive behaviour can improve their chicks' growth rate and their body condition and reduce the prefledging period. However, leaving the colony site also involves costs. Manoeuvring one's chick through and along colonies of breeding terns and gulls provokes serious attacks by the territory owners. We sometimes observed wandering chicks being pecked to death by neighbouring terns and gulls. It is therefore not surprising that, in particular, chicks in poor condition had moved to other sites on the island. Apparently these chicks suffered from high rates of kleptoparasitism and consequently their parents took the risk of guiding them to better spots. During observations in the enclosures it approved that parents that lost their fish to robbing gulls several times in succession, were restless and tried to lure their chick away to better sites (which was impossible as those chicks were enclosed). Abandoning the nest site is therefore likely to occur in colonies where the rate of kleptoparasitism is high. In colonies other than Griend, movements of broods away from the nesting area were observed, but have always been ascribed to factors other than food parasitism such as human disturbance or avoidance of infectious diseases (Cullen 1958; Chestney 1970; Campredon 1978). On Griend human disturbance is kept to a minimum and although seabirds are often heavily infected with ectoparasites or ants (Converse *et al.* 1976; Feare 1976; King *et al.* 1977; Spendelow 1982; Nisbet & Welton 1984; Boulinier & Danchin 1996) this has never been observed on Griend, leaving kleptoparasitism by Black-headed Gulls as the best possible explanation for the observed movements of the chicks.

Published data show considerable variation in the incidence of food piracy (*e.g.* Fuchs 1977a; Veen 1977; Ratcliffe *et al.* 1997; Garthe & Kubetzki 1998). Although the rate of kleptoparasitism in this study is within the range reported in literature, it might have been slightly overestimated because our observations were restricted to the hours around high tide, when the number of robbing gulls is highest (Veen 1977). The large between year difference in the incidence of robbery was not caused by differences in chick age or weather conditions, and although the supplied fish were longer in 1996 (1.94 ± 0.33 and 2.01 ± 0.37 bill lengths respectively in 1995 and 1996, Student's t test, $t_{1515} = 4.97$, $P < 0.01$) the difference seems too small to explain the large difference in kleptoparasitism. A less favourable food situation for the breeding gulls may have played an important role in this. Several authors mention that kleptoparasitism in terns occurs more frequently when alternative food for the pirates is scarce (Veen 1977; Monaghan *et al.* 1989; Gorke 1990; Oro 1996). Another factor in this respect may be the occurrence of a specialized pirate. Gorke (1990) clearly illustrated that there are specialists and generalists among the Black-headed Gulls. If the number of specialized pirates was higher in 1996 this also could explain the observed difference in consumption rate.

Table 5.7. The percentage of chicks of known fate that fledged in relation to the presence of suitable escape routes in the subcolony concerned.

Subcolony	No. of breeding pairs	Suitable escape routes present	Percentage fledged	N	Differences between subcolonies*
1	161	yes	100	6	2,3,4,5,6
2	807	yes	78.5	149	1,3,4,5,6
3	1776	no	24.3	423	1,2,4,5
4	1374	almost none	43.6	236	1,2,3
5	227	almost none	42.1	38	1,2,3
6	478	yes	40.0	15	1,2
Total	4823		43.8		

*The percentage of chicks fledging is significantly different ($P<0.05$) from that of the other subcolonies shown; chi-square or Fisher's exact test.

Veen (1977) described learning by Black-headed Gulls with respect to predation of eggs laid out near the colony. Over the first few days the eggs were exposed to the gulls 'the gulls reacted with fear to the eggs'. Only after ten days were the first eggs preyed upon. At that time, 'some gulls developed into experienced egg-predators'. Our results suggest that the same holds for kleptoparasitism, since it apparently took some time for the Black-headed Gulls surrounding the moved enclosure to learn that the more or less continuous supply of fish could be harvested. At first, the gulls showed almost no interest in this potential food resource. After a while, some gulls started to kleptoparasitise the terns and probably also attracted others. After 5 days, the rate of kleptoparasitism no longer differed between the permanent and the moved enclosures. However, on the first day after the second shift in 1996, the number of robbing gulls in the moved enclosure was relatively high and as a consequence the proportion of fish consumed by the chicks was low (Table 5.2). Wind was strong on this day, which may have attracted some occasional pirates to the enclosures, since the number of robbing gulls in the permanent enclosure was unusual high and consumption rates were extremely low. Unfortunately, we did not record the number of robbing gulls during the next few days when wind conditions improved. However, as the consumption rates improved (more than 50% eaten by the chicks 2 days later), the number of kleptoparasites probably diminished.

In natural situations, without enclosures, piracy may be even more reduced. In our experiment, the chicks were forced to stay at one location for at least 7 days. Outside the enclosures, parents can in theory react to piracy by black-headed gulls at any time by leading their youngsters to a new site. By abandoning an occupied site 5 days after settlement, or even sooner when robbing exceeds a certain threshold, terns can reduce piracy to a minimum, provided the new site has better opportunities for feeding their offspring. However, not all subcolonies provide suitable escape routes for chicks. In some subcolonies on Griend parents were forced to stay at the original breeding spot, simply because their chicks were trapped in a natural enclosure formed by dense vegetation. In 1996, half of the subcolonies on Griend were in locations where escape was impossible or difficult. Piracy was extremely severe in these subcolonies; we observed hundreds of Black-headed Gulls on guard here. The high rate of kleptoparasitism and the absence of suitable escape routes resulted in high rates of chick mortality in these subcolonies (Table 5.7); more than half of the ringed chicks of known fate were found dead before fledging. Since these subcolonies comprised 70% of the total population, reproductive success of the entire colony was extremely low in 1996. In this case, for many parents the decision to seek the gulls' protection proved fatal.

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Chapter 6

Variation in growth in Sandwich Tern chicks *Sterna sandvicensis* and the consequences for pre- and post-fledging mortality

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ASTRACT

Fitness consequences of variation in body mass growth and body condition were studied in a Sandwich Tern *Sterna sandvicensis* colony on Griend, Dutch Wadden Sea, during 1990-2000. Body mass increment during the linear growth phase predicted nestling survival probabilities accurately. Chicks growing less than 8 g.day^{-1} had low survival probabilities until fledging, but within a range of 8-11 g.day^{-1} growth had only small effects on chick survival. Effects of slow growth on survival became obvious after about 10 days after hatching. Slow growing chicks reached a much lower fledging mass, while slow growth had only small effects on structural size at fledging. Body condition of the chicks was highly variable and had strong effects on survival until fledging. However, body condition during the nestling stage did not influence post-fledging survival. Body condition at fledging had no effects on post-fledging survival and did not affect final mass or body size. It is argued that low fledging mass can be overcome soon after fledging, as parents take their fledglings closer to the foraging areas, thereby avoiding high rates of kleptoparasitism by Black-headed Gulls *Larus ridibundus*.

INTRODUCTION

Many birds show a great flexibility in growth. When food availability is low maturation of the chicks slows down and normal growth is resumed when the restrictions are lifted, without any consequences for final mass or morphology. However, in other species poor feeding conditions result in reduced fledging weight and may even affect adult size (Schew & Ricklefs 1998). Moreover, slow growth can increase chick mortality and may have negative effects on post-fledging survival or recruitment, as has been reported in many species (Gebhardt-Henrich & Richner 1998). Most seabirds depend on highly unpredictable food resources that show large temporal and spatial variations. Superimposed environmental conditions, such as weather and tide, demand an even greater flexibility of seabirds. One would therefore expect that adaptive features such as variable growth rate are well developed, especially in highly specialised seabirds that undertake long feeding trips, like Sandwich Terns *Sterna sandvicensis*. For Sandwich Tern parents, reduced growth of their offspring means a considerable reduction in the costs for rearing their young (Klaassen *et al.* 1992). This might be an important mechanism for this species to cope with unpredictable food resources. However, the estimates of Klaassen *et al.* (1992) were based on laboratory raised chicks. In the field, the limits of the parents are set by present and future costs for rearing their young. One may argue that if parental effort has consequences for their future survival, parents will probably lower feeding rates to the chicks when conditions are poor. On the other hand, if reduced growth also has fitness consequences in terms of chick mortality or post-fledging survival, this will potentially reduce the extent to which growth can be adjusted.

This paper focuses on the fitness consequences of poor development in Sandwich Terns. We hypothesise that growth rate of Sandwich Tern chicks is highly flexible and that reduced growth has minimal consequences for nestling and post-fledging survival. Sandwich Terns depend on only a few fish species that show strong fluctuations in their horizontal and vertical distribution (Stienen *et al.* 2000). They have to cope with strong variations in the amount of food they can offer to their chicks food due to variable weather conditions (Stienen *et al.* 2000) and food losses to kleptoparasitising gulls (Stienen *et al.* 2001; Stienen & Brenninkmeijer 2002). Here, we use data on growth and survival of Sandwich Terns chicks held in enclosures on Griend, the Dutch Wadden Sea, to examine the consequences of variation in growth rate and body condition for nestling survival. Next, we discuss the effects of poor growth during early development on the body weight at fledging. Using ring recoveries, we examine whether a poor body condition during the nestling phase or at fledging has repercussions for an individual's chance to recruit to the colony in later years. Because Sandwich Terns are not full-grown at fledging, we also investigate post-fledging growth patterns and the consequences of poor fledging condition for the final size of an individual.

STUDY AREA AND METHODS

The study was conducted on the isle of Griend during 1990-2000. Griend (57 ha) is situated in the western part of the Dutch Wadden Sea (53°15'N, 5°15'W). The island supports large colonies of Black-headed Gulls *Larus ridibundus* (about 23,000 pairs in the 1990s), Common Terns *S. hirundo* (about 2,100 pairs) and Sandwich Terns (about 7,000 pairs) and smaller colonies of Common Gulls *L. canus*, Herring Gulls *L. argentatus* and Arctic Terns *S. paradisaea*. During the study period, the population of Sandwich Terns fluctuated between 5600 (1996) and 8300 (1994) pairs, consisting of several subcolonies. In 1992-98, part of a subcolony, containing 50-100 nests, was fenced (enclosures) to prevent the chicks from walking away from the nest site (see also Stienen & Brenninkmeijer 1999). Accurate data on chick growth and survival was obtained from enclosed chicks. In addition, each year a number of free-living chicks, mainly of unknown age, were ringed and retrapped as often as possible. Statistical tests were performed using the SPSS/PC+ 4.0 (Norusis 1990) and the Genstat statistical package (Genstat 5 Committee 1993).

Enclosures

Within the enclosures, all chicks were ringed within 3 days after hatching and of each chick the hatching order was noted. The age of the chicks was estimated from the state of the egg during the previous control, feather characteristics, total head length, and whether or not the chick was still wet or had eggshell remains on its back. Preferably within 3 days from hatching and subsequently every third day, the chick's body weight and total head length (*i.e.* head and bill) were measured. To minimise disturbance in the colony stretched wing chord was measured less regular. Due to weather conditions and duration of the disturbance, not all chicks were measured during each visit. Dead chicks were sampled, after which the body mass and total head length were measured. The day of death was estimated by biometrics, smell, features of the eyeball and state of putrefaction. Chicks < 25 days that were missing from the enclosures, were categorised as lost to predators. If the age of a missing chick was more than 24 days, the chick was presumed to have fledged (see chapter 7 for more details). Probably the best way to describe fledging in Sandwich Terns is by using wing length as a reference for the ability to fly (Stienen & Brenninkmeijer 1999). However, because wing length was not known for some enclosed chicks, we used the age of the chicks instead. Although deviations were sometimes large, there was a strong relationship between age and wing length in enclosed chicks (Fig. 6.1). Within the enclosures parents on average laid 1.6 eggs per nest. Of all pairs that laid 2 eggs only 0.7% was able to fledge 2 chicks. Fledging success averaged 0.64 chicks per pair (see chapter 7 for more detailed information on chick survival).

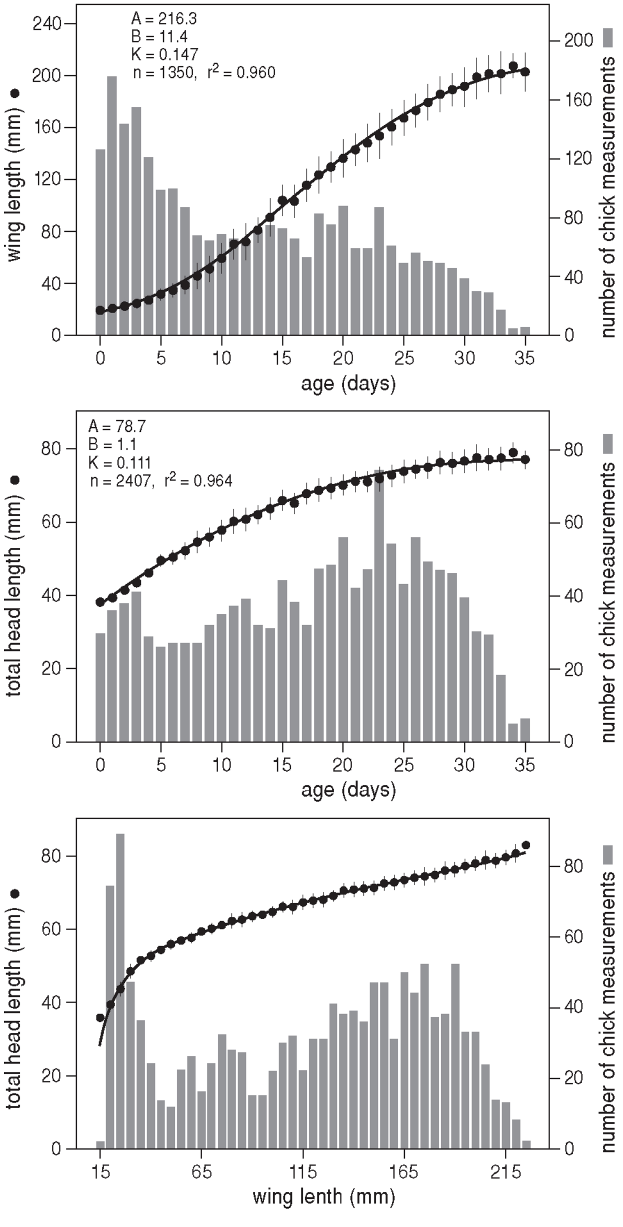

Figure 6.1. Development of wing and total head length (dots ± sd) with the age of enclosed Sandwich Terns on Griend in 1992-1998 (upper and middle graphs). Drawn lines are logistic growth curves (length = A / (1 + B * e^{-K*age}) for which the parameters are shown in the top of the graphs. The lower graph shows the relationship between wing length (15 = 12.5 - 17.4 mm, 20 = 17.5 – 22.4 mm, etc.) and total head length. The drawn line is a quadratic by linear curve: total head length = 57.1 + 69.5/(1-0.22*wing length) + 0.11*wing length, n = 1350, r^2 = 0.978). Bars denote the number of chick measurements (right axis).

Growth and condition

For age 0 to 24 days, missing body masses of enclosed chicks were interpolated assuming linear growth between two measurements. To avoid unrealistic biases of not fully digested meals, only measurements with an interval of more than two days were used. For each single or first-hatched chick for which at least three measurements of body mass were available and for which the first measurement was made when less than six days old, average growth rate was computed for the linear part of the growth curve (*i.e.* age 4-14). We used average growth rate instead of using regression analysis or parameters of logistic growth (*e.g.* Harris & Rothery 1985; Nisbet *et al.* 1998, 1999) because body mass development of the chicks often was very irregular. Among other things body mass growth showed large variations with weather conditions (Stienen & Brenninkmeijer in press).

For enclosed chicks, an index of body condition (CI) was defined as the proportional deviation of measured body mass (M, g) from average body mass (M_{exp}, g) of surviving chicks (*i.e.* age at final measurement ≥ 25 days) with similar total head length (equation 1).

$$CI = \frac{M - M_{exp}}{M_{exp}} \qquad \text{equation 1}$$

We used total head length as a reference for age because the age of most non-enclosed chicks was missing, allowing us to use the same index of body condition for non-enclosed chicks. In enclosed chicks there was a strong correlation between age and total head length on the one side and between wing length and total head length on the other side (Fig. 6.1).

Non-enclosed chicks

In addition, each year a number of non-enclosed chicks of varying age were ringed. Non-enclosed chicks were only used to analyse the effect of fledging condition on the probability to recruit to the colony in later years. Compared to enclosed chicks, most free-living chicks experience higher food intake rates and growth (Stienen & Brenninkmeijer 1999). By including non-enclosed chicks, the sample size was enlarged and variation in fledging condition increased.

For enclosed and non-enclosed chicks, fledging condition was defined as the average body condition of chicks with a total head length between 75 mm and 80 mm. Wing size of these chicks averaged 189.2 ± 14.4 mm. At this wing length about 43% of the chicks is able to fly (Stienen & Brenninkmeijer 1999). As the age of most non-enclosed chicks was missing, we applied an alternative definition of fledging. In all analysis referring to recruitment, enclosed and non-enclosed chicks were presumed to have fledged when total head length exceeded 75 mm. The average age of 62 enclosed chicks with a head of 75 mm was 27.6 ± 3.9 days.

Recruitment

From 1994 to 2000, effort was put into reading metal rings of adult Sandwich Terns. The rings were read by telescope from a moveable hide. Most rings were read during the birds' courtship display in the colony, at beaches near the colony where females fed on shell fractions just before egg laying (Brenninkmeijer *et al.* 1997) and at roosts near the colony. In addition, some ringed adults were caught on their nest. Although some birds of which the rings were read by telescope, were trapped on their nest later in the season, and most birds were engaged in courtship or nesting activities, there was no absolute certainty for all recovered birds that they actually started breeding on Griend, but for convenience we call them all recruits. Only a small proportion of the ringed birds present on the island was recovered, so the presented return probabilities can not be used as estimates of survival or recruitment. We further assume that the resighted birds are representative for the entire population. The number of chicks ringed and the number seen on Griend in later years are listed in Table 6.1. In total 850 ringed birds were seen on Griend, corresponding with 4.9% of all chicks ringed. Birds were first seen when 2 years old, but most were first seen when 3-5 years old. Since not all chicks that were born after 1997 might yet have returned to Griend they were omitted from the analyses.

Table 6.1. Number of Sandwich Tern chicks ringed on Griend per annum and the number of first recoveries in later years.

Year of ringing	Number of chicks ringed	Year of recovery 1994	1995	1996	1997	1998	1999	2000	Total
1990	150	3	9	2	0	0	0	1	15
1991	879	5	17	6	3	1	0	1	33
1992	2195	1	56	70	17	10	19	20	193
1993	1024	0	1	52	22	9	18	12	114
1994	3412		0	5	33	76	82	87	283
1995	3168			0	3	72	180	181	436
1996	2749				0	2	61	89	152
1997	2489					0	15	137	152

RESULTS

Body mass growth during the linear part of growth of 143 first-hatched and single Sandwich Tern chicks averaged 8.7 ± 2.1 g.day^{-1}. Survival probabilities of the chicks were closely linked to growth rate between 4 and 14 days (Fig. 6.2). Nestling survival sharply increased from 0.3 for chicks growing 1 g.day^{-1} to more than 0.8 when growth exceeded 8 g.day^{-1}. Presumably the effect of growth rate on survival probabilities is even more dramatic than presented in figure 6.2, because most slow growing chicks are not represented in the graph, as they had already died before they could be measured three times.

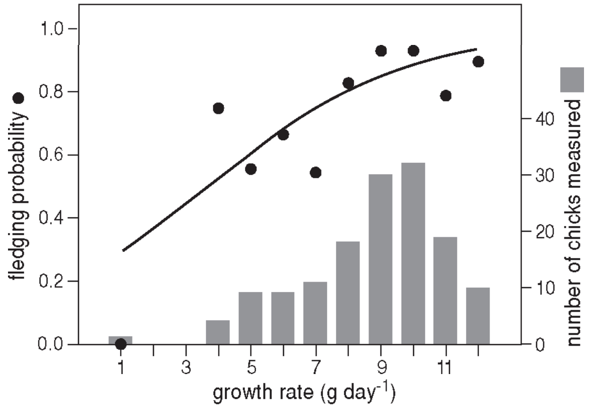

Figure 6.2. Relationship between body mass increase during the linear part of growth and survival probabilities until fledging (dots) of first-hatched and single Sandwich Tern chicks on Griend in 1992-1998. Drawn line represents logistic curve (logistic regression, survival probability = 1-(exp(1.207-0.326*growth)/(1+exp(1.207-0.326*growth))), deviance = 10.4, $P < 0.01$). Bars denote the number of chicks measured (right axis).

Growth and fledging condition

Body mass growth during the linear part of growth had no consequences for the condition of a chick at fledging (Pearson regression: $n = 92$, $r^2 = 0.02$, $P > 0.05$). On average, enclosed chicks which fledged in poor condition (*i.e.* fledging condition ≤ -10) experienced normal growth of body mass during the first 10 days of their lives, but deviated from the growth pattern of chicks in good fledging condition (*i.e.* fledging condition ≥ 10) after that age (Fig. 6.3). The deviation of structural growth (total head length and wing length) occurred somewhat later and was much smaller than the deviation of body mass growth. Asymptotic body mass of fledglings in poor condition amounted to 161.1 g; a difference of -27.4% compared with chicks fledging in good condition (asymptotic mass 222.0 g). This was accompanied by an average decrease in asymptotic total head and wing lengths of only 4.6% and 0.5%, respectively.

Pre-fledging mortality

To analyse whether body condition of a chick at any moment during the nestling period has consequences for its chance to survive until fledging, we divided the chick period into 5 categories of total head length, so that each category coincided with a difference in average age of 2-5 days (Table 6.2). In a logistic regression approach, we first controlled for hatching position (two groups: first-hatched or single chicks and second hatched chicks). For enclosed chicks with a total head length < 65 mm, hatching position had strong effects on nestling survival (Table 6.2), with second hatched chicks having much lower survival changes. If second hatchlings survived until a total head length ≥ 65 mm, their survival changes did no longer differ from first-hatched or single chicks. Body con-

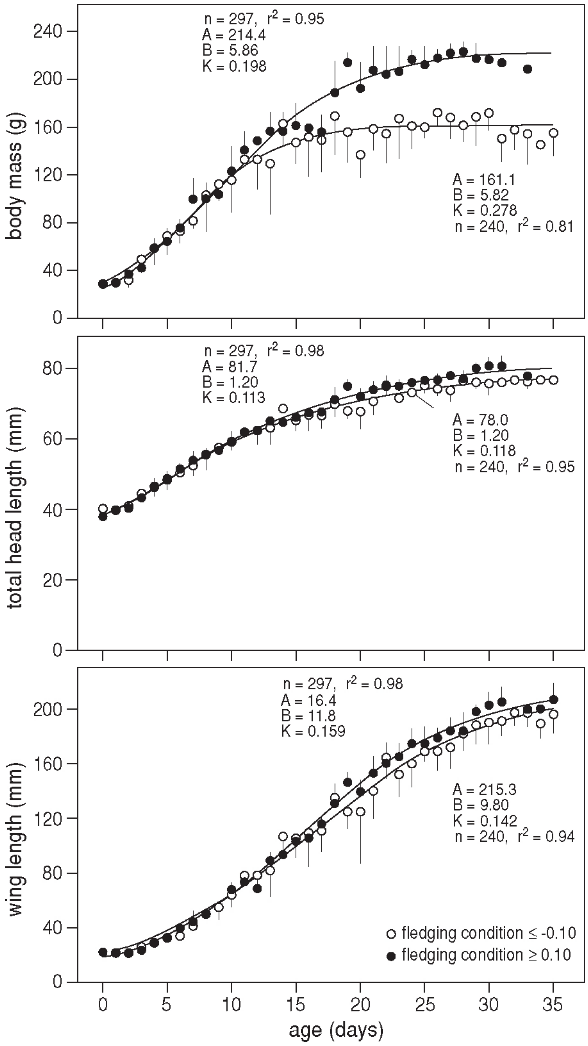

Figure 6.3. Pre-fledging development (means ± sd) of body mass (upper graph), total head length (middle graph) and wing length (lower graph) in Sandwich Tern chicks fledging in poor (fledging condition ≤ -0.10) and good condition (fledging condition ≥ 0.10). Only chicks that reached an age of 25 days were included in the analysis. Drawn lines represent logistic growth curves for which the parameters are shown in the top of the graph.

dition of very young chicks (total head length < 50 mm) did not influence their survival until fledging (Table 6.2). In the later periods until total head length ≥ 70 mm, chicks in poor condition experienced lower survival chances, while near fledging (70 mm ≤ total head length < 75 mm) body condition no longer influenced survival. Although some even older chicks (total head length ≥ 75 mm) were found inside the enclosures, their

Table 6.2. Logistic regression analysis examining the effect of hatching position (two categories: first-hatched or single chicks vs. second hatched chicks) and body condition on the probability of being found dead before fledging for different categories of total length size of enclosed Sandwich Tern chicks on Griend in 1992-98. In all cases hatching position was entered into the logistic regression model first, following body condition and the interaction term 'hatching*body condition'. *N* chicks: the number of chicks measured, the number of chicks found dead is shown between brackets. Age, wing length and body condition are means ± se. * = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$.

Total head (mm)	Age (days)	Wing (mm)	*N* chicks	Range in body condition	Change in deviance		
					Hatching position	Body condition	Hatching position* body condition
<40	0.8 ± 0.06	20.6 ± 0.24	170 (101)	-042 to 0.70	78.3 ***	0.0	1.3
40-49	3.1 ± 0.08	24.5 ± 0.24	288 (140)	-0.48 to 0.38	104.6 ***	1.5	0.1
50-59	8.0 ± 0.12	47.1 ± 1.03	218 (77)	-0.47 to 0.31	66.1 ***	10.2 **	0.4
60-64	13.2 ± 0.15	84.2 ± 1.12	154 (25)	-0.38 to 0.28	5.3 *	12.3 **	0.8
65-69	17.9 ± 0.20	121.9 ± 1.16	170 (21)	-0.50 to 0.69	1.4	46.3 ***	4.3 *
70-74	23.8 ± 0.21	159.0 ± 0.94	179 (2)	-0.23 to 0.49	0.0	0.1	0.0

survival could not be estimated because a part of these chicks had already fledged. Nevertheless, their survival probability seems very high. Of 2009 chicks (both enclosed and non-enclosed) with a total head length $\geq$ 75 mm only 27 were found dead on Griend, indicating that most left the island successfully. The interaction term 'body condition*hatching position' had significant effects only for chicks with 65 mm $\leq$ total head length $<$ 70 mm (Table 6.2), showing a slower increase of survival changes with body condition for second hatched chicks.

Post-fledging mortality

Next, the effect of body condition on the probability of being spotted in the colony some years later was analysed (further referred to as recruitment). For this analysis, we selected only those chicks that survived until fledging. To enhance the sample size also non-enclosed chicks were included in the analysis. Since the age of most non-enclosed chicks was missing, an alternative definition of fledging is used (see methods). In a logistic regression analysis examining the probability to recruit to the colony we first controlled for possible effects of year of birth (Table 6.3). For chicks that were measured around fledging (75 $\leq$ total head length $<$ 80) year of birth had significant effects on the probability to recruit to the colony (Table 6.3). Chicks born in 1990 had a relatively low chance to recruit to the colony, while chicks born in 1995 had the highest chance to be seen in the colony several years later. For all other groups of total head length year of birth had no significant effects. For none of the 'age'-groups adding of body condition and the interaction term 'year*body condition' to a model already containing year of birth resulted in a significant change in deviance (Table 6.3).

Table 6.3. Logistic regression analysing the effect of year of birth and body condition on the probability to be seen on Griend in later years for different categories of total head length of Sandwich Tern chicks in 1990-97. In all cases year was entered into the logistic model first, following body condition and the interaction term 'year * body condition'. *N* chicks: number of chicks measured, the numbers of chicks that were seen in the colony in later seasons are shown between brackets.
* = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$.

Total head (mm)	*N* chicks	Range in body condition	Change in deviance		
			Year	Body condition	Year * Body condition
<40	82 (13)	-0.24 to 0.37	7.2	1.5	6.7
40-49	254 (34)	-0.28 to 0.60	1.9	1.8	2.0
50-59	283 (34)	-0.30 to 0.34	4.4	0.2	5.7
60-64	204 (30)	-0.31 to 0.33	1.9	2.8	2.9
65-69	259 (29)	-0.25 to 0.28	10.2	0.7	2.0
70-74	273 (35)	-0.26 to 0.30	7.6	0.3	8.9
75-80	1620 (195)	-0.45 to 0.31	19.6 **	2.5	6.3
≥ 80	390 (43)	-0.33 to 0.23	11.3	0.0	5.6

The results suggest that in Sandwich Terns poor development as a chick influences survival until fledging and has large effects on the body mass at fledging, but less effect on the size at fledging. On the other hand, it shows that fledging condition has no consequences for post-fledging survival. In accordance with this, fledging condition of 24 juveniles, which were found dead within 3 years from fledging, did not differ significantly from that of 249 recruited terns (0.040 ± 0.086 and 0.008 ± 0.009, respectively, Student's T-test, $t_{271} = 1.75$, $P = 0.08$).

Post-fledging growth

Body mass, total head and wing length of 30-day old young that were still in the colony amounted to approximately 75, 73 and 62%, respectively, of that of incubating adults on Griend (Fig. 6.4). In total 13 juveniles of known age were mist-netted shortly after the breeding season in 1997 and 1998 at the isle of the Richel, situated 9 km northwest of Griend. Biometrics of these individuals indicate that growth of body mass and wing length is almost completed within 100 days from hatching, while at this time the total head length amounts to only 89% of adult total head length (Fig. 6.4).

A total of eight adults with known fledging condition were trapped on the nest on Griend some years later. Additionally, shortly after the ending of the breeding seasons of 1997 and 1998, four adults with known fledging condition were mist-netted at the isle of the Richel. These adults represent a range in fledging condition between –0.02 and 0.16. There were no significant effects of capture location (Griend or Richel) or fledging condition on any biometric measurement of adult Sandwich Terns (ANCOVA, ns in all cases) (Fig. 6.5).

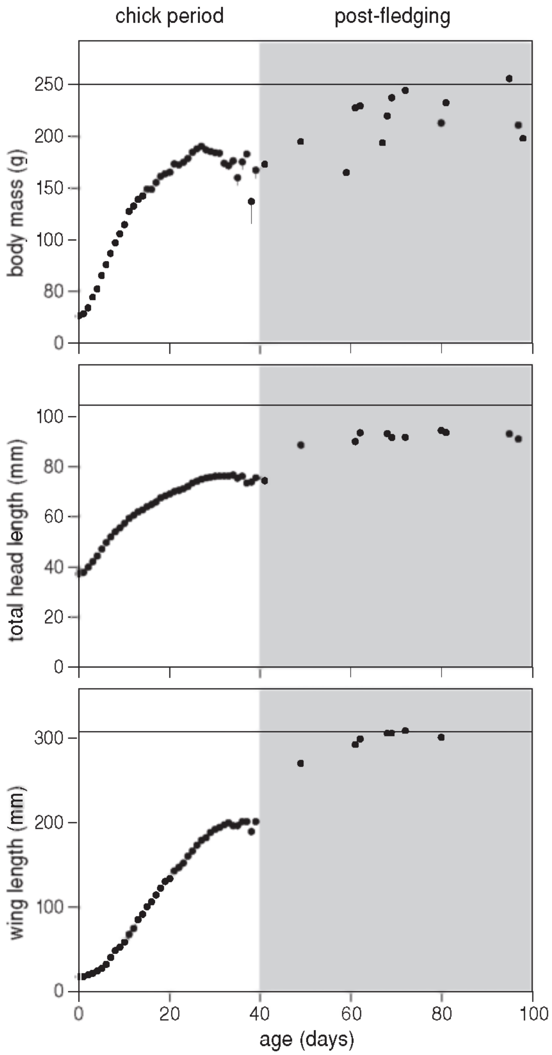

Figure 6.4. Pre- and post-fledging development of body mass, total head length and wing length in Sandwich Terns. Data on post-fledging development were derived from juveniles caught in mist nets at the isle of the Richel, 9 km north-west of Griend. Drawn lines indicate average body mass, total head length and wing length of 766 incubating adults of Griend in 1992-99.

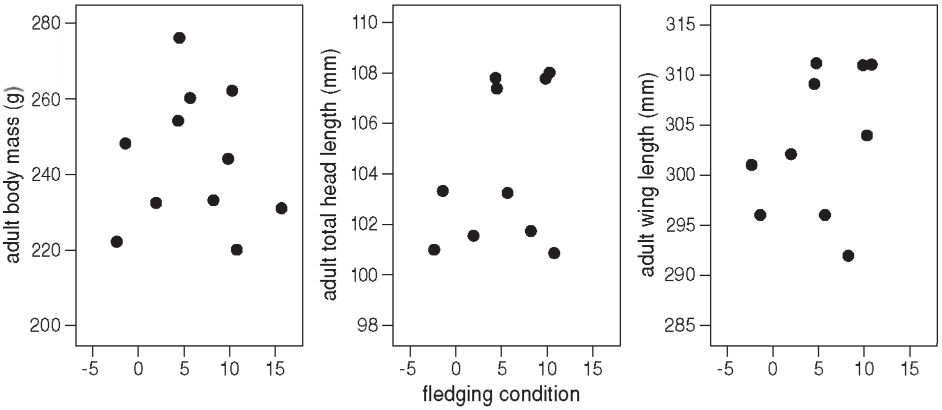

Figure 6.5. Relationship between fledging condition and adult biometrics in Sandwich Terns.

DISCUSSION

Nestling survival

The body condition of a chick reflects the amount of body tissue reserves that can be used during periods of food shortage. Therefore, a chick in poor condition might experience a decreased chance to survive on the short term. Indeed in Sandwich Terns, body mass increment during the linear part of growth as well as body condition showed a strong relationship with chick survival. Also in Roseate Terns *S. dougallii* growth predicted chick survival accurately (Nisbet *et al.* 1998, 1999). In Roseate Terns, survival could already be predicted from body mass growth in the first few days after hatching. In contrast, our results suggest that in Sandwich Terns body mass in the first few days after hatching is not important for survival, leading to the conclusion that poor nourishment during an early stage of life could be overcome by the parents. Nisbet *et al.* (1998) suggest that chick growth and survival in Roseate Terns is primarily determined by parental performance, which are already manifested during the first days after hatching. In Sandwich Terns, it seems relatively easy for most parents to meet the food requirements of their freshly hatched chicks. Only when the chicks grow and energy demands as well as the proportion of food parents lose to kleptoparasitising gulls sharply increase (Stienen *et al.* 2001), differences in parental quality might be manifested. Especially in years when the chicks' diet is dominated by sandeels, resulting in high rates of kleptoparasitism (Stienen & Brenninkmeijer 2002), aspects of parental performance might determine the chick's body condition and survival.

Post-fledging survival

On the long term, slow growth experienced during the chick stage might affect survival in a later stage. The sparse studies on this subject gave different results. In Kittiwakes

Rissa tridactyla, slow growing chicks had a lower chance to return to the area of birth (Coulson & Porter 1985), whereas Harris *et al.* (1992) found no difference in growth between Guillemots *Uria aalge* that survived until breeding and juveniles that were reported dead. Also in Sandwich Terns there seems to be no relationship between nestling development and post-fledging survival.

Several studies on seabirds report that a low body weight at fledging has negative effects on post-fledging survival or local recruitment, while other studies found no effect (Table 6.4). All species, for which a relationship between fledging weight and post-fledging or local survival has been found, become independent of their parents just before or directly after fledging. Juveniles of Guillemot, Razorbill and Sandwich Tern, but not of Puffin, are fed by their parents for some time after fledging (Cramp 1998). Dependency of parents thus might be a crucial factor that determines whether fledging weight affects post-fledging survival in seabirds. For juveniles of Sandwich Terns feeding conditions probably drastically improve after leaving Griend (*i.e.* a few days after fledging). In the first place, juveniles can be taken much closer to the feeding areas. Before fledging of the chicks parents have to travel, on average, about 12 km to the feeding grounds and feeding trips may last up to 3 hours (Stienen & Brenninkmeijer 2002). In addition, juveniles can be brought to sites that are free from Black-headed Gulls and other pirates otherwise imposing a high robbing pressure on prey brought to the ternery (Stienen & Brenninkmeijer 1999, Stienen *et.al.* 2001). For those reasons, food intake rates probably

Table 6.4. Relationship between body mass at fledging and post-fledging survival or local recruitment, and the age at which chicks become independent of their parents in several species of seabirds.

Species	Relationship between fledging weight and post-fledging survival/local recruitment	Age of independence	Authors
Sooty Shearwater *P.uffinus griseus*	Yes	Around fledging	Sagar & Horning 1998
Manx Shearwater *P. puffinus*	Yes	Just before fledging	Perrins et al. 1973
Cape Gannet *Sula capensis*	Yes	Soon after fledging	Jarvis 1974
Sandwich Tern *Sterna sandvicensis*	No	> 4 months after fledging	This study
Guillemot *Uria aalge*	No	At least a few weeks after fledging	Hedgren 1981
Razorbill *Alca torda*but	No	Cared for after fledging, period unknown	Lloyd 1979
Puffin *Fratercula arctica*	No	Just before fledging	Harris & Rothery 1985

greatly improve after fledging, making it possible for fledglings in poor condition to catch up on their backlog in growth relatively easy, thus resulting in a lack of an effect of fledging condition on post-fledging survival.

In some species, birds attain a smaller adult size when confronted with poor food conditions during early development, while in other birds no effect on final size was found (Schew & Ricklefs 1998). In turn, smaller size may affect dominance status of the birds (*e.g.* Garnett 1981, Drent 1983), and growing tall therefore might be of importance to occupy good nesting sites. In Sandwich Terns, poor body condition at fledging had no effects on adult body mass or size. Although the sample sizes were small, this suggests that early development is not important for the final size or dominance status.

Fluctuating food resources

Sandwich Terns on Griend depend on only a few species of prey fish for the rearing of their chicks. These prey species show large variation in numbers both between and within seasons (Fonds 1978; Corten 1990), and are patchy distributed (Stienen *et al.* 2000). Moreover, their availability for the terns depends on environmental conditions that affect vertical distribution of the prey and fishing success of the parents (Stienen *et al.* 2000). Such variation demands a great flexibility in features that are linked to food availability, like for example growth, in order to minimise the effects on chick survival. Indeed, Sandwich Terns seem to be well adapted to unpredictable food resources. Growth rate of the chicks proved to be highly flexible, which might help to overcome short periods of food shortage. In periods of food stress, chicks allocated resources to growth of structural components (total head and wing) rather sufficiently, while body mass growth was cut down. Body mass growth of chicks that survived the chick stage varied between 1 and 11 g.day^{-1} and is comparable to other studies on Sandwich Terns (Pearson 1968; Klaassen *et al.* 1992). Growth can be slowed down to about 8 g.day^{-1} without serious consequences for chick survival. Slowing down growth from 12 to 8 g.day^{-1} would mean a reduction in energy needs of the offspring of 13% (Klaassen *et al.* 1992). Within this window parents can fine-tune chick growth to prevailing food conditions, with almost no consequences for the survival of their chicks and without consequences for their post-fledging survival or final size.

In spite of the strong link between growth and nestling survival, 76.2% of all chicks with known growth rate grew at a rate of 8 g.day^{-1} or more. Although this percentage might be biased upwards because extremely poor growing chicks already died before they could be measured three times, it suggests that during the first two weeks post-hatching most parents experienced no difficulties in providing sufficient food to their chicks. The same is suggested by the fact that body condition in the first 5 days did not significantly contribute to the bird's survival chance. However, this might also be biased as the regression analysis of very young chicks is diluted with chicks initially in good condition but starving to death in a later stage. Nevertheless the last two weeks before hatching, when the condition of a chick has strong effects on its survival, probably is the most strenuous period for Sandwich Tern parents. At this stage energy requirements are maximal (Drent *et al.* 1992) and also the rate of kleptoparasitism is at a maximum level (Stienen *et al.* 2001). Apparently some parents were not able to further increase the amount of food transported to their offspring and consequently growth lagged behind. On the other hand the margins within witch a chick can survive are very large. In this study body mass of surviving chicks varied between 49% below to 77% above average body mass, showing that Sandwich Terns are well adapted to fluctuating food resources.

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Chapter 7

Consequences of brood size and hatching sequence for prefledging mortality in Sandwich Terns: why lay two eggs?

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ASTRACT

Mortality of Sandwich Tern *Sterna sandvicensis* chicks held in enclosures was studied in colonies on Griend, Dutch Wadden Sea, from 1992-1999 and Hirsholm, Danish Kattegat, in 1997. Survival until fledging of chicks amounted to 73% for chicks hatching from first-laid eggs or single egg clutches and 59-64% for partially hatched 2-egg clutches, whereas 6% of the second hatchlings survived until fledging. Less than 2% of all 2-chick broods actually fledged 2 chicks. Because 18% of the 2-egg clutches only hatched one egg, still 7% of the fledglings of 2-egg clutches originated from a second-laid egg. In nests where both eggs hatched, the number of chicks was generally reduced soon after hatching. Within 5 days from hatching, more than 50% of the second hatchlings died of starvation or were preyed upon. It appears that overproduction commonly occurs in Sandwich Terns and that it mainly serves as an insurance mechanism. On Griend and Hirsholm, chick productivity of 2-egg clutches was somewhat higher compared to 1-egg clutches. Undernourishment was an important cause of death, either directly by starvation or by selective predation of chicks in poor condition. This in combination with earlier published studies suggests that Sandwich Tern parents on Griend are exposed to a high food stress.

INTRODUCTION

Birds often lay clutches larger than they normally can rear. The surplus eggs may allow parents to track uncertain resources, to select offspring with the highest survival expectations, or they may serve as food-cache for parents or offspring (review in Forbes 1991). Also, the extra eggs might serve as an insurance against the failure of an egg or offspring (e.g. Mock 1984; Cash and Evans 1986; Anderson 1990). Producing surplus offspring requires that parents are able to efficiently reduce brood size if the surplus offspring is redundant, otherwise they may increase rather than decrease reproductive variance (Forbes 1991). Birds adopting a brood reduction strategy are thought to facilitate this process by producing a small final egg (Slagsvold *et al.* 1984) and by asynchronous hatching of the eggs (Cash and Evans 1986, Anderson 1989).

Being long-lived birds living in stochastic environments, seabirds may pay an especially large fitness cost for hatching chicks synchronously and therefore benefit from hatching clutches asynchronously in the long term (Pijankowski 1992, Mock & Forbes 1994). Laridae produce asynchronously hatching clutches, small final eggs and show differential survival of chicks within broods, with the last-hatched chick in a brood having the lowest probability of survival to fledging (e.g. Herring Gull *Larus argentatus*, Parsons 1970, Lesser Black-backed Gull *L. fuscus*, Royle and Hamer 1998, Kittiwake *Rissa tridactyla*, Coulson and Porter 1985, Common Tern *Sterna hirundo*, Langham 1972; Nisbet 1978; Nisbet and Cohen 1975; Bollinger *et al.* 1990, Roseate Tern *S. dougallii*, Nisbet 1978; Nisbet and Drury 1972; Nisbet and Cohen 1975; Burger *et al.* 1996, Gull-billed Tern *S. nilotica*, Eyler *et al.* 1999 and Sandwich Tern, Langham 1974; Veen 1977). Both hatching asynchrony and the decrease in egg size with hatching order in larids are consistent with the brood reduction strategy, but their functions are not always clearly understood (Bollinger 1994).

Studies on chick survival and brood size reduction in larids focussed on species with maximum clutches of three eggs, with the Roseate Tern probably being the best studied exception. Differential survival of Sandwich Tern chicks has been studied in detail by Langham (1974) and Veen (1977). Although sometimes clutches of three eggs can be found (probably originating from two females), Sandwich Terns generally lay one or two eggs. On Griend clutch size averages 1.6 eggs, with the volume of the second egg being on average 7% smaller than the first egg (Stienen and Brenninkmeijer 1996). The second chick of 2-chick broods hatches about three days after the first (Veen 1977). At least at our study sites on Griend, The Netherlands, and on Hirsholm, Denmark, the survival probability of the second hatchling is extremely low. In seven years covered by the present study, Sandwich Terns seldom raised more than one chick to fledging. This paper analyses pre-fledging mortality of Sandwich Tern chicks held in enclosures on Griend and Hirsholm in relation to egg sequence and rank within the brood. We will discuss possible benefits for the terns of producing a clutch size larger than they generally rear. The reduction of the brood size is discussed in the light of the availability of food resources.

MATERIALS AND METHODS

The main study was carried out on the Isle of Griend, situated in the Dutch Wadden Sea (53°15'N, 5°15'E), where several species of gulls (mainly Black-headed *Larus ridibundus*, Common *L. canus* and Herring Gull *L. argentatus*) and terns (mainly Sandwich, Common *S. hirundo* and Arctic Tern *S. paradisaea*) nest. During the study period (1992-99) the population of Sandwich Terns on Griend fluctuated between 5600 and 8300 breeding pairs, each year consisting of several subcolonies. The island consists of a sandy ridge that was constructed in 1988 to protect the lower marshy inner part of the original island. The salt marsh is dominated by a pioneer vegetation of *Salicornia procumbens, S. europaea, Armeria maritima, Pucinellia maritima* and *Limonium vulgare*. The higher parts are dominated by *Halimione portulacoides, Matricaria maritima, Atriplex littoralis* and grasses (mainly *Elymus farctus, E. repens, Leymus arenarius* and *Festuca rubra*). For comparison in 1997 a Sandwich Tern colony on Hirsholm, Danish Kattegat (10°38'N, 57°29'E), was studied. In contrast to Griend, Hirsholm is inhabited by man, has a stony undersoil and highly divers vegetation ranging from pioneer vegetation to shrubs and trees. In 1997, 1250 pairs of Sandwich Terns nested on Hirsholm as well as 6500 pairs of Black-headed Gulls and smaller colonies of Common Gull, Herring Gull, Lesser Black-backed Gull *L. fuscus* and Arctic Tern.

Enclosures

Each year on Griend and on Hirsholm in 1997 a part of a subcolony containing 50-100 nests was selected for further study. To reduce possible effects of hatching date, the subcolonies under study were chosen in a way that the hatching date of most chicks coincided with the peak of hatching of the entire island population. Only in 1993, an additional subcolony of later hatching date was studied on Griend, so that hatching dates ranged from day 140-172 (median hatching day = 152).

Within the selected study sites, most nests were marked with numbered sticks within 3 days after laying of the first egg. If possible, in each nest the eggs were marked in sequence of laying with a permanent marker. A few days before hatching of the first eggs, part of the selected study site was enclosed with wire netting. In total 434 enclosed nests with known laying sequence of the eggs were selected for this study (Table 7.1). In 1994 on Griend, hatching success and fledging success were measured in different subcolonies, so that the results were not used for this study. If possible, all enclosed nests and broods were checked every three days and the chicks were ringed within 3 days after hatching. The hatching date of a chick was estimated from the state of the egg during the previous control, feather characteristics of the chicks, the size of the yolk sac, total head length (*i.e.* exposed culmen length) and whether or not the chick was still wet. Under favourable weather conditions the chicks' body mass, total head length and stretched wing chord were measured during each control. If a chick was missing from the enclosure it was presumed to be preyed upon. In such case the date of predation was set as the middle day between last live measurement and the day that the chick was missing

Table 7.1. Clutch size, hatching success and sample size of enclosed Sandwich Tern nests on Griend and Hirsholm in the period 1992-1999. Only nests of which laying sequence of the eggs was known are listed.

Location:	Griend	Griend	Griend	Griend	Griend	Griend	Griend	Hirsholm	
Year:	1992	1993	1995	1996	1997	1998	1999	1997	Total
1-egg clutch									
No chick	3	3	1	7	1	6	0	4	25
1 chick	15	24	11	41	27	6	17	7	148
2-egg clutch									
No chick	0	3	1	4	5	5	1	3	22
a-chick	3	5	2	1	4	6	2	3	26
b-chick	5	1	1	2	5	5	2	1	22
2 chicks	30	27	26	11	19	32	36	10	191

from the enclosure. If the age of a missing chick exceeded 24 days, however, the chick was presumed to have fledged. At this age wing length can exceed 175 mm, which is the minimum wing length required for flying in Sandwich Tern chicks (Stienen and Brenninkmeijer 1999). A chick was categorised as dead if it was found dead or when it was missing from the enclosure when still not able to fly. The latter losses were mainly due to avian predators that either preyed upon living or dead chicks (both Griend and Hirsholm hold no ground predators). During observations in the colony, we mainly observed Black-headed Gull, and occasionally Common and Herring Gull preying upon Sandwich Tern chicks. On Hirsholm in 1997, predation by Herring Gulls occurred more often than on Griend (own observation). Except for avian predation, there were two other reasons why chicks could be missing from the enclosures. Sometimes very young chicks (age < 5 days) did not completely swallow a fish that was fed by a parent, thus part of the fish was sticking out of the chick's bill. In such case it could happen that a gull tried to rob the fish while the chick was still attached to it. Consequently, the chick was transported a few meters through the air and sometimes came lose outside the enclosure. Occasionally dead chicks were removed from the enclosure by Sandwich Tern parents (Stienen *et al.* 1997). However, the intra-specific removal of dead chicks and gull-enhanced transport of living chicks were very rare events (own observations) and have only small effects on the results of this study.

Body condition (BC) of the chicks was defined as the proportional deviation of the measured body mass (M, g) from the average body mass (M_{exp}, g) of chicks of the same age that survived the first 25 days:

$$BC = \frac{M - M_{exp}}{M_{exp}} \qquad \text{equation 1}$$

Chicks were divided into the following five categories dependent on the egg from which it hatched and the rank within the brood at hatching: a_1 = chick from a 1-egg clutch, a_{12} = first-hatched chick from a 2-chick brood, b_{12} = second-hatched chick from a 2-chick brood, a_{11} = single chick originating from the first-laid egg of a 2-egg clutch of which the second egg did not hatch and b_{11} = single chick originating from the second-laid egg of a 2-egg clutch of which the first egg did not hatch.

Of the 434 nests listed in Table 7.1, 47 did not hatch any chick because of egg predation by gulls or Oystercatcher *Haematopus ostralegus*, addled eggs or chicks that died in the process of hatching. Not all chicks of the remaining 387 nests could correctly be matched to corresponding nest or egg and some very young chicks lost their metal ring. In total 527 hatchlings originating from 352 nests could be justly classified of which 141 a_1-chicks, 171 a_{12}-chicks, 164 b_{12}-chicks, 24 a_{11}-chicks and 27 b_{11}-chicks. Through the large size of the enclosures coloniality was preserved, but it was impossible to measure all chicks within the enclosure at each occasion without causing an unacceptably long disturbance. Therefore, 82 randomly chosen broods were put out of the enclosures when more than 10 days old. For the 445 remaining chicks that were held in enclosures from hatching until fledging, we found no significant effect of hatching date on the fledging probability after controlling for effects of year, location and chick category (Table 7.2). Therefore, hatching date will not be considered in further analyses.

For each period of 5 days, mortality rate was computed by dividing the number of non-surviving chicks (found dead and missing from the enclosures) by the total number of chicks present at the onset of the 5-day period. Chicks that were put out of the enclosures were included in the computation of mortality rate until they were exiled. Dead chicks were sampled, their body mass and total head length were measured, and the day of death was estimated by smell, features of the eyeball and state of putrefaction and were subsequently removed from the enclosures.

Table 7.2. Generalised linear regression analysis examining the effect of location, chick category and hatching date on the fledging probability of 445 Sandwich Tern chicks that were held in enclosures from hatching until fledging on Griend (1992-1999) and Hirsholm (1997).

Variable	(change in) Deviance	df	P-value
Null model	609.6	444	
Final model	351.0	407	
Location	31.9	7	< 0.001
Chick category	176.7	4	< 0.001
Location*chick category	48.3	25	0.003
Hatching date	1.5	1	n.s.

Statistical analyses

Generalized linear models for the analysis of mortality rates (using binomial distribution) were performed with the Genstat statistical package (Genstat 5 Committee 1993). For data analysis and all other statistical tests we used the SPSS/PC+ 4.0 statistical package (Norusis 1990). We report differences at a probability level of $P < 0.05$ as significant. To compare mortality rates between groups of chicks we first controlled for effects of year and location. Interaction terms were only included if they were significant. The parameters location (*i.e.* a combination of year and colony, 8 levels), age category (6 levels), chick category (a_1-chick, a_{12}-chick etc., 5 levels) were entered in the analyses as factor variables. All generalized linear models were corrected for overdispersion.

RESULTS

Mortality rate

Mortality rates of Sandwich Tern chicks did not differ between Griend and Hirsholm, but significantly differed between age categories (Table 7.3). Further adding of chick category to the regression analysis resulted in significant effects on chick mortality rates and also the interaction term location*chick category had significant effects on chick mortality rates. Of a_1- and a_{12}-chicks, respectively 73.4% and 73.1% survived until fledging, while only 6.2% of the b_{12}-chicks survived (Fig. 7.1). Within five days from hatching, more than 50% of the b_{12}-chicks had died and in some years this figure was even higher. In total, only nine b_{12}-chicks survived until fledging. Of these chicks, four originated from nests of which the a_{12}-chick had died before hatching of the b_{12}-chick. Of the remaining five surviving b_{12}-chicks, three had a more slowly growing a_{12}-sibling that eventually died. Thus only two nests actually fledged two chicks, corresponding with 1.1% of all 2-chick broods ($n = 171$). Another three b_{12}-chicks were put out of the enclosure before fledging. Of these chicks, two had an a_{12}-sibling that had died by the time the b_{12}-chick was exiled, while one b_{12}-chick that was put out of the enclosure at 24 days old had an a_{12}-sibling sibling that had already fledged. If we assume that the latter b_{12}-chick has

Table 7.3. Generalised linear regression analysis examining the effect of location, age and chick category on the mortality rate of enclosed Sandwich Tern chicks on Griend and Hirsholm.

Variable	(change in) Deviance	df	P-value
Null model	609.0	175	
Final model	234.4	133	
Location	11.8	7	n.s.
Age category	36.2	4	< 0.001
Chick category	272.1	4	< 0.001
Location*chick category	54.6	27	0.001

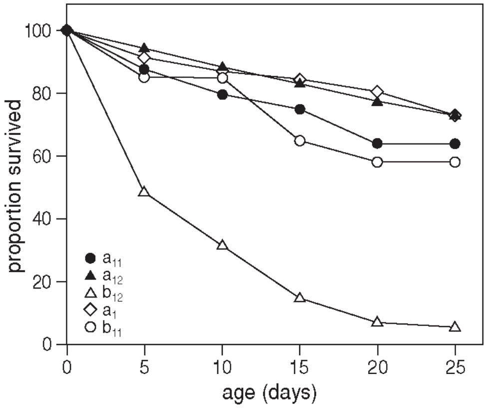

Figure 7.1. Cumulative survival of Sandwich Terns chicks held in enclosures on Griend in 1992-1999 and Hirsholm in 1997 in relation to laying sequence of the egg, rank within the brood and age. A_{11} = chick originating from the first-laid egg of a partially hatched clutch, a_{12} = first-hatched chick of a 2-egg clutch, b_{12} = second-hatched chick of a 2-egg clutch, a_1 = chick of a 1-egg clutch, b_{11} = chick originating from the second-laid egg of a partially hatched clutch.

actually fledged, 1.8% of all initial 2-chick broods fledged two chicks. A_{11}- (64.3% survival) and b_{11}-chicks (58.5%) experienced significantly higher mortality rates than a1- and a_{12}-chicks (Fig. 7.1). Of the 7 b_{12}-chicks of which the a_{12}-chick died before hatching of the b-chick 57.1% survived, very similar to the survival of b_{11}-chicks.

When hatching success and fledging success are combined (Table 7.4) it follows that producing 2-egg clutches has slight advantages for Sandwich Terns in terms of chick production. Of all 1-egg clutches 63% successfully raised a chick, whereas breeding success amounted to 0.69 fledglings per pair in 2-egg clutches. Of the 2-egg clutches 82.4% of all

Table 7.4. The effects of clutch size on hatching and breeding success of Sandwich Terns on Griend and Hirsholm. Chick survival rates were derived from figure 2.

Clutch size	Number of nests	Chick category	Hatching success	Chick survival	Breeding success (fledgling per pair)	Overall breeding success (fledgling per pair)
1 egg	173	no chick	14.5%		0.00	0.63
		a1 chick	85.5%	73.4%	0.63	
2 eggs	261	no chick	8.4%		0.00	0.69
		a11 chick	10.0%	64.3%	0.06	
		b11 chick	8.4%	58.5%	0.05	
		a12 chick	73.2%	73.1%	0.54	
		b12 chick	73.2%	6.2%	0.05	

eggs hatched successfully; somewhat lower than in 1-egg clutches (85.5%), but the difference was not significant (chi-square test, $\chi^2 = 0.93$, n.s.). Still, the probability of a complete hatching failure of the nest was 6.1% lower in 2-egg clutches.

Hatching mass significantly differed between a_{12}- and b_{12}-chicks (Table 7.5), in accordance with the generally smaller size of the second-laid egg (Stienen and Brenninkmeijer 1996). Hatching mass of a_1-chicks was similar to that of a_{12}-chicks. Structural size (total head length) did not differ between these groups, thus b_{12}-chicks hatched with lower body reserves. Nevertheless, early chick mortality seems independent of the laying sequence of the egg. Although b_{12}-chicks experienced a much higher early mortality rate than a_{12}-chicks, there was no significant difference between a_{11}- and b_{11}-chicks (Table 7.6). Early mortality rate of chicks of partially hatched nests (a_{11}- and b_{11}-chicks) was much higher than that of fully hatched nests (a_{12}- and a_1-chicks), but the difference was not significant.

Causes of death

The proportion of non-surviving chicks that was missing from the enclosure differed between locations (Table 7.7). It was extremely low on Griend in 1995 (< 5% were not found) and highest on Hirsholm where 70.6% of all non-surviving chicks were missing from the enclosure. Controlling for effects of location, the proportion of missing chicks significantly differed between age-categories (Table 7.7). Of non-surviving chicks in the age of 0-4 and 5-9 52.1% and 44.4%, respectively, was missing from the enclosure. The proportion of missing chicks decreased to 20.0-20.8% for chicks between 10 and 19 days and was only 11.8% for chicks of 20-24 days.

The body mass of Sandwich Tern chicks was highly variable (Fig. 7.2). The body condition of chicks that survived until fledging varied between –0.63 and 0.47. Body mass of chicks measured within three days from death (further called last live body mass), generally was much lower than that of surviving chicks (Fig. 7.2). The last live body mass of chicks that were found dead or were missing from the enclosures averaged 31.9% and 22.6%, respectively, below the average body mass of surviving chicks. Of these groups 47.9% and 43.5%, respectively, had a last live body mass that was even lower than the minimum recorded body mass of surviving chicks. This suggests that most non-surviving chicks suffered from undernourishment and ultimately starved to death or were taken by predators. Still, 6.0% of the chicks that were found dead ($n = 119$) and 21.7% of the missing chicks ($n = 46$) had last live body conditions that were higher than or equal to the average body condition of surviving chicks. Most (80.0%) of the missing chicks in good body condition ($BC \geq 0.0$) were a_{12}-, a_1-, a_{11}- or b_{11}-chicks, whereas missing chicks in poor condition ($BC < -0.1$) mainly (81.8%) concerned b_{12}-chicks (last live body condition of preyed a_{12}-, a_1-, a_{11}- or b_{11}-chicks vs. b_{12}-chicks, -0.02 (SD 0.18, $n = 17$) and –0.34 (SD 0.24, $n = 29$), Student's t-test: $t = 4.75$, $P < 0.001$). The last live body condition of missing a_{12}-, a_1-, a_{11}- and b_{11}-chicks did not differ significantly from the body condition of surviving chicks (-0.02, SD 0.18, $n = 17$ and 0.00, SD 0.10, $n = 185$, respectively, $t = 0.58$, $P > 0.05$).

Table 7.5. Body mass and head length (mean ± SD) of freshly hatched Sandwich Tern chicks on Griend in relation to brood size and hatching position. Text within brackets denotes significant differences (Scheffé-test, $F_{2,82} = 7.62$ and 1.11, $P < 0.001$ and n.s., respectively).

Chick category	Number of chicks	Body Mass (g)	Head size (mm)
a_1	31	27.05 ± 2.53 (b_{12})	37.60 ± 1.18
a_{12}	21	26.98 ± 2.10 (b_{12})	38.03 ± 1.05
b_{12}	32	25.00 ± 2.45	37.59 ± 1.26

Table 7.6. Mortality rate of Sandwich Tern chicks during the first five days after hatching in relation to chick category. The number of non-surviving chicks is shown between brackets. Differences in mortality between groups were tested by means of chi-square or Fisher's exact test. Only significant differences ($P < 0.05$) are shown.

Chick category	Number of chicks	Mortality	Differences
a_{12}	171	0.05 (9)	
a_1	141	0.09 (12)	
a_{11}	24	0.13 (3)	
b_{11}	20	0.15 (3)	
b_{12}	171	0.51 (87)	1,2,3,4

Table 7.7. Logistic regression analysis examining the effect of location and age of Sandwich Tern chicks on the proportion of non-surviving chicks that were missing from the enclosures.

Variable	(change in) Deviance	df	P-value
Null model	101.7	35	
Final model	47.8	44	
Location	41.7	7	< 0.001
Age category	12.2	4	0.02

Low food intake rate causing poor body condition apparently was an important cause of chick mortality in enclosed Sandwich Tern chicks at Griend and Hirsholm. Therefore one might expect that having two chicks is disadvantageous for their growth and that the duration that two chicks are present in the brood has consequences for survival of the first hatchling or at least for its body condition. To test these assumptions, a-chicks were divided into 5 categories according to their age at the moment the b-chick died. Indeed, the time of death of the b-chick significantly affects survival rate of the a-chick (Table 7.8), but the direction was unexpected (Fig. 7.3). In nests where the b-chick died 0-4

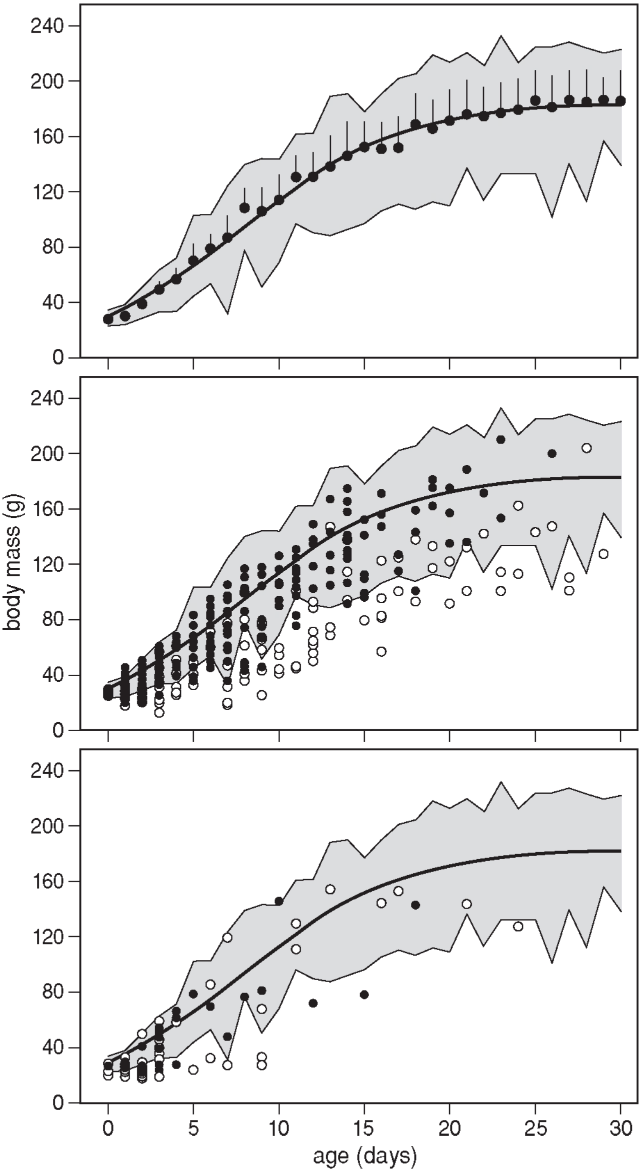

Figure 7.2. Body mass (means + SD and ranges) of enclosed Sandwich Tern chicks on Griend and Hirsholm that survived until fledging (upper graph) and body mass of chicks that were found dead (middle graph) or were missing from the enclosures when not yet able to fly (lower graph) in relation to age. Drawn lines represent logistic growth curve fitted through data of fledged chicks (body mass (g) = 183.3/(1+5.08*exp(-0.212*age)), n = 1532, r^2 = 0.87). Black dots = body mass > 3 days before death or before they were missing from the enclosure, open circles = body mass within 3 days from death or missing.

Table 7.8. Logistic regression analysis examining the effect of location and age category on the mortality rate of a_{12}-chicks in relation to the age at which the b_{12}-chick died (5 levels: died when a_{12}-chick was 0-4, 5-9, 10-14 or > 14 days, and b_{12}-chick survived until fledging).

Variable	(change in) Deviance	df	P-value
Null model	124.0	75	
Final model	50.5	60	
Location	13.5	7	n.s.
Age category	46.4	4	< 0.001
Age of death	13.6	4	< 0.01

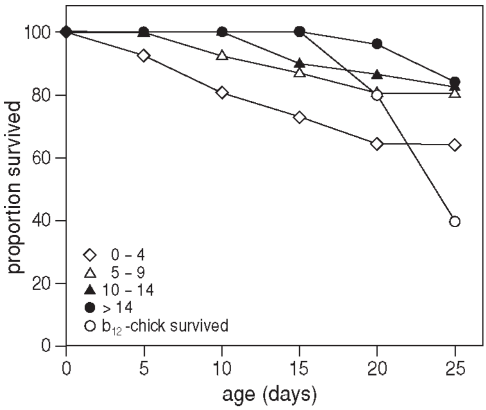

Figure 7.3. Cumulative survival of first hatched Sandwich Tern of 2-chick broods in relation to the time the second hatchling was present. 0-4 = second hatched chick died between day 0 and day 4 from hatching of the first chick, etc.

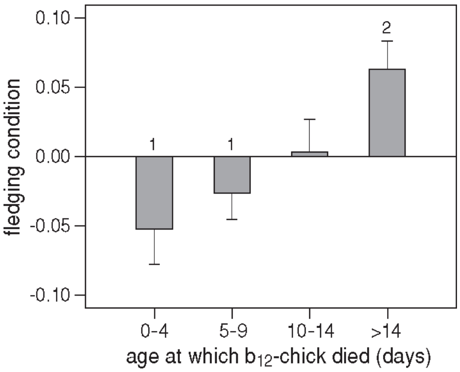

Figure 7.4. Fledging condition of first-hatched Sandwich Tern chicks in relation to the time of death of the second hatchling. 0-4 = second hatched chick died between day 0 and day 4 from hatching of the first chick, etc. Numbers above bars denote significant differences.

days after hatching of the a-chick, the a-chick had relatively low survival chances (64.5% survived until fledging, so very much the same as a_{11}-chicks and somewhat higher than b_{11}-chicks). If the b-chick survived the first five days but died afterwards, survival chances of the a-chick ranged from 80.8–84.0%. In the few nests where the b-chick survived until fledging survival rate of a-chicks was only 40.0%. The fledging condition (*i.e.* average BC of the chick when older than 24 days) depended on the time of death of the b-chick (ANOVA, $F_{3, 82} = 3.7$, $P = 0.02$). However, where a decrease in fledging condition with increasing duration of the time that two chicks were present was expected an increase is found (Fig. 7.4).

DISCUSSION

Reproductive output

Parents in this study that produced only one egg took the risk of losing the egg before hatching. If, however, the egg hatched successfully, the chick had high survival chances and fledged in average body condition (fledging condition did not differ between chick-categories; ANOVA, $F_{4,190} = 0.1$, n.s.). A second category of parents produced two eggs, but hatched only one. Survival chances of their chicks were somewhat lower (mainly because of high chick mortality during the first five days), but fledging condition was comparable to the first category. For unknown reasons, the eggs and chicks of these parents were more prone to predation, but the parents apparently had no difficulties with providing enough food to their chick. A third category in which brood size was reduced in an early phase and whose surviving chick had poor survival changes as well. Their chicks were in relatively poor body condition at fledging. These parents apparently had no difficulties in protecting their eggs and chicks from predators, but had difficulties with providing enough food to the chicks. Finally, there was a small group of high quality parents that were able to hatch two eggs and keep two chicks alive for a relatively long period and to raise a fledgling that was in good body condition. Obviously, these parents invested more energy in the production of eggs and the rearing of their chicks than other parents, but reached high survival rates of their a_{12}-chick and even had a small chance to rear two chicks to fledging.

A reproductive output of less than one chick per breeding pair and a poor survival of second hatchlings are not unique for Griend or Hirsholm, but rather seem commonplace in Sandwich Terns. In a Sandwich Tern colony at Zeebrugge, Belgium, no pair was able to fledge 2 chicks in any of the 4 years during the period 2001-2004 (own observations in enclosed subcolonies). Isenmann (1975) mentions that in the Camarque, France, only 7% of all pairs had 2 chicks close to fledging. All other measurements of breeding productivity in Sandwich Terns in the literature are doubtful, as either only counts of 'large' chicks were made or breeding success was estimated from the numbers of dead chicks found. Sometimes, no method is described at all. Nevertheless, these studies hardly ever found a breeding success much higher than 1 fledged chick per pair (Schmidt 1969;

Chestney 1970; Langham 1974; Walsh *et al.* 1990). Only Campredon (1978) mentions a breeding success of more than 1.7 fledglings per pair, but he based this figure on the number of dead chicks found in the colony (which would have excluded losses due to predators, if any). At first sight, Veen (1977) also found higher survival rates on Griend in the period 1971-1972. He suggests that up to 84% (49.3-83.8%) of the a_{12}-chicks and up to 20% (11.8-20.0%) of the b_{12}-chicks survived until fledging. In contrast, however, to our study where fledging age was set at 25 days, Veen defined chicks older than 14 days as fledglings. If we use the same definition of fledging as Veen did, mortality rate in the 1970s is comparable to that in the 1990s when 83.5% and 15.2%, respectively of the a_{12}- and b_{12}-chicks survived the first two weeks posthatching (Fig. 7.2).

It remains puzzling to what extent our results can be compared to that of studies where chicks were not held in enclosures. After all, by preventing the chicks to move away from the colony site by retaining them in enclosures they suffer from increased rates of kleptoparasitism and consequently mortality rates might have been higher than in natural situations (Stienen & Brenninkmeijer 1999). On the other hand, one would expect that enclosing chicks would only affect older chicks, because (1) also in natural situations very young chicks stay in the vicinity of the nest and (2) kleptoparasitism by Black-headed Gulls is still rather low during the first week after hatching (Stienen *et al.* 2001). In our study, however, most b_{12}-chicks died in an early stage of life when possible negative effects of the enclosures are not yet to be expected. In non-enclosed subcolonies on Griend and Hirsholm we also found many dead b_{12}-chicks of less than 1 week old and during observations of Sandwich Terns parents feeding fledglings at the beaches around Griend we very rarely observed more than one fledgling per parent, suggesting a generally low survival rate of second hatchlings.

Overproduction and brood reduction

The extremely low survival rate of b_{12}-chicks is surprising when considering that Sandwich Terns on Griend on average produce 1.6 eggs per nest (Stienen and Brenninkmeijer 1996). Apparently Sandwich Terns produce more eggs than they normally can raise chicks and often the brood size is reduced in an early stage if both eggs hatch successfully. Overproduction is widely spread among plants and animals (including several seabirds) and may serve various functions (review in Mock and Parker 1998): (1) it may allow parents to select the fittest offspring, (2) it may serve as a mechanism for resource-tracking (extra offspring may be affordable in the case of unpredictable improvement of the food situation), (3) it may facilitate sibling survival (if extra offspring serve as helpers or meals for other siblings) or (4) it may be an insurance against accidental failure of an egg or defective offspring.

In Sandwich Terns, overproduction serving resource tracking (2) seems rather costly as in 10 years time (1992-2001; data from this study and non-published data) almost no pair was able to fledge 2 chicks on Griend. However, given that Sandwich Terns can become more than 25 years old, and if the costs involved in producing an extra offspring are relatively low (but see Heaney and Monaghan 1995), it might be affordable to produce two eggs even if 'good' years occur at a very low frequency. The present food situation around Griend and the high rates of kleptoparasitism causes a lot of food stress for Sandwich Terns parents (Stienen & Brenninkmeijer 2002) and undernourishment is an important cause of death for Sandwich Tern chicks (this study). This suggests that resources were low during the 1990s. Sibling facilitation (3) in terms of the youngest sibling helping or serving as an extra meal for the first hatchling does not occur in Sandwich Terns. There might be a small advantage of having a younger sibling, because parents that have two chicks increase the rate of food transport to the nest. This would be temporarily advantageous to the first hatchling, namely during the first few days when the first hatchling consumes almost all food brought to the brood (Stienen *et al.* 2000). The extra egg serving as an insurance (4) in combination with selection of the fittest offspring (1) seems to be the most plausible explanation for overproduction in Sandwich Terns. The failure of the first egg or the death of the first chick in an early stage occurred relatively often in our study plots. In 18.4% of the 261 2-egg clutches only 1 egg hatched, 7.2% of the fledglings of 2-egg clutches originated from second-laid eggs and parents that laid two eggs had a somewhat higher breeding success (Table 7.4).

As 2-egg clutches seem to be slightly more productive, one might expect that Sandwich Terns on Griend nowadays tend to lay larger clutch than in the past. There is, however, no evidence for this. Brouwer (1930) mentions a clutch size of 1.75 in 1929 on Griend, in 1970-72 clutch size averaged 1.81 (Veen 1977) and in the 1980s clutch size averaged 1.6 (Brenninkmeijer & Stienen 1992). The apparent advantages of producing a 2-egg clutch thus might be nullified by parental reproductive costs involved in producing and rearing a large clutch.

It is thought that birds adopting a brood reduction strategy may facilitate this process by producing a small final egg (Slagsvold *et al.* 1984) and by asynchronous hatching of the eggs (Anderson 1989; Cash & Evans 1986) as is the case in Sandwich Terns (Veen 1977; Stienen & Brenninkmeijer 1996). Experimental studies on other Laridae suggest that lower survival rate of the last-hatched chick is primarily caused by hatching asynchrony while egg size difference is less important (Parsons 1975; Bollinger 1994; Royle & Hamer 1998), which is also suggested by our results (Table 7.6). In an experimental study in the Caspian Sea, Gauzer (1989) found that 73.9% of synchronously hatched Sandwich Terns broods produced 2 fledglings, compared to 23.3% in the control group that hatched chicks asynchronously. Gauzer (1989) found that Sandwich Terns were even able to raise three chicks to fledging provided that in the experimentally enlarged clutch the three eggs hatched synchronously. Although we were not able to extract Gauzer's (1989) definition of fledging, the study demonstrated that asynchronous hatching of the eggs facilitates brood reduction in Sandwich Terns. It also appears that the food situation in Gauzer's study area was much more profitable than on Griend and Hirsholm. In our study hatching asynchrony results in a knock-out race and facilitates the death of the youngest sibling. If both chicks would have hatched synchronously periods of food stress might very well result in the death of both siblings.

Food availability

Stienen & Brenninkmeijer (2002) showed that in the presence of kleptoparasitising gulls food availability on Griend is not sufficient to rear two chicks to fledging. This study confirms that undernourishment resulting in a decrease in body condition that finally leads to starvation was an important cause of death in enclosed Sandwich Tern chicks on Griend and Hirsholm. A large proportion of the chicks that were missing from the enclosures lagged behind in body mass as well. The high proportion of missing chicks on Hirsholm (70.6% of all non-surviving chicks were missing) is probably the result of high removal rates of both living and dead chicks by Herring Gulls (own observation). On Griend, predominantly Black-headed Gulls preyed upon Sandwich Tern chicks. Despite large differences in the proportion chicks that were missing from the enclosures, survival rates did not differ between Griend and Hirsholm. Although this study does not differentiate between predation and starvation, the results suggest that predators selectively took smaller chicks in poor body condition (mainly b_{12}-chicks) that would otherwise have died from starvation and/or they removed chicks that had starved to death. Selective predation on chicks in poor condition was also found in Common Terns (Nisbet 1975) and was earlier described in Sandwich Terns on Griend by Veen (1977).

In conclusion, in most pairs of Sandwich Terns on Griend and Hirsholm the brood was reduced to only one chick at an early stage mainly through starvation of the second hatchling. Also for first hatchlings and singletons starvation was an important cause of death, suggesting a high degree of food stress. Earlier studies on Griend (Stienen *et al.* 2001, Stienen & Brenninkmeijer 2002) show that this is a combined effect of a poor food situation and high rates of kleptoparasitism. This gives the terns little leeway during periods of bad weather when feeding conditions deteriorate and food loss to the gulls increases.

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Chapter 8

Feeding ecology of wintering terns in Guinea-Bissau

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ASTRACT

We studied the feeding ecology of Little Terns *Sterna albifrons*, Sandwich Terns *S. sandvicensis* and Royal Terns *S. maxima* in the Archipélago dos Bijagós (11°40'N, 15°45'W) in Guinea-Bissau (West-Africa) during the winter of 1992/1993. More than 95% of all prey taken by these terns were roundfish, ranging in weight between 0.3 and 40 g. Usually birds fed alone, but sometimes they were observed feeding in mixed species flocks consisting of 15-200 individuals. Capture rate (n of fish per hour foraging) in these flocks was higher than that of solitary birds. However, smaller fish were caught while foraging in flocks, so food intake rate (g/h) did not differ between solitary and flock feeding birds. Especially the relationships between foraging behaviour of the three tern species and abiotic factors, such as time, tide and water clarity, have been investigated. Capture rate of Royal Terns increased with water clarity. For Little Terns and Sandwich Terns, food intake rate was lower in the most turbid waters compared to clearer waters. There was very little foraging activity during high tide. For Little Terns and Royal Terns, food intake rate was about twice as high during receding and low tide than during incoming tide. Food intake rate averaged 8 g/h in Little Terns, 60 g/h in Sandwich Terns and 45 g/h in Royal Terns. With a rough model, we provisionally estimate the maximum rate of daily energy expenditure of terns wintering in the tropics at 3BMR. From an energetic point of view, wintering Sandwich Terns in Guinea-Bissau seem to have an easy living.

INTRODUCTION

During the last century, some populations of marine tern species in Europe, Middle America and Asia have shown large fluctuations in numbers (Cramp 1985; Del Hoyo *et al.* 1996). Besides hunting (Mead 1978, Meininger 1988) and poisoning (Koeman & Van Genderen 1966), crashes have been caused by decreases in prey fish availability (Heubeck 1988; Monaghan *et al.* 1992; Wright 1996; Suddaby & Ratcliffe 1997). Fish stock size and abiotic factors, such as water clarity (Eriksson 1985; Haney & Stone 1988), wind speed (Dunn 1973; Veen 1977), water temperature, salinity and water current (Hunt & Schneider 1987), have been suggested to influence fish availability by affecting the behaviour of fish as well as the behaviour of their potential avian predators. Crashes were not always followed by a complete recovery, which may have been due to problems in the wintering as well as in the breeding areas (Brenninkmeijer & Stienen 1992; Stienen & Brenninkmeijer 1992).

We studied the feeding ecology of wintering Little Terns *Sterna albifrons*, Sandwich Terns *S. sandvicensis* and Royal Terns *S. maxima* in the coastal waters of Guinea-Bissau. The total number of terns wintering in 1992/93 in these waters has been estimated at 62,000 (Asbirk 1993; J.S. Salvig unpubl. data). Most of the Royal Terns in Guinea-Bissau probably breed in Senegal or Mauritania (Keijl *et al.* 2000), whereas the Little and Sandwich Terns originate from European breeding colonies (Cramp 1985). The coastal waters of Guinea-Bissau are of great international importance to terns, since more than 25% (10,000) of the 40,000 Western Palearctic Little Terns, 5% (7,500) of the 150,000 Western Palearctic Sandwich Terns and 10% (7,500) of the 75,000 West African Royal Terns spend the northern winter in the area. In this paper, relationships between the foraging behaviour of the three tern species and abiotic factors, such as time, tide and water clarity, are discussed. Furthermore, a simple model shows the energetic consequences of different feeding behaviour of the three species.

METHODS

Study site

Field work was carried out at 32 days between 15 November 1992 and 7 February 1993, at 12 sites in the Archipélago dos Bijagós (11°40’N, 15°45’W), a group of islands and intertidal mudflats off the coast of Guinea-Bissau (Fig. 8.1). Each site was visited by boat for a period of one to eight days. The sites holding the highest tern densities were chosen for study, although not all sites were accessible by boat or provided suitable observation opportunities. The lowest density of foraging terns was measured in the harbour of Bissau (1 tern.km^{-2}), while high densities were found around the Isle of Orangozinho (197 terns.km^{-2}, Brenninkmeijer *et al.* 1998). The maximum density of foraging terns at the 12 study sites averaged 46.9 ± 47.1 (sd) terns.km^{-2}, which is close to the average density of terns in the entire area (62 000 terns at 1570 km2 of tidal area, J.S. Salvig unpubl. data). However, at the study sites even more terns were present, as always some terns were roosting at the beaches or on the tidal flats, suggesting that the sites chosen for study held relatively high numbers of terns.

Study on fish

For logistic and technical reasons (most sites were not suitable for hauling a net over the bottom), species composition was measured at only two sites in the centre of the Archipélago (Maio and Rubane). Yet species composition of roundfish was essentially the same at all sites but Bissau (Van der Veer 1998). Species composition was measured by hauling a beach seine net (length 22 m, depth 1 m, mesh width 10 x 10 mm) over the bottom towards the shore over a distance of approximately 500 m. Simultaneous with our tern investigations, on 11 (Maio), 25 (Rubane), 30 December 1992 (Maio) and 18 January 1993 (Maio), in total 22 catches were conducted at regular intervals over a full tidal cycle. The total length of each fish caught was measured in 0.5 cm classes.

Because the mass of individual small fishes could not be measured accurately on a rolling vessel, we determined fish volume instead by putting fish in a beaker with water. Subsequently, the water volume increase, being the fish volume, was read off with an accuracy of 0.1 ml. Fish volume was converted into fresh mass assuming a specific mass of 1 g/cm^3. Throughout the paper, fish mass is given as fresh mass, unless otherwise indicated.

Behavioural observations on birds

Foraging terns were observed between 7:00 h and 19:00 h on 32 observation days for a total of 214 hours. The number of terns using the observation area, measuring approximately 12,500 m^2 (taking a semicircular area of about 90 m in radius), was counted at least once per hour by telescope (magnification 20-60 times). Of all terns flying in the observation area, one was selected randomly to study its feeding behaviour as long as possible. Flying immatures were not distinguished from adults, since their winter dresses are very similar. Although sometimes terns were foraging in flocks, most observations refer to terns foraging alone. Observations stopped when the tern flew out of the observation area, since prey size could not be estimated accurately from a distance larger than 90 m. Nevertheless, sometimes it was impossible to estimate prey length in the field. Afterwards, these unknown preys were given the average fish length per category of the known preys. Terns that did not dive for fish during the observation period, were omitted from further analysis. Because of the method used, individual foraging periods were highly variable and lasted between 19 and 2280 sec (average 299 ± 280 (SD) sec). Foraging behaviour was observed for a total of 16.8 h in Little Terns, 11.9 h in Sandwich Terns and 7.8 h in Royal Terns. Prey size (total length, cm) was estimated with reference to the tern's bill length (this culmen length, from tip to feathers, is for Little Tern: 2.9 cm; Sandwich Tern: 5.4 cm; Royal Tern: 6.2 cm; Cramp 1985) and classified in 3 cm length classes. Prior to data collection, fish size estimates of each observer were calibrated by holding fishes of various sizes in front of a stuffed tern. Capture rate (the number

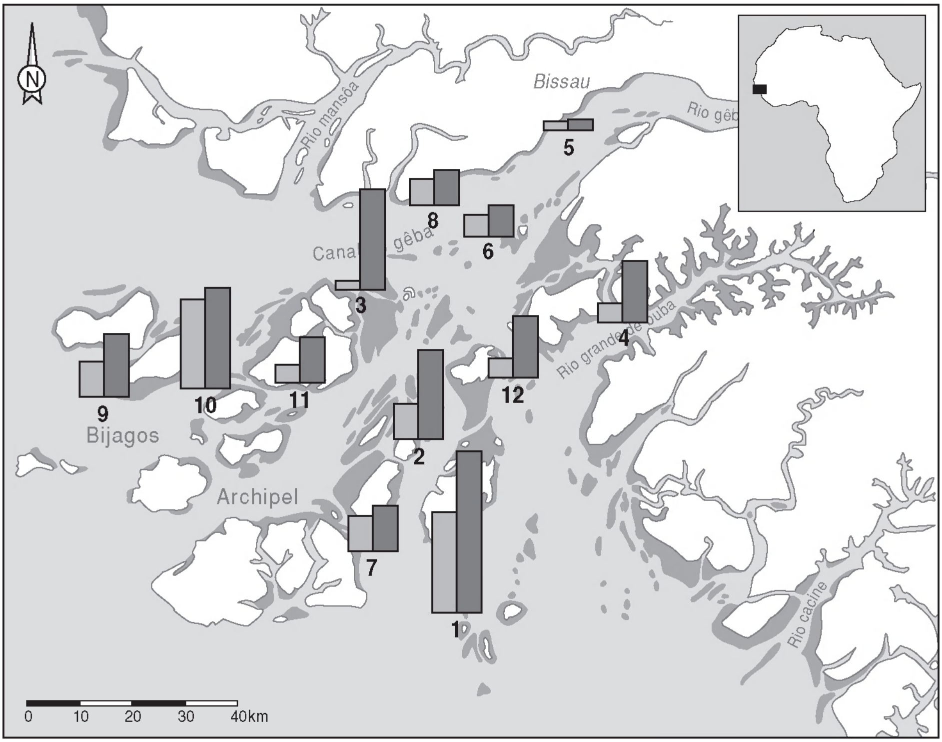

Figure 8.1. Study area in Guinea-Bissau with average min. and max. water clarities (m) per study site (1: Cavalos 2.00-3.25 m, 2: Rubane 0.70-1.75 m, 3: Maio 0.20-2.00 m, 4: Bolama 0.45-1.50 m, 5: Bissau 0.20-0.25 m, 6: Areias 0.40-0.60 m, 7: Orangozinho 0.70-0.90 m, 8: Prabis 0.50-0.70 m, 9: Porcos 0.70-1.25 m, 10: Enu 1.75-2.00 m, 11: Egumbane 0.35-0.90 m, 12: Galinhas 0.40-1.25 m).

of prey per hour foraging) was determined for each bird observed. Data on prey size were pooled per tern species and per category (flock or solitary foraging, water clarity, phase of the tidal cycle). Food intake rate (gram per hour foraging) was calculated for each category by multiplying capture rate with the average prey mass.

Abiotic measurements

For the analyses of foraging behaviour, four tidal phases were distinguished: high tide HT (from 45 min before HT until 45 min after HT), receding tide RT (from 45 min after HT until 5.15 h after HT), low tide LT (from 45 min before LT until 45 min after LT), and incoming tide IT (from 5.15 h before HT until 45 min before HT); data from Admiralty Tide Tables. The daylight period (7.00 h - 19.00 h) was divided into five periods (before 10.00, 10.01-12.00, 12.01-14.00, 14.01-16.00, after 16.00 h).

Water clarity was measured with a Secchi disk, at hourly intervals during most foraging observations and beach seine days. Most terns foraged near the shoreline, where water clarity generally increased gradually from beach towards channel. To obtain a characteristic water clarity value per site per hour, water clarity was measured in a transect of approximately 250 m perpendicular to the shoreline, of which the average was taken. Per site, there was no significant day to day variation in water clarity when tidal phase was considered. Therefore, for each site and tidal phase an average clarity value was used in the statistical analyses of foraging behaviour.

Statistics

Data processing and statistics were conducted using SPSS/PC, versions 4.0 and 6.0. Two-tailed tests and confidence intervals of 0.05 were used in all cases. All figures and tables show weighted means (for time) of capture rate and food intake rate.

RESULTS

Water clarity

Water clarity varied from 0.2 m in the shallow, brackish waters near the capital of Bissau to 3.5 m in the very south of the Archipélago dos Bijagós (Fig. 8.1). Corrected for place, there was no relationship between water clarity and time of day (ANCOVA, $F_{4,154} = 0.385$, $P = 0.819$), nor between water clarity and tide (ANCOVA,$F_{3,155} = 4.068$, $P = 0.077$).

Prey selection

More than 95% of the 263 observed prey items taken by terns were roundfish. Unfortunately, roundfish captured by terns could not be identified at the species level. A total of 3645 roundfish were captured in beach seine samples. This accounted for more than 85% of all prey items caught, the remainder being stingrays, flatfish and crabs (Table 8.1). Mullets (*Mugil* sp., *Liza* sp.) occurred in all but one sample, representing

Table 8.1. The occurrence of roundfish in 22 samples between 11 December 1992 and 18 January 1993 in the central part of the Archipélago dos Bijagós. Four different species of mullets (*Liza ramada, L. grandisquamis, Mugil cephalis* and *M. curema*) were lumped.

Species[a]	N catches with species	N fish	Average fish length (cm) ± sd
Mullets	21	831	8.9 ± 6.0
Eucinostomus melanopterus	18	756	7.8 ± 2.2
Pomadasys peroteti	17	520	10.4 ± 3.0
Galeiodes decadactylus	17	198	10.2 ± 3.4
Sardinella maderensis	10	202	9.4 ± 1.9
S. rouxi	10	81	7.7 ± 1.7
Ilisha africana	2	1046[b]	12.9 ± 1.5

[a] Nomenclature after Sanches 1991.

[b] All but 6 individuals occurred in one haul.

almost 25% of all roundfish caught. Another potentially important prey species for terns was *Ilisha africana*. However, this species had a very patchy distribution: virtually all 1046 individuals occurred in one single catch.

About 80% of the roundfish captured in the beach seine samples measured between 7.5 and 16.5 cm (Fig. 8.2). The size of prey items taken by Royal and Sandwich Terns roughly resembled the distribution in beach seine samples, although prey larger than 13.5 cm were rarely caught by the terns. Little Terns clearly selected smaller prey. Fish smaller than 7.5 cm were significantly more abundant in their diet (90%) than in the beach seine samples (18%) ($\chi_1^2 = 13.69, P < 0.001$).

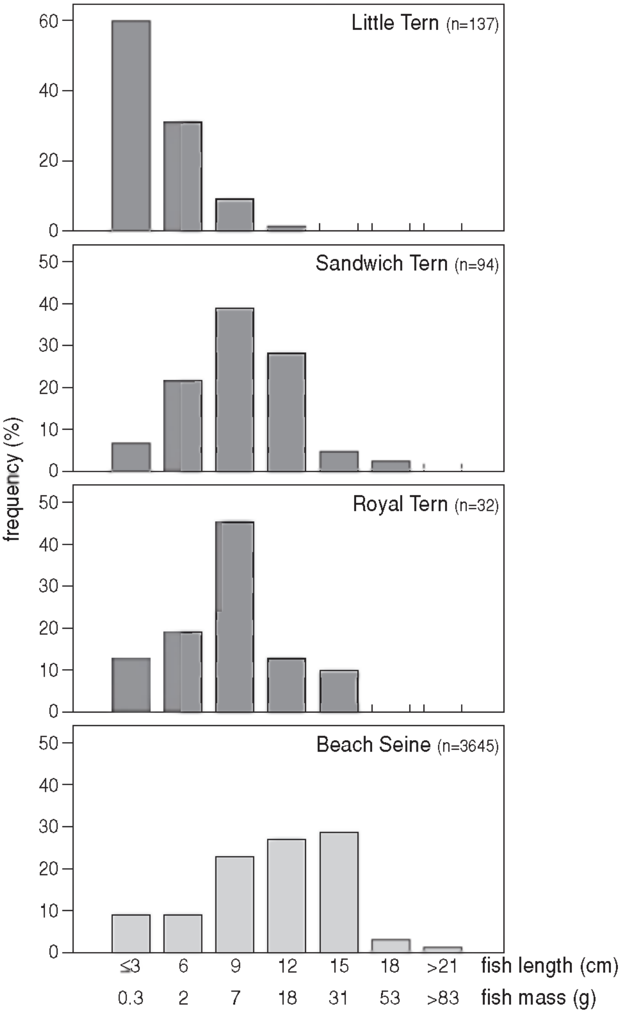

Figure 8.2. Frequency distribution of fish size (length and mass) caught by Little Tern (LT), Sandwich Tern (ST), and Royal Tern (RT) and by beach seine (BS). Mann-Whitney U-tests LT - BS: Z = -2.51, P = 0.012; ST - BS: Z = -1.25, P = 0.212; RT - BS: Z = -1.29, P = 0.196.

Fresh mass of roundfish increased exponentially with length (Fig. 8.3). Since we were unable to identify which species were captured, we had no better option than to use the overall regression equation to estimate the mass of prey taken by the terns:

$$\text{Mass (g)} = 0.01167 \times \text{Length}^{2.915} \text{ (cm)} \qquad r^2 = 0.94, n = 184.$$

Fortunately, fish longer than 16.5 cm were only occasionally taken and within this size range most species fell on the same curve (Fig. 8.3). Only the patchily distributed Ilisha africana had prey masses 39-47% lower than predicted by the curve, while masses of Eucinostomus melanopterus were 16-28% higher.

Food intake rate

Food intake rate per hour foraging averaged 8 g in Little Terns, 60 g in Sandwich Terns and 45 g in Royal Terns (Table 8.2). Despite large sample sizes, the standard errors amounted to 16-29% of the average values, indicating large variation in the underlying data. Some of this variation may be of environmental origin due to differences related to phase of the tidal cycle, water clarity and whether birds forage in flocks or alone. These issues are addressed below.

Occasionally, terns foraged in mixed species flocks consisting of 15-200 individuals. Fish capture rate in flocks was always higher than that of birds foraging alone, but this did not translate into a higher food intake rate, since birds foraging in flocks caught smaller fish (Table 8.2). Because food intake rate did not differ between birds foraging individually and those in flocks, we decided to combine all data.

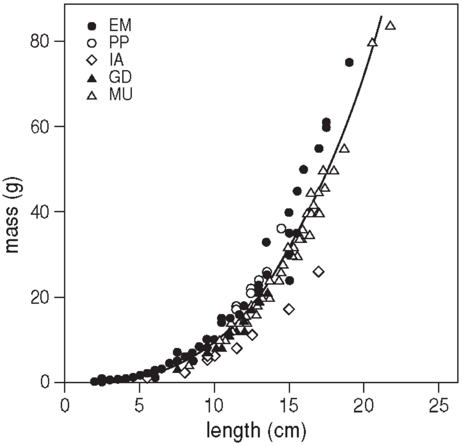

Figure 8.3. The relationship between mass (g) and total length (cm) of roundfish, caught on different places in the Archipélago dos Bijagós from October to December 1992 by beam trawls by H. Witte. Mass (g) = 0.01167*Length (cm) $^{2.915}$, $r^2 = 0.94$, n = 184; EM = *Eucinostomus melanopterus*, GD = *Galeiodes decadactylus*, IA = *Ilisha africana*, MU = mullet (*Liza grandisquamis, L. ramada, Mugil cephalus* or *M. curema*) and PP = *Pomadasys peroteti.*

Table 8.2. Foraging success and calculated food intake rate of terns foraging individually or in flocks during the winter of 1992/1993 in Guinea-Bissau. For all three species, the average food intake rate was calculated combining all the data irrespective of time of day, tidal phase, water clarity or whether the bird foraged individually or in a flock (Student's paired t-test: Little Tern $t_{198} = 0.793$, $P > 0.20$, Sandwich Tern $t_{136} = 0.985$, $P > 0.15$, Royal Tern $t_{41} = 0.013$, $P > 0.40$).

	Individually	In flocks	All terns
Little Tern			
N of terns observed	197	3	200
Time observed (h)	15.0	0.5	15.44
N fish captured	130	7	136
Capture rate (fish/h) ± se	8.69 ± 0.76	14.61 ± 5.52	8.88 ± 0.76
Average fish mass (g) ± se	0.94 ± 0.14	0.38 ± 0.14	0.91 ± 0.13
Food intake rate (g/h) ± se	8.13 ± 1.41	5.55 ± 2.93	8.05 ± 1.34
Sandwich Tern			
N of terns observed	113	25	138
Time observed (h)	9.3	1.8	11.13
N captures	76	18	94
Capture rate (fish/h) ± se	8.14 ± 0.93	10.03 ± 2.36	8.44 ± 0.87
Average fish mass (g) ± se	7.68 ± 0.90	4.59 ± 0.77	7.09 ± 0.75
Food intake rate (g/h) ± se	62.52 ± 10.23	45.98 ± 13.29	59.85 ± 8.84
Royal Tern			
N of terns observed	37	6	43
Time observed (h)	5.0	0.7	5.75
N captures	24	8	32
Capture rate (fish/h) ± se	4.79 ± 0.98	10.95 ± 3.87	5.57 ± 1.14
Average fish mass (g) ± se	9.46 ± 2.10	4.11 ± 0.92	8.13 ± 1.64
Food intake rate (g/h) ± se	45.30 ± 13.68	45.02 ± 19.08	45.26 ± 13.01

Terns spent most of the high water period on their roosts, while food was collected throughout the remainder of the tidal cycle. Foraging terns were observed for only 2.5% of 15.8 hours of observations during high tide. Foraging terns were observed about six times more frequently during the other phases of the tidal cycle (receding tide: 16.6% of 93.1 hours; low tide: 17.5% of 37.5 hours; incoming tide: 14.7% of 67.3 hours). During this observation time, not only foraging terns were followed, yet also terns were counted, and water clarity was measured regularly. Therefore, these percentages cannot be used to calculate the amount of time spent by terns on foraging. Yet it gives a fair indication of the large foraging differences during the tidal cycle. Food intake rate was highest during receding tide and low tide, and declined during incoming tide (Table 8.3). This reduction amounted to 50%, but the average food intake rate pooled for receding and low tide, differed significantly from incoming tide only for Little Tern (Student's paired t-test: $t_{198} = 2.939$, $P < 0.01$) and Royal Tern (Student's paired t-test: $t_{41} = 2.325$, $P < 0.05$).

Table 8.3. Foraging observations and the calculation of food intake rate of wintering terns in Guinea-Bissau during different phases of the tidal cycle.

	N terns observed	Hours observed	N fish caught	Capture rate (fish/h) ± se	Fish mass (g) ± se	Food intake rate (g/h) ± se
Little Tern						
High Tide	2	0.10	0	0	-	-
Receding Tide	96	7.03	55	7.82 ± 1.05	1.32 ± 0.29	10.3 ± 2.7
Low Tide	48	3.71	43	11.85 ± 1.77	0.73 ± 0.15	8.7 ± 2.2
Incoming Tide	54	4.59	39	8.50 ± 1.36	0.54 ± 0.11	4.6 ± 1.2
Sandwich Tern						
High Tide	5	0.24	2	8.34 ± 5.90	8.74 ± 3.46	72.9 ± 59.1
Receding Tide	63	4.46	42	9.41 ± 1.45	7.64 ± 1.43	71.9 ± 17.4
Low Tide	34	2.21	18	8.16 ± 1.92	7.17 ± 0.82	58.5 ± 15.3
Incoming Tide	36	4.22	32	7.58 ± 1.34	6.21 ± 1.06	47.1 ± 11.6
Royal Tern						
High Tide	1	0.06	0	0	-	-
Receding Tide	24	3.95	21	5.32 ± 1.16	8.68 ± 2.08	46.2 ± 15.0
Low Tide	9	0.63	7	11.08 ± 4.19	8.72 ± 4.25	96.6 ± 59.6
Incoming Tide	9	1.10	4	3.63 ± 1.82	4.20 ± 1.49	15.2 ± 9.3

Capture rate increased with water clarity in all three species (Fig. 8.4, upper column), yet this was only significant in the Royal Tern (Student's paired t-test: clarity < 50 cm vs. ≥ 50 cm: $t_{41} = 3.62$, $P < 0.05$). Water clarity had a quadratic effect on the size of the fish captured (Fig. 8.4, middle column), since the largest fish were captured at a water clarity of only 0.5-0.9 m. For Little Tern and Sandwich Tern, food intake rate was lower in the most turbid waters (visibility < 50 cm) compared to clearer waters (≥ 50 cm) (Student's paired t-test: Little Tern: $t_{198} = 2.03$, $P< 0.05$, Sandwich Tern: $t_{136} = 3.41$, $P < 0.001$) (Fig. 8.4, lower column).

Foraging time

From a nutritional perspective, the quality of a wintering area can be expressed as the time required to meet the daily food requirements. We assume that wintering terns in Guinea-Bissau have to at least maintain in energetic equilibrium so that energy income equals energy expenditure. Energy income (kJ/day) is calculated as the product of time spent foraging t_{for} (h/day) and the rate of energy acquisition REA (kJ/h) while foraging.

$$\text{Energy Income} = t_{for} \times \text{REA} \qquad (1)$$

Energy expenditure under thermoneutral conditions is largely determined by the proportions of time spent in flying and non-flying activities. The rate of energy expenditure

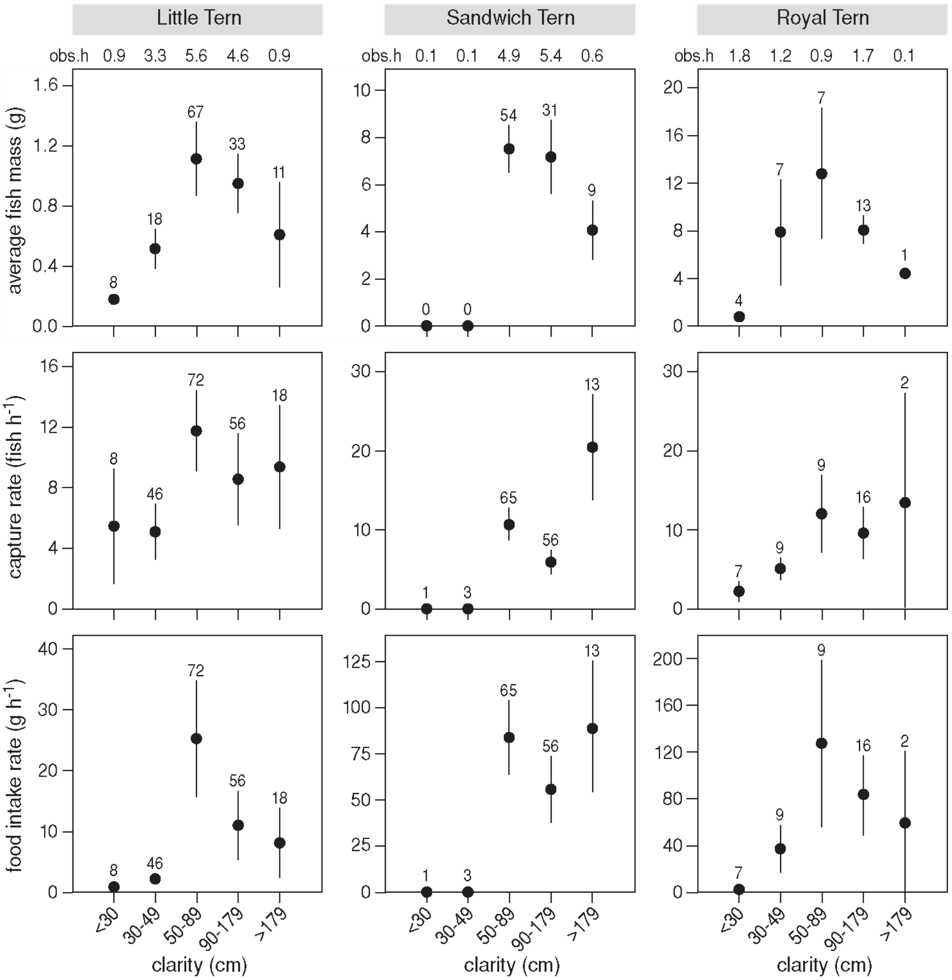

Figure 8.4. Relationship between water clarity and average fish mass (fish/h) (upper column), capture rate (g) (middle column), and food intake rate (g/h) (lower column, Student's paired t-test: Little Tern t_{198} = 2.0316, $P < 0.05$, Sandwich Tern t_{136} = 3.4099, $P < 0.001$, Royal Tern t_{41} = 1.4156, $P > 0.05$) with standard error and the number of fish caught or the number of terns of Little Tern (left panel), Sandwich Tern (middle panel) and Royal Tern (right panel). Clarity is divided logarithmically into five categories: < 30 cm, 30 - 49 cm, 50 - 89 cm, 90 - 179 cm, and ≥ 180 cm. At the upper x-axis stands the observation time (in h).

during flight in the tropical Sooty Tern *Sterna fuscata* was estimated at 4.77 x BMR from doubly labelled water measurements, whereas metabolism averaged 1.62 x BMR during the remainder of the time (Flint & Nagy 1984). Adopting these values for the tern species in Guinea-Bissau, we estimate daily energy expenditure as

$$\text{Energy Expenditure} = t_{flight} \times 4.77BMR + (24 - t_{flight}) \times 1.62BMR \quad (2)$$

So, when income equals expenditure:

$$t_{for} \times \mathrm{REA} = t_{flight} \times 4.77\mathrm{BMR} + (24 - t_{flight}) \times 1.62\mathrm{BMR} \qquad (3)$$

Because food is patchily distributed and does not remain accessible for a long time on the same place, terns spend quite some time on the wing looking for exploitable patches. Consequently, flight time is appreciably longer than actual foraging time. In our model, it is convenient to express total flight time as a multiple of foraging time. Substituting $t_{flight} = m \times t_{for}$, equation (3) can be solved for t_{for}

$$t_{for} = 12.34/(0.32(\mathrm{REA}/\mathrm{BMR}) - m) \qquad (4)$$

The rate of energy acquisition is the product of food intake rate, energy content of food and its digestibility. Several authors provide data on the energy content of tropical roundfish and their digestibility (Table 8.4). We used the average values of 6.37 (kJ/g) and 76.8%, in combination with the average food intake rate of all our measurements (Table 8.2), to calculate the rate of energy acquisition of each tern species (Table 8.5).

Table 8.4. Fish length (in cm), body composition (in %), energy content (of wet weight, in kJ/g) and digestibility Q (in %) of small (sub) tropical roundfish.

Fish species	Length (cm)	Composition			Energy content (kJ/g)	Q (%)	Predator species
		Water	Fat	Protein			
Anchovy *Engraulis capensis*[a]		66.3			8.0	76.5	Jackass Penguin chick *Spheniscus demersus*
Anchovy *Engraulis capensis*[b]						77.7	Cape Gannet juvenile (78 days) *Sula capensis*
Anchovy *Engraulis capensis*[c]	6.2-16.0	73.2		19.7	6.74		Cape Gannet *Sula capensis*
Saury *Scomberesox saury*[c]	7.8-41.6	74.3		19.4	6.20		Cape Gannet *Sula capensis*
Horse Mackerel *Trachurus capensis*[c]		73.2		18.9	5.63		Cape Gannet *Sula capensis*
Stockfish *Merluccius capensis*[c]		80.2		18.3	4.07	69.2	Cape Gannet juvenile (80 days) *Sula capensis*
Pilchard *Sardinops ocellata*[c]	6.8-22.0	68.4		19.9	8.59	79.4	Cape Gannet juvenile (80 days) *Sula capensis*
Common Bullies *Gobiomorphus cotidianus*[d]		74.6	3.1	17.3	5.36	81.1	Australasian Harrier *Circus approximans*
Average					6.37	76.8	

[a] Cooper 1977. [b] Cooper 1978.
[c] Batchelor & Ross 1984.
[d] Tollan 1988.

Table 8.5. The rate of energy acquisition of wintering Little Terns, Sandwich Terns and Royal Terns in Guinea-Bissau.

	Little Tern	Sandwich Tern	Royal Tern
Body mass[a] (g ± sd, N)	42.2 (± 3.2, 131)	219.0 (± 14.9, 59)	351.4 (± 30.4, 35)
Food intake rate (g/h)	8.1	59.9	45.3
Rate of Energy Acquisition (kJ/h)	39.5	292.3	221.0
BMR (kJ/h)	0.90	3.55	5.26

[a] Body mass taken from terns caught in Guinea-Bissau during the expeditions of 1986/1987 (L. Zwarts, unpubl. data) and 1992/1993 (pers. obs.).

In literature, we found BMR estimates for nine different species of terns (Ellis 1984, Klaassen 1994, 1995a) to which we were able to add one additional unpublished value for Sandwich Terns, measured on the Isle of Griend in The Netherlands, using the same method and setup as used by Klaassen (1994) (M. Klaassen & A. Brenninkmeijer, unpubl. data; n = 6, mass = 255 ± 9 (sd) g, BMR = 202 ± 21 (sd) kJ/d). Using non-linear regression, we compiled an allometric relation for BMR, where M is mass (in g). Standard errors (se) have been put between brackets.

$$\mathrm{BMR} = 1.793\ (\pm\ 1.879)\ M^{0.822\ (\pm\ 0.195)},\ r^2 = 0.663 \tag{5}$$

The effect of latitude on BMR in birds is a well-known phenomenon (e.g. Ellis 1984, Klaassen 1994, 1995b). The inclusion of latitude L (in ° N or S) in this relation appeared to have a significant effect (Fig. 8.5).

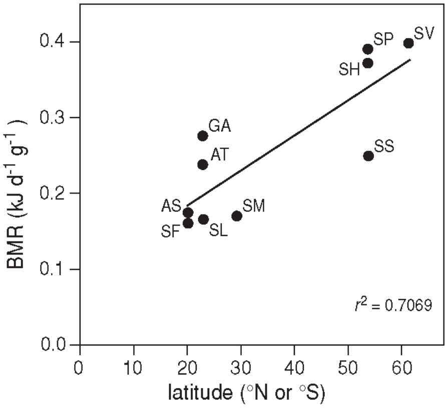

Figure 8.5. Basal Metabolic Rate (BMR, in kJ per day per mass$^{1.21}$) that different terns (*Sterna lundata, S. fuscata, S. maxima, Anous stolidus, A. tenuirostris, Gygis alba, S. vittata, S. paradisaea, S. hirundo, S. sandvicensis*) have on various latitudes L (in ° N or S).

$$\text{BMR} = [0.617\ (\pm\ 0.313) + 0.029\ (\pm\ 0.012) \times \text{L}]\ \text{M}^{0.833\ (\pm\ 0.075)},\ r^2 = 0.963 \qquad (6)$$

There is also evidence accumulating that an individual's BMR is flexible changing seasonally and with latitude in a similar fashion as BMR changes inter-specifically with latitude (Kersten *et al.* 1998). Therefore we tentatively used equation (6) to predict BMR for terns in our study. The foraging time required to meet daily energy expenditure is calculated as a function of m (total time in flight divided by the actual time spent foraging) (Fig. 8.6A).

Daily food requirements can be met in a remarkably short time (1-4 hours), as long as the time required to locate exploitable patches is short relative to actual foraging time (m < 3). When the time spent on the wing in order to search for exploitable food patches increases, actual foraging time increases more rapidly in Royal Terns and Little Terns than in Sandwich Terns. The results indicate that wintering terns in Guinea-Bissau should be able to meet their daily food requirements in a couple of hours foraging. However, terns may become time restricted when it takes a long time to find exploitable food patches. Terns are essentially diurnal and spend about two hours inactive at the roost around high tide. Consequently, the time available for finding and collecting food is about 10 hours. This seriously limits the range of *m*-values over which terns are able to meet their daily food requirements (Fig. 8.6B). In order to survive, m should not exceed 5.9 for Royal Terns, or 6.2 for Little Terns. Sandwich Terns are able to deal with much more patchily distributed food; m-values up to 8.0 are for them acceptable.

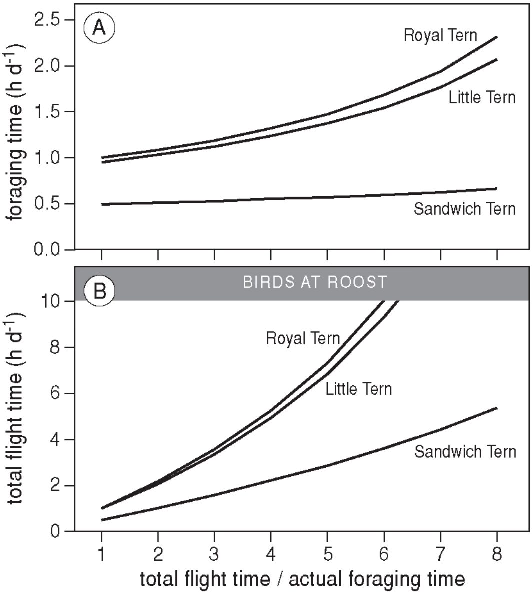

Figure 8.6. Foraging time (A) and total flight time (B) required to meet daily energy requirements of three species wintering in Guinea-Bissau in relation to the ratio between total flight time and actual foraging time (*m* in equation 4, see text). Total flight time consists of foraging time plus time spent on the wing in order to find patchily distributed prey.

DISCUSSION

Food intake rate

Because we were unable to determine which fish species were actually eaten by the terns, our estimates of food intake rate rely on the assumption that those fish species were consumed which were also present in the beach seine samples. Stomach contents of Sandwich Terns and Royal Terns provide evidence in support of this assumption, since these same fish species, or close relatives, figured prominently in the diet of birds wintering in Sierra Leone and Ghana (Dunn 1972a).

Relatively large standard errors surround the rates of food intake calculated from our data. This is due to the stochastic nature of prey captures in combination with the large variation in mass of individual fish captured. For instance, the few fish in the largest size classes accounted for more than 50% of the biomass consumed in each tern species. Theoretically, this problem can be solved by longer observations, but given the high mobility and low site tenacity of foraging terns, this is impossible in practice. Consequently, we have to accept that only major environmental factors affecting food intake rate can be detected.

In our study, terns did not benefit from flock foraging. Despite a higher capture rate, food intake rate did not increase because terns foraging in flocks caught smaller fish. Other studies on fish-eating birds have shown that birds foraging in flocks have higher capture rates than those foraging solitarily (Krebs 1974, Götmark *et al.* 1986; Hafner *et al.* 1993; Van Eerden & Voslamber 1995; Reid 1997). Yet only two studies measured also higher food intake rates (Krebs 1974; Hafner *et al.* 1993). Although our observations indicate that food intake rate was similar in flocks to that in solitary feeding, the terns probably gain greatly from joining a flock because this shortens search time.

Surprisingly, water clarity had a more pronounced effect on the size of fish captured than on capture rate. Average fish mass was highest at water clarity between 50 and 90 cm. We have no idea why the average fish mass declined when water clarity improved beyond 90 cm. Fish captured in clear water were considerably larger than those captured in the most turbid waters, but few very large individuals were captured. Recently, Mous (2000) reported on the vertical distribution of fish in relation to water clarity in Lake IJsselmeer, The Netherlands. He showed that larger fish move towards the surface as water turbidity increases. This suggests that changes in fish availability rather than visibility were responsible for the fact that fewer large fish were captured in the clearest waters. Consequently, food intake rate increased with water clarity until 50-90 cm, but not beyond. In general, water clarity increased with distance from the mainland, which is where most tern concentrations were also encountered. The most turbid waters occurred at the river mouth of the Rio Geba, around Bissau, Areias and Prabis (localities 5, 6 and 8, Fig. 8.1). With the exception of Areias (6), which is an important roost area for terns, only small numbers of terns were observed on these sites.

Wintering area quality

The question arises: is Guinea-Bissau a good wintering area for terns? Capture rates of wintering Sandwich Terns in Guinea-Bissau were 12-41% lower than of conspecifics in Sierra Leone (Dunn 1972b). For Royal Terns in Guinea-Bissau, capture rates were 29-57% lower compared with conspecifics wintering on Bonaire, Netherlands Antilles (Buckley & Buckley 1974). Unfortunately, there is no comparable information about foraging Little Terns in other wintering areas. So, compared with Bonaire and Sierra Leone, Guinea-Bissau appears to be less good as a wintering area. However, feeding conditions between Guinea-Bissau and other wintering areas are difficult to compare, because the most important factor, food intake rate, is only known from Guinea-Bissau.

Besides large standard errors, there are several other sources of random and systematic errors, such as fish length estimation in the field (with an inaccuracy of a quarter of a bill length), the conversion of fish length into fish mass, and the assumption of BMR and flight cost, which make the model less accurate. Still, it was useful to make this rough model. Not only does it show the differences between the three tern species, yet it also gives a - very rough - indication of the capacity of Guinea-Bissau as a wintering area for terns. Hopefully this will stimulate other researchers to conduct similar investigations in wintering areas.

In our model, daily energy expenditure was calculated as the sum of energies expended during flight and non-flight activities. Daily energy expenditure increases linearly with flight time, because the presumed rate of energy expenditure was almost three times as high during flight (4.77BMR) as during non-flight (1.62BMR). When food becomes more patchily distributed, terns need more time to locate exploitable patches and flight time increases until a maximum of 10 hours per day. Consequently, daily energy expenditure will reach its maximum under these circumstances. This maximum rate of daily energy expenditure of terns wintering in the tropics can be provisionally estimated: $DEE = ((10 \times 4.77BMR + 14 \times 1.62BMR) / 24) =$ about 3BMR. This is a rather moderate value, given that sustainable rates of energy expenditure in other bird species are in the order of 4-5BMR (Drent & Daan 1980).

Actual rates of daily energy expenditure are almost certainly lower, since terns are not likely to forage all day. Therefore, from an energetic point of view, wintering terns in Guinea-Bissau seem to have an easy living. Since the observed rates of food intake while foraging are high (Table 8.5), the crucial factor determining whether terns are able to meet their food requirements is the time required to locate exploitable food patches. With respect to this parameter, Sandwich Terns are better off than either Little Terns or Royal Terns. Sandwich Terns can afford to search for more than one hour in order to find a patch, which they can exploit for 10 minutes. Little Terns and Royal Terns should find a similar patch within half an hour.

Consequently, we expect that Sandwich Terns are more widely distributed throughout the Archipelago dos Bijagos than the other two species. Sandwich Terns may occupy parts of the archipelago where the density of exploitable patches is too low for Little Tern and Royal Tern. Finally, we predict that, in those parts of the archipelago where the three species occur together, Sandwich Terns spend more time inactive during low water than the other two species.

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Chapter 9

Echoes from the field:
towards a causal nexus explaining population fluctuations in European Sandwich Terns

LIVING WITH GULLS

It was long believed that Black-headed Gulls *Larus ridibundus* were a threat to breeding Sandwich Terns *Sterna sandvicensis* because they prey upon tern eggs and small chicks, and rob the fish meant for the tern chicks. Therefore Black-headed Gulls were controlled at major tern colonies in The Netherlands and for many years their numbers were kept at a minimum to protect the terns (*e.g.* Brouwer *et al.* 1950). Midway the twentieth century there was a vivid discussion in Dutch ornithological literature on the impact Black-headed Gulls had on terns (Brouwer *et al.* 1950, Van den Assem 1954, Rooth 1958, 1960, 1965). Veen (1977) dedicated an extensive study to the question why Sandwich Terns often choose to breed together with Black-headed Gulls, which is hard to explain if these gulls have such a negative impact on reproductive success in the terns. From 1966-1972, he studied the predation behaviour of the gulls on Griend, Dutch Wadden Sea. Consistent with earlier studies, Veen found that a significant proportion of Sandwich Tern eggs (14 % of all eggs) and chicks (12%) were lost to predating gulls. He argued that predation had, however, no overall impact on the reproductive output of the terns because the gulls mainly took non-viable eggs and chicks. He concluded that the anti-predator function of neighbouring Black-headed Gulls (the gulls form a buffer against intruders and chase away predators) outweigh the disadvantages of the losses of eggs and chicks. The study of Veen led to a change in the attitude towards Black-headed Gulls, resulting in a halt in the management programme to control them in Dutch colonies.

My work was designed to carry on these studies at the same colony with a focus on events throughout the chick phase. Especially during brooding and during the onset of chick rearing, Black-headed Gulls offer protection to the non-aggressive terns, but as the tern chicks grow and become less prone to be caught by predators the need for protection decreases. At the same time, Sandwich Terns experience increasing disadvantages of the breeding association with Black-headed Gulls. With the aging of the tern chicks, a number of gulls develop into specialised robbers of fish meant for the tern chicks. They exert a growing pressure on prey-carrying adults causing prey delivery time to increase (chapter 5) and resulting in an increasing rate of food loss (chapter 3). Two weeks after hatching, about 25% of all prey offered to Sandwich Tern chicks on Griend was robbed and another 9% was lost outside the observer's view mainly when Black-headed Gulls were chasing after a prey-carrying tern parent. During the first two weeks post-hatching, food piracy by Black-headed Gulls is still relatively low and potential negative effects can largely be overcome. Afterwards negative effects on chick growth and survival become obvious, in particular during longer periods of strong winds (chapter 3).

The present study on the feeding ecology of Sandwich Tern was mainly performed on chicks held within enclosures made of wire netting. Enclosing chicks makes it possible to follow them from hatching to fledging as they are forced to stay within the vicinity of the nest. Sandwich Tern chicks are semi-precocial and in natural situations often leave the nest soon after hatching. In non-enclosed situations, nest departure normally occurs

3-6 days after hatching of the first egg in a nest (Veen 1977). The first days after leaving are spent hiding in the vegetation or in nest scrapes in the direct surroundings of the original nest. About two weeks after hatching, however, many laying sites have been deserted. Most chicks have then spread and are found in the vegetation surrounding the colonies. During the following weeks, the chicks further disperse and are found scattered over the entire island. In chapter 5 we argue that leaving the nest site is a behavioural trait to avoid the heavy attacks from the kleptoparasitising gulls. The timing for leaving the nest vicinity critically depends on the trade-off between a decreasing need for protection from the gulls and an increasing robbing pressure. By leaving the original laying site the chicks are led away from the robbing gulls and by spreading over the island aggregations of food input are avoided and thus the conditions for kleptoparasitism to occur are minimised. Although moving chicks probably still encounter gulls, most of these gulls have not yet learned to steal food from terns. We argue that when the chicks keep moving around, gulls can not develop into specialised kleptoparasites (chapter 5). Yet, on Griend exceptionally high robbing pressures were measured in free-living chicks as well, especially in chicks that had become trapped in natural fykes formed by the vegetation (Geschiere 1993, own observations). Similar high attack rates were observed in Sandwich Tern colonies that were surrounded by dense vegetation from which the tern chicks could hardly escape. It is not clear to what extent and when free-living chicks do leave the nest site in natural situations. It also remains unstudied if and how chicks move over breeding sites and how this relates to the spatial distribution of vegetation, and the probability of meeting conspecifics and potential kleptoparasites. It further is uncertain if and to what extent our frequent visits in some colonies have contributed to the departure from the nesting site. Around fledging Sandwich Tern chicks sometimes gather in flocks along the beach. In those flocks piracy by the gulls seems to revive, although the success rate of gulls has never been studied in these circumstances. Future studies could make use of radio transmitters to monitor Sandwich Tern chicks from hatching until fledging and to further examine the evasive behaviour of the terns.

The high incidence of food loss to Black-headed Gulls recorded in this study (19% of all food items were robbed by the gulls) is, however, not restricted to enclosed or trapped chicks only but is typical in Sandwich Terns. During the period 1966-1970, Veen (1977) found that on average 18-38% of the fish brought to non-enclosed chicks on Griend was stolen by Black-headed Gulls. At the former Dutch colony “De Beer”, Hoek of Holland, up to 25% of the fish meant for the tern chicks was robbed (Rooth 1965) and Garthe & Kubetzki (1998) report that in 1997 11% of the food brought to Sandwich Tern chicks on Juist, German Wadden Sea, was lost to kleptoparasitising gulls. At the Hompelvoet colony in the Dutch Delta area losses of 20-50% were not uncommon in the 1970s (Beijersbergen 1976). Fuchs (1977) recorded lower rates of kleptoparasitism (~ 6%) at the Sands of Forvie, Scotland, in 1973-1974 and Dies & Dies (2005) report similar low rates (5%) in Eastern Spain. Several authors mention that exceptionally high rates of kleptoparasitism (> 50%) occur during spells of bad weather (Rooth 1965, Smith 1975, Veen 1977, Glutz von Blotzheim & Bauer 1982, own observations).

The rate of food loss strongly depends on the size of the prey brought to the chicks (Dunn1972, Ratcliffe *et al.* 1997, this study chapter 2, 3). Of the two main prey types that were brought to the chicks on Griend (clupeids and sandeel; chapter 2) the gulls preferred to rob the longer sandeel. Thus, the composition of the diet of Sandwich Tern chicks on Griend greatly influenced the probability of losing the prey to kleptoparasitising gulls. Consequently, we found a strong negative relationship between the average yearly proportion of clupeids in the chicks' diet and the proportion of the food that was robbed by the gulls (chapter 4). Figures on robbing incidence and diet composition extracted from Veen (1977) suggest a very similar relationship (Fig. 9.1). In Veen's dataset lower proportions of the food were robbed, probably because that author followed younger chicks (in chapter 4 chicks > 15 days were selected) and because in the present study prey-consumption probabilities (including other causes of prey loss) were used rather than losses to robbing gulls. Veen ascribed the increased piracy on Griend in the period 1966-70 to a relative increase of the Black-headed Gull population compared to that of Sandwich Terns, but in retrospect this can also be explained by dietary changes as his data fit the expected effect of changes in diet composition very well (Fig. 9.1).

By evolving a close breeding association with gulls, Sandwich Terns trade-off food against predation. In chapter 4 we describe how Sandwich Terns can organise their foraging behaviour in order to maximise prey intake rates of their chicks in the presence of kleptoparasitising Black-headed Gulls. Presupposing that enough herring is available in the foraging areas and given the relationship shown in figure 9.1, parents that face high food losses could theoretically shift the diet towards more clupeids in order to reduce the losses. However, in most years parents did not bring more clupeids to the nest when food losses increased (chapter 4), suggesting that the availability of clupeids was limited. Instead, both parents left the island to forage leaving their chicks unattended at the nest more often and thus increased the food transport. Increased foraging effort in years with

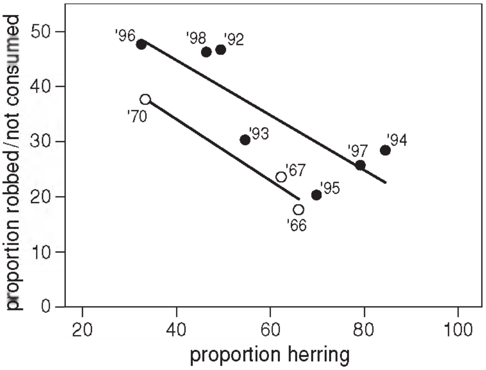

Figure 9.1. Relationship between the diet composition of Sandwich Tern chicks on Griend and the proportion of the food that is robbed or not consumed by the chicks. Black dot = non-consumed proportion in 1992-1998 extracted from chapter 4; open dot = robbed proportions in 1966-1970 extracted from Veen (1977)

low clupeid proportions in the diet enabled the parents to counterbalance an imminent food shortage. Simultaneous foraging of the parents commenced when the chicks were about 2 weeks old when they are too large to be swallowed by the major predators on Griend. Leaving the chick unprotected at the colony at that age did not result in increased predation rates. The observed variation in diet composition did not translate into differences in growth or survival of the Sandwich Tern chicks despite the differences in parasitic losses. Apparently, Sandwich Terns are well adapted to the kleptoparasitic behaviour of their associative breeding species. If they can not avoid the attacks of the gulls by moving away from them, they increase their foraging effort and compensate for these losses.

FEEDING ECOLOGY OF SANDWICH TERNS

During the breeding season, Sandwich Terns feed their chicks on a restricted number of species of marine fish. In The Netherlands, chicks are predominantly fed with herring *Clupea harengus*, sprat *Sprattus sprattus*, sandeel *Ammodytes tobianus* and greater sandeel *Hyperoplus lanceolatus* (Veen 1977, this study). Adult terns locate the fish visually and the prey is mainly caught by plunge diving, down to a maximum depth of two metres (Borodulina 1960, Dunn 1972). On Griend, the food is predominantly found within 15 km distance from the colony, but in some other colonies foraging flights > 25 km might be more common (Veen 1977, Baptist & Meininger 1984, Fasola & Bogliani 1990, Raaijmakers *et al.* 1993, own observations). Sandwich Tern parents breeding on Griend forage mainly in shallow waters and in channels around the islands of Terschelling and Vlieland (Stienen & Brenninkmeijer 1994, Fig. 9.2). Investigations in 1993 on parents equipped with radio-transmitters indicate that the foraging areas of Sandwich Terns on Griend have somewhat shifted to the southwest compared to the 1960s when the northeastern part of Terschelling was also frequently used for foraging (Veen 1977), but the foraging range is very comparable (Fig. 9.2). Parents transport the captured fish to the colony one by one (only in exceptional cases do they carry two prey items), holding it crosswise in the bill. The length of fish parents offered to the chicks on Griend ranged from 1.5 to 21.5 cm. On average, sandeel brought to the colony were somewhat longer (11 cm) than clupeids (9 cm).

The abundance of the Sandwich Terns' prey species can differ greatly from year to year (Corten 1990, 2001, Corten & van de Kamp 1979, 1996). Superimposed on this, the prey fish show distinct patterns of horizontal migration within a year (Fonds 1978, Corten 1996) causing strong changes in the species composition, distribution and length of available prey fish during the breeding season of the terns. The prey fish also move vertically in the water column with changing light conditions and tidal movements (Thorpe 1978), resulting in cyclic fluctuations in prey availability for the terns during the day. Predator fish and sea mammals cause unpredictable horizontal and vertical movements of the prey as well. This causes strong spatio-temporal variation in the availability and the quality of the Sandwich Terns' food and requires a great flexibility of these spe-

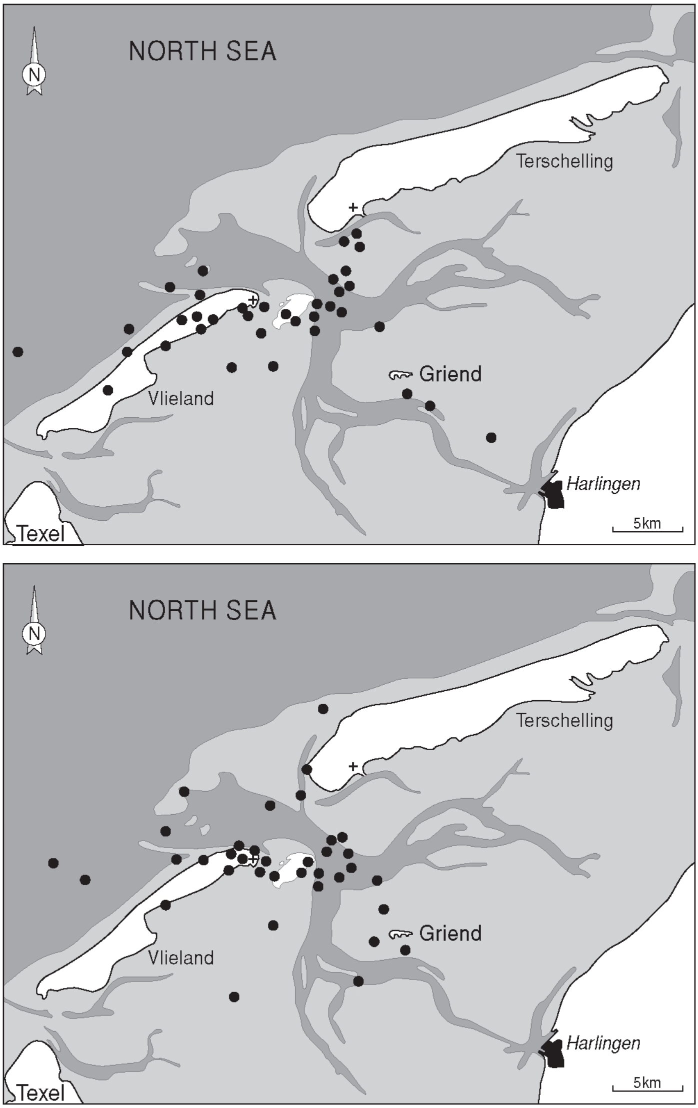

Figure 9.2. Positions (dots) of two radio tagged Sandwich Terns during chick rearing in 1993. The foraging terns were located by radio antennas placed on Griend, Terschelling and Vlieland (latter two locations indicated by +). Light shaded areas surround the mean low water coastline.

cialised foragers. Chapter 2 describes how patterns in diet composition of Sandwich Tern chicks reflect the cyclic variation in prey fish availability, for example the downward migration and shoaling of herring and sprat during the day and the dispersal and upward migration at dusk (Blaxter & Parrish 1965, Laevastu & Hayes 1981, Cardinale *et al.* 2003, Nilsson *et al.* 2003). This rhythmicity means that clupeids are typically available for the day active terns during the early morning and at dusk, matching the increased proportions of clupeids in the chicks' diet at that time.

The patterns in diet composition described in chapter 2 are the averaged results of 7 years of observation in the colony at Griend. Patterns in diet composition derived from a particular year can, however, be very deviant from this average pattern. In 1994, for example, chicks received high proportions of clupeids throughout the day. An unambiguous explanation for such an aberrant pattern can not be given. It is most likely, however, that the high availability of clupeids in 1994 (IBTS data given below) caused an increased availability of herring and sprat near the surface even during the day. A low availability of sandeel may, however, also lead to the same pattern, as terns will then be forced to feed on clupeids throughout the day. This emphasizes that it is impossible to use shifts in the diet composition of seabirds as reliable indicators for shifts in the availability of their food, even if the diet composition mirrors the underlying food composition. For predators that have an even broader choice of prey species, diet composition is without any doubt a very poor indicator of food availability, although it is often interpreted as such.

In order to link patterns in the diet of seabirds to spatio-temporal changes of their prey one must concurrently study food availability locally in the foraging areas as well as the seabird's biology (*e.g.* Litzow *et al.* 2000, Mous 2000). It is, however, not easy to measure food availability of Sandwich Terns because their fish prey occur in shallow water, are patchily distributed and perform species-specific diel vertical migration, schooling and feeding behaviour (Cardinale *et al.* 2003). The fish-sampling programme conducted in the terns' foraging area in 1995-1998 by The Netherlands Institute of Fishery Research (RIVO) suggests particularly strong effects of water clarity on prey fish availability (Fig. 9.3). Especially clupeids, but also sandeel were caught more frequently in turbid water. Since we sampled fish in the upper water layer (0-2 m), this indicates that the fish move to the surface when water transparency decreases. This implies that turbid waters might offer better foraging conditions to the terns. In the present study, it could not be excluded that more fish were caught in turbid waters simply because the fish saw the approaching fishing gear less well and therefore experienced a lower probability to escape than in clear waters. However, using acoustic recordings Mous *et al.* (2000) found very similar results in Lake IJsselmeer, where increased water transparency resulted in a decreasing availability of surface-dwelling prey fish for terns. Mous *et al.* could link the spatial distribution of foraging Black Terns *Chlidonias niger* directly to the clarity of the water. This implies that species diving for fish near the surface, like Sandwich Terns, may depend on turbid waters despite the fact that they locate their prey visually.

POPULATION LIMITATIONS IN SANDWICH TERNS

Seabird populations critically depend on the dynamics in the availability of their prey and are often limited in size by the availability of their food (reviews in Birkhead & Furness 1985 and Croxall & Rothery 1991). Several studies on seabirds linked measurements of

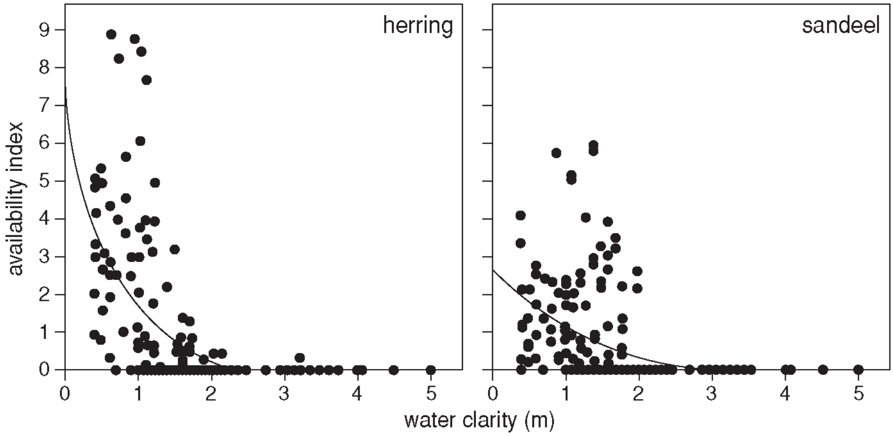

Figure 9.3. Relationship between water clarity (measured with Secchi disk) and the occurrence of herring and sandeel near the water surface. Prey fish availability was obtained by log transforming the mass of fish caught with an Isaac's Kidd Midwater Trawl net (IKMT-net) with a mesh size of 6 mm in the upper 2 m of the water layer (see Stienen & Brenninkmeijer 1998a for more details).

food abundance with the number of breeding pairs, the reproductive output, chick growth or adult survivorship of seabirds (reviews in Crawford & Shelton 1978, Cairns 1987, Furness 1989) and experimental supplementary food can increase the reproductive output of seabirds (examples in Newton 1998). Throughout the world and in many species, the population size and breeding success of seabirds has been linked with dynamics in prey stock abundance (review in Furness 1989). The most striking and best documented cases are the dramatic changes in breeding performance and population size of seabirds along the coast of central Norway in the late 1960s, in the Barents Sea in the mid-1980s and at Foula, Shetland in the mid-1980s due to the collapse of components of the seabirds' food stock (Barrett *et al.* 1987, Heubeck 1988, Monaghan *et al.* 1989, Vader *et al.* 1990, Bailey 1991, Hamer *et al.* 1991, Suddaby & Ratcliffe 1997).

The species of seabirds that tend to be the most sensitive to changes in fish abundance are small birds with restricted foraging ranges and energetically expensive foraging methods, feeding on species present near the water surface and with fast growing chicks (Furness & Ainley 1984, Furness 1989). Sandwich Terns meet all criteria and are therefore ranked among the five most vulnerable seabird species to reductions in food supply in the North Sea (Furness & Tasker 2000). The unpredictable nature of their food combined with highly variable amounts of food loss to the gulls cause a high degree of food stress for Sandwich Terns during the breeding season. In particular when years of unfavourable diet composition (poor clupeid years) coincide with adverse weather conditions strong effects on the breeding performance of the terns may be expected. During the 7 years of study on Griend we found no effect of apparent changes in food availability (reflected by fluctuations in diet composition) on the reproductive output of the terns. Also growth of the chicks was not affected by changes in prey fish availability (chapter 4). In poor clupeid years, when sandeel dominated the chicks' diet, parents worked harder (sometimes at maximum levels) and were thus able to counterbalance the high proportions of food loss to the gulls. In the present study, years of poor availability of clupeids coincided with reasonable weather conditions and yet the tern parents already reached maximum buffer capacity. Therefore, strong negative effects on chick growth and survival can be expected when wind conditions are less favourable in poor clupeid years. This implies that a poor availability of clupeids has the potential to reduce chick survival but that this critically depends on the wind conditions.

Increased foraging effort of the parents in poor clupeid years might lead to reduced fecundity in the following year, as has been demonstrated in other seabirds (Wernham & Bryant 1998) as well as in a wide variety of short-living species (*e.g.* Røskaft 1985, Smith *et al.* 1987, Gustafsson & Sutherland 1988, Verhulst 1995). Being long-lived, seabirds are believed to respond most strongly to fluctuating food resources with variation in their diet, working levels and breeding success rather than adult survival rate (Drent and Daan 1980). There is, however, growing evidence that poor food availability even affects adult survival in long-lived species (Reid 1987, Jacobsen *et al.* 1995, Davis *et al.* 2005). If indeed higher working levels affect adult survival in Sandwich Terns, then a decreased clupeid availability can lead to reduced adult survival and even small reductions could have strong effects on population dynamics.

Another, more direct, link between food resources and population dynamics would be the adjustment of the non-breeding population to current food abundance. Adults that have bred the year before may decide not to breed if the conditions for breeding are not favourable in the subsequent year(s). In some seabirds, large proportions (15%-25%) of the population may not breed in unfavourable years (*e.g.* Aebischer & Wanless 1992, Bradley *et al.* 2000). Intermittent breeding would allow terns a fast response to changes in the food situation that is adaptive in highly variable environments. Non-breeding of adults explains the fast rate of decline of the Arctic Tern populations on Orkney and Shetland during 1980 and 1989 when the sandeel stock collapsed (Avery et. al. 1993). Where some other tern species exhibit a strong fidelity to their natal colony and a strong tenacity to previously used breeding areas and nesting sites within those areas (Austin 1949, Nisbet 1978, González-Solís *et al.* 1999, own observation), Sandwich Terns exhibit a highly flexible choice of nesting sites. They often change breeding sites within an established breeding area (own observations) and easily switch between breeding sites when conditions are affected by predators or other disturbances or sometimes for unidentified reasons (Courtney & Blokpoel 1983, Ratcliffe *et al.* 2000, Noble-Rollin & Redfern 2002, Ratcliffe 2004). Nomadic behaviour enables Sandwich Terns to respond to discrete events at the breeding grounds (such as disturbance, predation or competition with other species) and more importantly to adjust to the strong fluctuations of their prey fishes.

CHANGES IN FOOD RESOURCES

Overexploitation by fisheries was long believed to be the primary factor regulating fish stocks in the North Sea after World War II. Industrial fishery for sprat and herring caused a collapse of the North Sea herring stock in the 1970s, which lead to the closure of fishery from 1977 to 1983 and fishery quota in the subsequent years (Corten 2001). The heavy exploitation by the fishing industry of predatory fish (*e.g.* cod, herring and mackerel) is thought to have relieved the predatory pressure on their prey such as sandeels and sprats, allowing the latter to become more abundant (Corten 2001). The past decades increasing attention has been directed towards environmental variability that can similarly lead to strong fluctuations in the abundance and spatial distribution of fish stocks (Bakken & Bailey 1990, Corten 2001, Ottersen *et al.* 2001, Beaugrand *et al.* 2003). During the second half of the twentieth century, the combination of fishery mortality and environmental variability led to strong fluctuations of fish stock biomass in space and time and thus strongly influenced food supply for seabirds in the North Sea.

How such changes can influence terns was illustrated in the 1980s when the collapse of the local sandeel stock around Shetland caused widespread breeding failure and population decline in terns and several other seabirds (Heubeck 1988, Bailey 1991). This led to the closure of the Shetland sandeel fishery for several years and also to intensive research on the dynamic links between sandeels and seabirds. It was finally concluded that the depletion of the Shetland sandeels and thus the seabird breeding failures were not caused by the fishery on sandeel but by natural factors acting in the early life-history of sandeels (Bailey 1991, Corten 2001). One of the most strongly affected seabird species in the Shetland crisis was the Arctic Tern *S. paradisaea* (Monaghan *et al.* 1989); a species with a very specialised diet choice similar to the case of the Sandwich Tern. Changes in food resources might therefore be important determinants of the Sandwich Tern population trend. However, long-term data on fish abundance in the southern North Sea is not available for all prey species and certainly not on a local scale. For that reason, various indices of prey fish abundance in the North Sea are used here, in the hope of finding signals that indicate changes in the availability of prey fish for Sandwich Terns. Also data on the underlying ecological processes that determine food availability for seabirds in the North Sea are used. Here I use the variation in the atmospheric pressure in the North Atlantic (the North Atlantic Oscillation or NAO) that forces the ecology of the North Atlantic Ocean and the North Sea. The NAO influences wind speed, sea temperature and salinity in the North Sea and thus strongly influences the population dynamics of marine species at different trophic levels (Stenseth *et al.* 2004). Fluctuations in the fish stocks of herring, cod and salmon are linked to the variability in the NAO (Corten 2001, Beaugrand *et al.* 2003, Stenseth *et al.* 2004). The climatic variability thus strongly influences the food availability of piscivorous seabirds and indices of NAO might be a very robust determinant that captures a package of weather conditions as well as biological variability. Data on NAO is further very useful because it spans the entire twentieth century and therefore fully overlaps with data on the Dutch Sandwich Tern population, whereas most data on fish abundance only covers the past few decades.

PAST AND FUTURE PROSPECTS OF THE SANDWICH TERN IN THE NETHERLANDS

With a total of 14 500 breeding pairs (Stienen 2002), at the end of the twentieth century The Netherlands held about one quarter of the northwest European population (53 000 – 57 000 pairs according to Delany & Scott 2002). Within The Netherlands there are currently important colonies on Griend in the Wadden Sea (7920 pairs in 2000) and on Hompelvoet (2800 pairs) and The Hooge Platen (3000 pairs) in the southern Delta area. During the past decades, smaller settlements often of a less permanent character were found at almost all other Dutch Wadden Sea islands (Texel, Terschelling, Ameland, Schiermonnikoog and Rottumerplaat) and at several localities in the Delta area. Ring recoveries indicate that the colony in the harbour of Zeebrugge in adjacent Belgium is closely connected with the colonies in the southern part of The Netherlands and for that reason the Zeebrugge colony is here included in the Delta population.

The Dutch Sandwich Tern population fluctuated strongly during the twentieth century (Fig. 9.4). During the first half of the century, it was mainly direct anthropogenic pressure that shaped the population. At the beginning of the century, large-scale egging for consumption and shooting of adult terns for use in the manufacturing industry of ladies' hats caused the population to decrease rapidly. The exact impact of these practices is not very well documented, as surveys were poor and incomplete in those years. It is, however, clear that due to this persecution by man the population reached a low around 1910. In 1908, Dutch law prohibited collecting of eggs and shooting of terns. Along with the guarding of the most important colonies during the breeding season from 1912 onwards, this resulted in a gradual increase of the Dutch population to 35 000 – 46 000 breeding pairs in the 1930s. During World War II, disturbances, shooting of terns and egg collecting caused the numbers to drop again, but the population recovered soon in the years after the war. At the end of the 1950s, numbers dropped markedly and the population was reduced to only 875 pairs in 1965. This collapse was the result of a pollution of the Dutch coastal waters with organochlorine pesticides (Koeman 1971, 1975). This heavily affected tern colonies and other waterbirds in a wide area ranging from the Delta area in the south of The Netherlands (Den Boer *et al.* 1993, Brenninkmeijer & Stienen 1992, Arts & Meininger 1994, Stienen & Brenninkmeijer 1998b) to the German Wadden Sea (Südbeck *et al.* 1998). In 1967, the spill of pesticides was stopped and from then on the numbers gradually increased. This time the population recovered much more slowly than during the previous recovery periods. In the period 1911-1940 after the population had been reduced to a level comparable to the low of 1965, the annual increase averaged more than one thousand pairs (1 336 by linear regression). Interestingly, a similar rate of increase was evident in the period 1944-1956 (annual increment 1 257 pairs) despite the

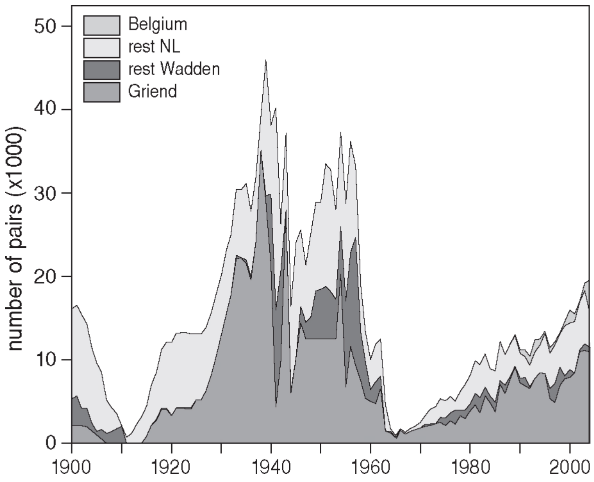

Figure 9.4. Number of breeding Sandwich Terns (pairs) in The Netherlands and Belgium during 1900-2004 (completed from Brenninkmeijer & Stienen 1992, data summarised in appendix 9.I).

fact that the low was only 16 200 pairs in 1944. In sharp contrast, in the period 1965-2004 annual growth averaged only 388 pairs, with the northern population in the Dutch Wadden Sea recovering somewhat faster than the population in the Delta area. By the end of the twentieth century, the Dutch population amounted to about 14 500 breeding pairs and in 2004 numbers had further increased to almost 19 500 pairs (including Belgium). Still this is only about half of the breeding numbers prior to the pollution incident.

The collapse of the Dutch Sandwich Tern population in the 1960s was followed by several years of a very low abundance of herring (Fig. 9.5). Yet, during this period the number of Sandwich Terns gradually increased. In the 1980s the growth of the Dutch population stagnated; first in the Delta area (period 1980-1990) and later in the Wadden Sea (1985-2001). From 1981-1998 the Dutch population slowly increased at an annual rate of 208 pairs (linear regression), but at the very end of the century numbers increased again and a maximum of 19 486 pairs was counted in 2004. During the past two decades both the Delta and Wadden Sea population showed sudden and sharp declines that can not be explained from adult mortality or poor breeding success (Delta population crashed in 1977, 1998 and 2002, and the Wadden Sea population in 1985, 1992 and 1996). Such periods of sudden population decline are most likely explained by non-breeding and/or emigration to other colonies. Apparently, these sudden population declines were not caused by the loss or degradation of the breeding grounds. Most likely they are indicative for poor feeding conditions. In the next paragraphs, the link between population changes of Sandwich Terns and food abundance will be discussed in detail using various indices of food abundance.

In the first place ICES data on the North Sea spawning stock biomass of herring were used to explain the population changes in sandwich Terns (Fig. 9.5). These surveys show

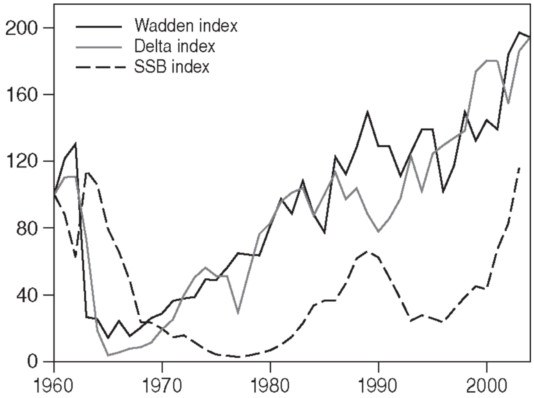

Figure 9.5. Index of the development of the Sandwich Tern populations breeding in the Wadden Sea and the Delta area (including Belgium) compared with the index of the spawning stock biomass of North Sea herring (SSB index). The population sizes in 1960 were arbitrarily set at 100%.

that at the time that the Dutch Sandwich Tern population crashed in the early 1960s, the North Sea herring stock size peaked. The herring stock did not collapse until 1965, suggesting that the poisoning of the coastal waters in the years before was the primary cause of the crash in the Sandwich Tern population and that poor food availability did not play a role. The recovery of the Dutch tern population after the crash, however, might very well have been hampered by the poor herring stock during the 1970s and early 1980s. Remarkably, the stagnating growth of the Dutch population during the 1980s was apparent long before the decrease in the herring stock in 1991. Also the peak in Wadden population in 1989 precedes the peak in the herring stock in 1990. This suggests that although herring is an important part of the diet of Sandwich Terns a link between the Dutch Sandwich Tern population and the North Sea herring stock is not a simple one. Yet, some parallels between the herring stock and the Wadden Sea population (peak at the end of the 1980s followed by a decade of low numbers and finally a strong increase in population size around 2000) invite for a further examination of the data, and for this reason a subset of another dataset has been examined.

When the more detailed ICES-data of the International Bottom Trawl Surveys (IBTS) on clupeid abundance (*i.e.* data on herring and sprat combined) in the southeastern North Sea from 1977-2004 are employed, again some striking parallels with the development of the Dutch Sandwich Tern populations appear. Peaks in clupeid abundance in 1981, 1989, 1994 and 1998, for example, coincided with peaks in the number of Sandwich Terns breeding in the Wadden Sea. Also lows in the Wadden Sea population in 1992 and 1996 correlated with a low abundance of clupeids in the southeastern North Sea. There was, however, no relationship between the breeding performance (either clutch size or reproductive output) of Dutch Sandwich Terns and the clupeid abundance

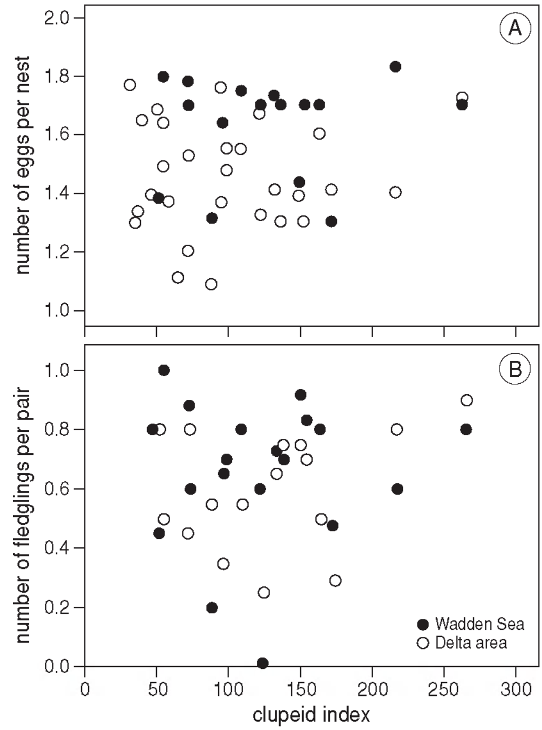

Figure 9.6. Relationship between IBTS clupeid abundance in the southeastern North Sea (population size in 1977 was set at 100%) and clutch size (averaged annual number of eggs per nest; A) and breeding success (averaged annual number of fledglings per pair; B) in the colonies on Griend in the Wadden Sea (1986-2004) and Hompelvoet/Markenje in the Delta area (1977-2004 and 1989-2004, respectively for clutch size and breeding success). Note that clutch size and breeding success are generally lower in the Delta area than in the Wadden Sea.

in the southeastern North Sea (Fig. 9.6). We conclude that if the changes in the Sandwich Tern populations are related to fish availability it will probably be an immediate response of the adult population to changes in food abundance rather than a delayed response through the reproductive output of the terns.

The reproductive output of the Sandwich Tern populations on Griend (recorded in 1986-2004) and on Hompelvoet/Markenje (1977-2004) yield a prediction of the number of recruits that may enter the populations a few years later (assuming that fledglings recruit to the natal colony 3 years later and using a recruitment rate of 0,3[1]). Assuming that breeding adults of the previous year return to the same colony (using an adult mortality rate of 0,18[1]) generates a prediction of the size of the respective populations. The relative difference between the predicted population size and the actual population size is then a measurement of the changes in the population caused by processes of immigra-

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[1] Adult mortality and recruitment rate are derived from Green *et al.* (1990) and are very similar to values for the Dutch population given by Brenninkmeijer & Stienen (1992).

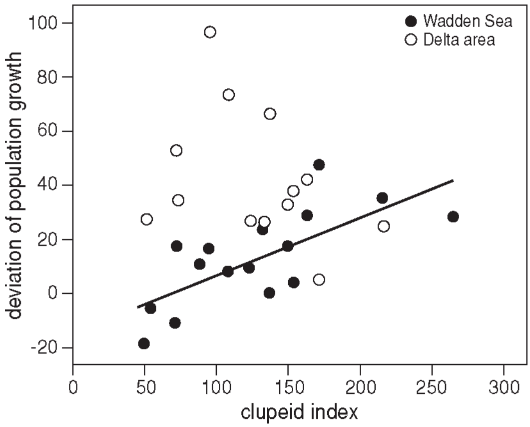

Figure 9.7. Relationship between IBTS clupeid abundance in the southeastern North Sea and the Δ – population growth of the Wadden Sea and Delta populations of Sandwich Tern (see text for more details).

tion/emigration and/or intermittent breeding (further called Δ–population growth). A strong positive relationship (linear regression, r^2 = 0,52, $P < 0.01$) between the IBTS clupeid abundance in the southeastern North Sea and the Δ–population growth of the Wadden Sea population was found (Fig. 9.7). This result is in accordance with the hypothesis that the recent changes in the Dutch Sandwich Tern population are linked to fluctuations in prey fish stocks, although the relationship seems not to hold for the Delta population. As was supposed earlier in this chapter there seems to be a direct link between the amount of food available in determining how many terns decide to breed or not to breed in the Wadden Sea, but so far as we know, there is no simple relationship to the terns' subsequent reproductive successs (confirming chapter 4). It remains puzzling what caused the population changes in the Delta area. This population might more critically depend on the stock size of Downs herring that spawns in the English Channel or other local prey stocks that are not very well represented in the IBTS surveys. Alternatively, the southern population might be driven more by other ecological processes (*e.g.* wind, predation, habitat changes etc.). It must also be mentioned that the restricted data used here (*e.g.* no reliable data on sandeel availability and clupeid abundance may differ locally) may be insufficient to explain all patterns in detail.

During the twentieth century, three periods of positive population growth can be distinguished during which the Dutch Sandwich Tern population grew faster than was expected from survival parameters (Fig. 9.8). A first positive phase can be seen around 1920, resulting from the wardening of colonies and protection against egging and shooting. The increase was apparent in the Delta area and not in the Wadden Sea because at the Dutch Wadden Sea was not very important as a breeding station for Sandwich Terns at that time. The strong growth of the Wadden population between 1920 and 1940 was most probably the result of an influx of immigrants into the Wadden Sea (partly but not

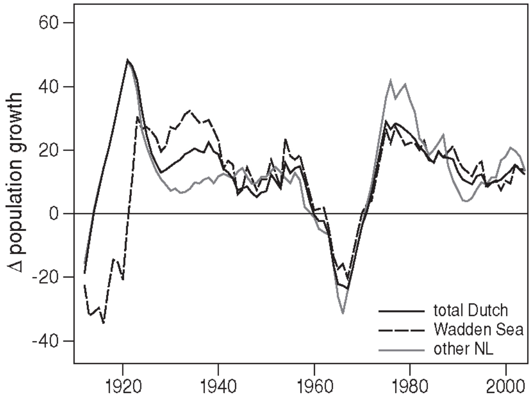

Figure 9.8. Outline of the development of the total Dutch population as well as the populations in the Wadden Sea and other parts in The Netherlands during 1910-2004. The lines represent the 10-year running means of the Δ – population growth (assuming a breeding success of 0.7 fledglings per pair).

entirely originating from the Delta area). In 1959, both the Delta and Wadden Sea populations entered a period of strong negative population growth caused by the poisoning of adults and chicks. This period was followed by a strong population increase that presumes a strong net influx of terns. Again the influx was more apparent in the Delta area than in the Dutch Wadden Sea. Figure 9.8 further suggests that by the end of the twentieth century, the processes of emigration/mortality and immigration/recruitment were more in balance with each other. The strong growth of the Delta population during 1999-2004, however, again suggests a net influx of individuals originating from other colonies. So the Delta population seems to depend more on processes of immi- and emigration than the Wadden Sea population.

A BIOGEOGRAPHICAL PERSPECTIVE

The longer periods of positive population growth (*e.g.* in the Wadden Sea from 1920-1940 and in the Delta area after the recovery of the crash in 1965) may point towards periods of increased reproductive output or may result from immigration from other colonies, whereas shorter periods of strong population changes may reflect intermittent breeding. Ring recoveries indeed confirm that there is considerable interchange between colonies throughout large parts of NW-Europe (Møller 1981, Brenninkmeijer & Stienen 1997, Noble-Rollin & Redfern 2002). Recoveries of foreign ringed terns on Griend come from pulli ringed in colonies in Great Britain & Ireland, Belgium, Germany, Denmark, Sweden and Estonia (Fig. 9.9). There is also considerable exchange with other Dutch colonies. On the other hand, pulli ringed on Griend have been reported breeding in the

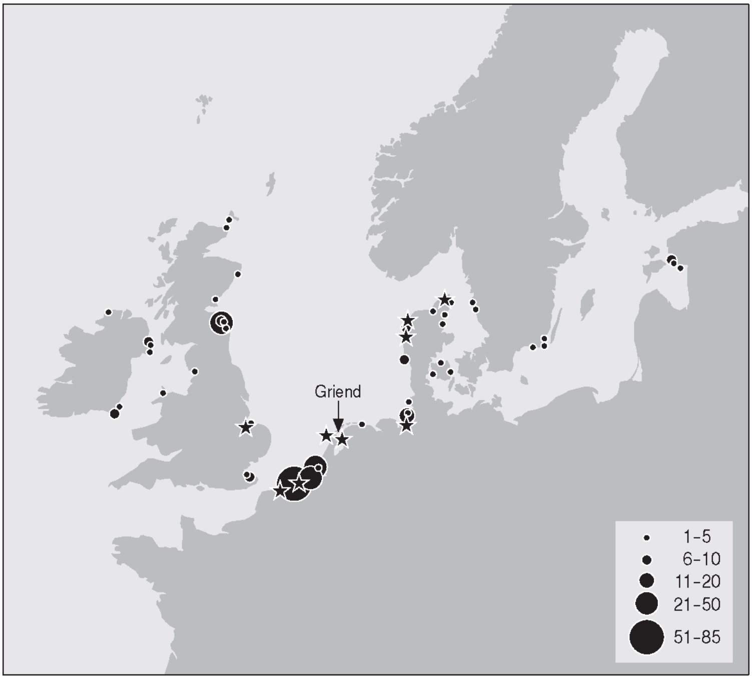

Figure 9.9. Ringing locations of 349 Sandwich Terns recovered on Griend during the breeding season (May-June) and ringed as pulli elsewhere (dots). The asterisks show recovery locations of 32 Sandwich Terns ringed as pulli on Griend and recovered elsewhere in a subsequent breeding season when of breeding age (> 2 cy). Hatched circle = Griend. Data Vogeltrekstation Arnhem.

UK, France, Belgium, Dutch colonies other than Griend, Germany, and Denmark. According to the recoveries analysed by Brenninkmeijer & Stienen (1997) about 23% of the Sandwich Terns nesting on Griend in the 1990s originated from colonies other than Griend, with Griend having strong connections with colonies in the Dutch Delta area, and to a lesser extent with colonies in the UK and Denmark (and probably from Germany where not so many birds have been ringed as in the other countries).

Sandwich Terns have ample opportunities to mix with terns from other colonies. Sandwich Terns from The Netherlands share common wintering quarters with Irish, British, Belgian, German and Danish colonies. When migrating northwards from the African wintering areas to the breeding areas European terns visit various colony sites located to the south of their natal colony. At each breeding location they can decide to stay if conditions for breeding are good or alternatively to continue their flight northwards. After breeding, parents and fledglings from Dutch colonies first move northwards (up to Denmark) before starting their southward migration to the African wintering areas. There is post-fledging dispersal of British and Belgian birds to The Netherlands and Denmark as well (Møller 1981, Noble-Rollin & Redfern 2002, own data). By visiting non-natal breeding sites individuals can sample the food situation in large parts of the Atlantic and the North Sea, and they can monitor the number of fledglings in various other colonies (which may be indicative for feeding conditions). The connectivity with other colonies and the high rates of interchange between colonies imply that population dynamics in Sandwich Terns must be dealt with on a European scale. Most studies, however, only consider fluctuations in the breeding numbers at the colony, region or county level and often link local changes in breeding numbers to discrete events (*e.g.* Südbeck & Hälterlein 1997, Lloyd *et al.* 1991, Merne 1997, Ratcliffe *et al.* 2000, Ratcliffe 2004) and have not considered exchange of birds between European colonies.

Before the crash of the Dutch population in the 1960s, the European Sandwich Tern population amounted to about 50 000 pairs. At that time, The Netherlands supported about 70% of the total European population. For that reason, the collapse of the Dutch population caused a temporary decrease of the European population to a low of about 15 000 pairs in 1965. After the Dutch population crash, numbers gradually increased and in the early 1990s Europe again supported about 50 000 pairs. However, the distribution over the various countries had drastically changed. The Netherlands only supported less than 25% of the European population, while other European colonies had gained in importance (Brenninkmeijer & Stienen 1997). A comparison of the population trends in the Dutch populations (Wadden Sea and southern North Sea) with those in the adjacent populations of the United Kingdom, Ireland and Germany (data available from 1969 onwards) shows that after the crash of the Dutch population a strong increase was apparent in all northwest European populations, except for those in Great Britain and Ireland (Fig. 9.10). Particularly high rates of population growth were found in the North Sea/Channel, Dutch Wadden Sea and Germany, whereas numbers increased much less rapidly in eastern UK waters. After 1980, growth stagnated in many regions or even became negative; first in the German North Sea population (1981-1986), followed by the eastern UK colonies (1983-1998), the southern North Sea (1986-1994), the Dutch Wadden populations (1990-2000) and again in Germany (1997-2001). Remarkably, in all parts of Europe those periods of recessions were followed by a revival of the population growth at about the same rate as prior to the stagnation. In contrast to the population changes prior to the 1970s that were all related to human impact (egging, shooting of adults, pollution), this time the changes were probably not directly anthropogenic and most probably related to food availability. The stepwise pattern of the Sandwich Terns' population growth in various parts of Europe may point towards sudden shifts within the North Sea ecosystem. During the past decades similar shifts, so-called regime shifts, were noted at different levels of the North Sea ecosystem, spanning the lower trophic levels, via fish to birds and marine mammals (*e.g.* Edwards et. al. 1999, 2001, Corten 2001, Reid *et al.* 2001, Ottersen *et al.* 2001, Weijerman *et al.* 2005). In the North Sea and Wadden Sea sudden and stepwise ecosystem changes occurred in 1988 and 1998 imposed on more gradual trends as a result of an increased inflow of oceanic water (Reid *et al.* 2001), so largely coinciding with the shifts in the Sandwich Tern populations in many parts of Europe.

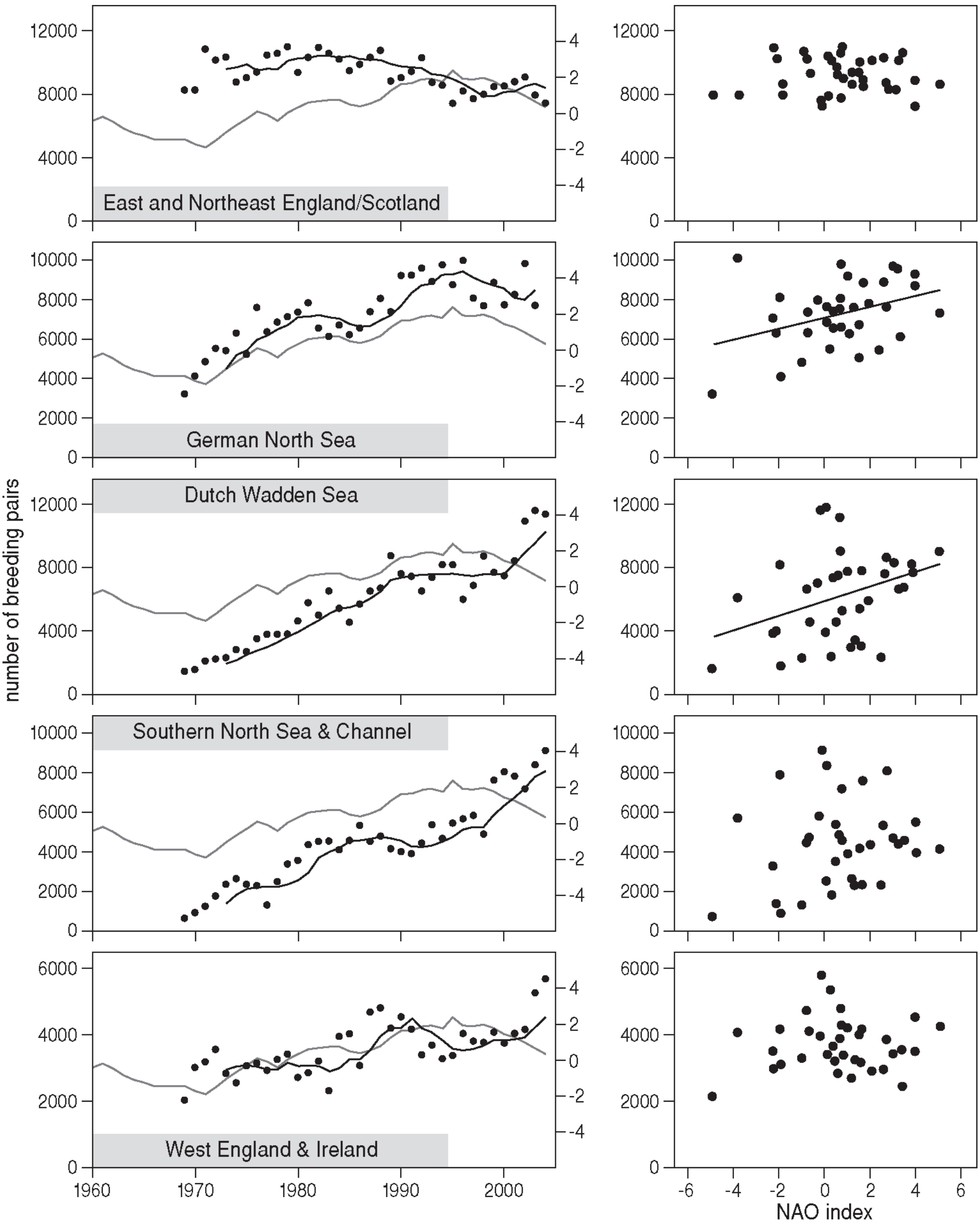

Figure 9.10. The left panel shows the number of Sandwich Tern (dots) in various regions in Europe during 1969-2004. Drawn lines are 5-year-running means of the population sizes. The grey line represents the 10-year-running mean of the index of the North Atlantic Oscillation during December-March (data from Hurrell 2005) and is plotted against the right axis. The right graphs show the relationship between the NAO-index and the number of breeding pairs in each region.

THE NORTH SEA ECOSYSTEM AND THE NAO

The functioning of the North Sea ecosystem is highly complex and not very well understood, but the major driving forces are the periodical changes of the NAO influencing sea surface temperature and the sudden inflows of nutrient rich oceanic water into the North Sea (Reid *et al.* 2003). The NAO has major impact on fish stocks in the North as well as the transport of fish larvae across the North Sea (Corten 2001, Beaugrand *et al.* 2003, Stenseth *et al.* 2004). When the NAO is in a positive phase herring larvae are transported from the spawning grounds in the eastern UK waters to the nursery areas in the Wadden Sea and the Skagerrak/Kattegat (Corten 2001). During negative phases the larvae fail to reach the nursery areas. Because herring is a very important food source for Sandwich Terns one may expect that the NAO strongly influences the feeding condition of Sandwich Terns nesting in the more eastern parts of the North Sea. With the collapse of the herring stock in the 1970s (at least in part due to the industrial fishery) the NAO was in a negative phase and herring larvae failed to reach the nursery areas in the eastern North Sea. With the failure of herring larvae to reach the eastern North Sea, the sprat stock in the western North Sea expanded enormously (Corten 2001). In other words: while the feeding conditions for Sandwich Terns deteriorated in the eastern North Sea, conditions improved in the western North Sea. In the mid 1980s, the NAO reverted to a positive phase and the transport of herring larvae returned to normal while the sprat stock in the western North Sea declined (Corten 2001). After 1985, therefore, feeding conditions for Sandwich Terns improved in the eastern and deteriorated in the western North Sea. In accordance with this, around 1985 growth resumed in the German Sandwich Tern population, while the eastern UK population started to decline (Fig. 9.10). In fact the German North Sea population closely followed fluctuations in the NAO throughout the period 1969-2004, and also in the Dutch Wadden Sea the number of breeding pairs were positively correlated with the NAO-index. Although the population development of the German North Sea population and the Dutch Wadden Sea population largely overlap, there are some interesting differences. During periods of positive NAO-indices in 1985-1995, the German North Sea population increased while at the same time growth stagnated in the Dutch Wadden Sea. When the NAO-index changed to negative values after 1996, breeding numbers decreased in Germany and strongly increased in the Dutch Wadden Sea. This suggests a link between the populations in the Dutch Wadden Sea and colonies in the German Wadden Sea and a high degree of exchange of individuals linked to fluctuations in feeding conditions in the more eastern colonies. Similarly, when feeding worsened in the eastern UK waters after 1985 birds may have migrated to German (and Dutch) colonies where feeding conditions had improved. Ring recoveries of breeding adults on Griend confirm that a disproportionately large number of immigrants from UK-colonies were ringed in the 1980s, whereas recoveries of birds ringed in Danish colonies were more evenly distributed over the past four decades (Table 9.1).

Table 9.1. Number of Sandwich Terns per decade ringed as pulli in the United Kingdom and Denmark, and recovered in a subsequent breeding season (May and June) on Griend in 1971-2003. Data derived from Vogeltrekstation Arnhem.

Year of birth	Number of UK- immigrants (%)	Number of DK- immigrants (%)
1960-1969	10 (9.4)	11 (28.9)
1970-1979	13 (12.3)	6 (15.8)
1980-1989	62 (58.5)	8 (21.1)
1990-1999	21 (19.8)	13 (34.2)

From the above we may conclude that there is substantial evidence that the NAO is the driving force that changes the distribution and composition of fish stocks in the North Sea and ultimately determines the distribution of Sandwich Terns over Europe. It still remains puzzling how the population changes in the southern North Sea, Channel, Ireland and west England are related to this. The strong links between the European populations and the supposed link with the dynamics of their prey fish argue for a close cooperation between various countries in resolving this puzzle. As Sandwich Terns are indicators of the food situation par excellence and because reproductive parameters and the demography of the populations can be measured relatively easily, a European wide study on breeding numbers and reproductive output and a better organisation of ringing and ring recovery than was done hitherto is called for. The results of this study should then be coupled with a North Sea wide study on the dynamics of clupeids stocks as well as sandeel.

THREATS TO THE EUROPEAN SANDWICH TERN

So far we have seen that Sandwich Terns are highly vulnerable to reductions in food supply in the breeding areas and to pollutants that accumulate in the food web. Sandwich Terns have a restricted choice for breeding habitats and breed gregariously in a few very dense colonies. Northwest Europe only harbours a few large colonies (10-20 depending on the definition) of this species. If anything happens to one of these colonies, this can have major consequences for the size of the European breeding population as a whole. This happened in the 1960s in The Netherlands, when poisoning of the Dutch coastal waters caused that about two-thirds of the total European population perished. Likewise persecution by humans (large-scale egging and shooting of adults) has heavily reduced the European population in the beginning of twentieth century.

The highly gregarious behaviour of this species also poses a threat during wintering. All European Sandwich Terns share the same wintering areas and the distribution over the wintering areas does not differ between terns of various breeding origin (Møller

1981, Brenninkmeijer & Stienen 1999). The main wintering grounds are situated along the coast of West Africa, with Senegal and Ghana as strongholds (Müller 1959, Møller 1981, Urban *et al.* 1986, Brenninkmeijer & Stienen 1999). This implies that it is not likely that the distinct changes in numbers in the various European countries are caused by factors acting in the wintering areas, although at the same time changes in the wintering area can have large effects on the European population as a whole. At present, the food situation during winter is probably not limiting the size of the European population (chapter 8), but other factors such as the trapping of terns in the wintering areas may limit the growth of the population.

Local people living near the terns' main wintering grounds in Senegal and Ghana, are notorious for their habit of tern trapping (Mead 1978, Dunn 1981, Meininger 1988, Staav 1990). On an annual basis several thousands of terns are the victims of this practice, with Sandwich Tern being one of the most affected species (Stienen *et al.* 1998). However, the exact impact of this practice remains unknown, as the estimates are very imprecise and based on incomplete coverage of the wintering area. In countries where tern trapping is a common habit, the recovery rate of ringed terns will be higher than elsewhere. In Mauritania for example the density of the human population is extremely low and tern trapping is not commonly practiced, resulting in relatively low recovery rates from this country. Estimates of the number of terns wintering in Mauritania (Perennou 1991) are much higher than expected from the distribution based on ring recoveries (Brenninkmeijer & Stienen 1999). Integral counts of the number of terns wintering in Africa have never been made and counts carried out in the wintering areas are scarce and widely scattered in time and space.

In many West-African countries a strong increase in commercial fishery took place during the past decades. At present, the coastal waters along West Africa are heavily exploited by European, Russian and Asian vessels and effects on the marine ecosystem are already obvious. There is a particularly high fishing pressure on pelagic fish (Alder & Sumaila 2004) that can potentially have a large impact on piscivorous birds like Sandwich Terns. There is a strong need for a scientifically based fishery policy and regulation of commercial fishery in West African waters to avoid overexploitation and to reduce the impact on the ecosystem (Kaczynski & Fluharti 2002, Alder & Sumaila 2004).

Another recent threat to European Sandwich Terns is the growing economic interest in coastal areas by the offshore wind industry. With the first offshore power plants already in operation and many more projects under consideration, wind farms will soon be a widespread phenomenon along the Atlantic and North Sea coasts. For economical reasons shallow coastal waters will be the most interesting sites to situate offshore power plants and thus the accumulated impact of offshore wind farms (barriers and increased mortality as well as possible effects on the fish stocks) may particularly affect near-coastal migrants like Sandwich Terns.

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Appendix 9.1. Number of breeding pairs of Sandwich Tern in various parts of The Netherlands and in Belgium during the period 1900-2004. Data before 1960 are reconstructed (interpolated at the colony level accounting for known trends in adjacent colonies) from figures given in literature (see Brennikmeijer & Stienen 1992 for more details). From 1960 onwards, almost all Dutch colonies were counted annually and figures are much more reliable.

Year	Griend	rest Wadden	rest NL	Belgium
1900	2000	3085	11000	0
1901	2000	3485	11000	0
1902	2000	2085	11000	0
1903	2000	2085	10000	0
1904	1500	595	9000	0
1905	1000	185	8000	0
1906	500	1100	7000	0
1907	0	1000	4000	0
1908	0	1250	3000	0
1909	0	1500	2000	0
1910	0	1750	500	0
1911	0	0	500	0
1912	0	0	1000	0
1913	0	0	2000	0
1914	3	0	3000	0
1915	300	50	4000	0
1916	2000	50	5000	0
1917	2500	50	6000	0
1918	4100	50	7000	0
1919	4100	50	8000	0
1920	3000	0	9000	0
1921	4200	0	9000	0
1922	4200	0	9000	0
1923	4000	150	9000	0
1924	4000	50	9000	0
1925	5000	50	8000	0
1926	5000	50	8000	0
1927	6000	50	8007	0
1928	8000	25	8002	0
1929	10000	4	8381	0
1930	12500	21	8000	0
1931	15000	19	8800	0
1932	17500	4	7860	0
1933	22000	300	8082	0
1934	22000	0	8305	0
1935	21465	300	9436	0
1936	18640	450	8650	0
1937	25000	110	9500	0
1938	35000	110	10750	0
1939	27500	2010	8550	0
1940	15000	15005	10210	0
1941	4000	10000	12220	0
1942	8000	15016	10100	0
1943	25000	3035	9225	0
1944	5000	200	11000	0
1945	8000	550	15500	0
1946	15000	1153	9260	0
1947	12500	1535	7310	0
1948	12500	2800	10549	0
1949	12500	5750	10560	0
1950	12500	5875	10460	0
1951	12500	6000	15000	0
1952	12500	5500	14760	0
1953	12500	4000	11510	0
1954	22500	3292	11435	0
1955	6500	8905	13321	0
1956	12500	10332	13314	0
1957	10000	14882	7490	0
1958	7500	6622	4860	0
1959	5500	3906	4079	0
1960	5250	715	4057	0
1961	5000	2352	4514	0
1962	7000	858	4489	0
1963	1500	92	3004	0
1964	1500	15	752	0
1965	725	90	60	0
1966	1500	2	193	0
1967	900	2	298	0
1968	1200	2	364	0
1969	1600	0	436	0
1970	1700	1	717	0
1971	2100	70	1019	0
1972	2100	236	1640	0
1973	2200	53	2100	0
1974	2700	270	2354	0
1975	2250	687	2105	0
1976	2700	752	2102	0
1977	2500	1385	1200	0
1978	3300	603	2203	0
1979	2950	851	3150	0
1980	4000	616	3400	0
1981	4650	1212	3923	0
1982	4100	1150	4106	0
1983	6000	633	4100	0
1984	5050	305	3500	0
1985	3900	610	4170	0
1986	6900	500	4700	0
1987	5900	750	3985	0
1988	7600	12	4250	1
1989	9000	130	3414	250
1990	7300	300	3204	300
1991	7000	750	2524	950
1992	6600	0	2778	1100
1993	7600	0	3300	1650
1994	8300	0	3351	800
1995	8200	60	4850	250
1996	5600	496	4601	670
1997	5000	1987	4975	425
1998	7000	2050	4500	73
1999	7800	0	6350	720
2000	7918	737	5800	1550
2001	8207	17	6350	920
2002	10970	142	6200	46
2003	11260	500	6700	823
2004	11275	351	3793	4067

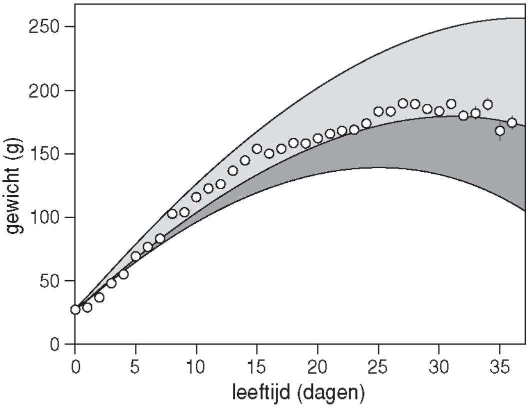
Nederlandse samenvatting

De zandige, laaggelegen kusten van Nederland vormen een belangrijk broedgebied voor kustbroedvogels en waren in de twintigste eeuw van groot belang voor de Grote Stern *Sterna sandvicensis*. Halverwege de twintigste eeuw broedde maar liefst 75% van de Europese populatie van deze soort langs onze kust. In de jaren zestig kwam daar verandering in. Een grootschalige verontreiniging van de Nederlandse en Duitse kustwateren met organische chloorverbindingen reduceerde het aantal broedparen van meer dan 35.000 in de jaren vijftig tot een minimum van slechts 865 in 1965. Nadat de lekkage van de gifstoffen was gestopt, herstelde de Nederlandse broedpopulatie beduidend langzamer dan in eerdere periodes van herstel. Bij aanvang van deze studie in 1994 waren de aantallen van de jaren vijftig nog lang niet bereikt. Er broedden toen nauwelijks meer dan 10.000 paren in Nederland. Bovendien was de Nederlandse populatie onderhevig aan sterke schommelingen die niet goed begrepen werden en niet konden worden verklaard vanuit de overleving van oudervogels of vanuit de broedresultaten. Bij aanvang van deze studie werd verondersteld dat de voedselbeschikbaarheid wel eens een belangrijke rol kon spelen bij het langzame en onvolledige herstel van de populatie en dat fluctuaties in de voedselbeschikbaarheid mogelijk de oorzaak waren van de sterk fluctuerende aantallen. Een relatie met voedsel lag immers voor de hand omdat de Grote Stern een voedselspecialist is met een zeer beperkte keuze van prooisoorten en –lengtes. Bovendien hadden Brenninkmeijer en Stienen (1994) een positieve correlatie gevonden tussen het aantal broedparen in Nederland en de hoeveelheid jonge haring in de Noordzee. Dat alles was reden om de voedselecologie van de Grote Stern uitgebreid te bestuderen in de hoop dat deze kennis zou leiden tot een beter begrip van de populatiedynamica van deze soort.

Als studiegebied werd gekozen voor het eiland Griend in de Waddenzee omdat hier van oudsher een grote broedkolonie was gevestigd. Er was al veel onderzoek verricht naar de sterns op Griend en een redelijk deel van de broedpopulatie was geringd wat belangrijke informatie kon opleveren over eventuele verplaatsingen van en naar andere broedgebieden. Dankzij een uitgebreide studie van Veen (uitgevoerd rond 1970) was er al veel bekend over de broedbiologische aspecten van de Grote Sterns op Griend. De resultaten van de studie van Veen hadden de houding ten opzichte van Kokmeeuwen *Larus ridibundus* sterk veranderd. Voor die tijd werd verondersteld dat de meeuwen een bedreiging vormden voor Grote Sterns omdat ze hun eieren en kuikens roofden. De studie van Veen bevestigde het roofgedrag van de meeuwen, maar toonde tegelijkertijd aan dat de meeuwen vooral eieren en kuikens roven die sowieso al niet levensvatbaar waren en dat het roofgedrag geen nadelige effecten heeft op het broedsucces van de sterns. Veen stelde vast dat Grote Sterns juist de nabijheid van broedende Kokmeeuwen opzoeken omdat die hen bescherming bieden tegen roofdieren. De gevolgen van het kleptoparasitisme (*i.e.* het roven van voedsel) door de meeuwen werden in eerdere studies echter onvoldoende onderzocht. De huidige studie toont aan dat Grote Sterns niet alleen eieren en kuikens inruilen tegen bescherming, maar ook een behoorlijk deel van de vis - die eigenlijk voor hun kuikens is bedoeld - verliezen aan rovende meeuwen. De huidige studie onderzoekt hoe Grote Sterns zijn aangepast om de gevolgen van het kleptoparasitisme zo gering mogelijk te houden.

Als viseters staan Grote Sterns aan de top van de mariene voedselketen. Tijdens het broedseizoen is hun voedselkeuze beperkt tot een klein aantal soorten prooivissen. In Noordwest-Europa bestaat het menu van Grote Sternenkuikens voor meer dan 90% uit haring- en zandspieringachtigen. Dit zijn vissen met een hoge voedingswaarde die het kostbare foerageergedrag van de oudervogels en de hoge groeisnelheid van de kuikens moeten dekken. Door hun gespecialiseerde voedselkeuze zijn Grote Sterns bijzonder gevoelig voor veranderingen in de beschikbaarheid van een van hun prooivissen. Foeragerende sterns lokaliseren hun prooien visueel en de prooivissen worden meestal met een stootduik bemachtigd waarbij ze tot maximaal twee meter diep kunnen vissen. De belangrijkste foerageergebieden rond Griend liggen bij Vlieland en Terschelling zo'n 10-15 km van de kolonie. In tegenstelling tot veel andere zeevogels hebben Grote Sterns geen krop. Ze transporteren de prooivissen één voor één en in hun geheel zichtbaar in de snavel naar hun kuikens. Deze opvallende voedingswijze in combinatie met het feit dat Grote Sterns in zeer dichte kolonies broeden, maakt hun zeer kwetsbaar voor kleptoparasiterende meeuwen. Om dezelfde redenen is onderzoek naar de voedselkeuze van deze soort heel aantrekkelijk omdat relatief gemakkelijk veel gegevens kunnen worden vergaard over het menu van hun kuikens en over het roofgedrag van de Kokmeeuwen. Toch was er bij aanvang van deze studie relatief weinig bekend over het voedsel van Grote Sterns. De schaarse literatuurgegevens beschreven meestal alleen het menu tijdens de eerste levensdagen van de kuikens wanneer die nog in de nabijheid van het nest verblijven. De onderhavige studie is de eerste waarin het foerageergedrag van de oudervogels en de samenstelling van het voedsel van Grote Sterns is onderzocht tijdens de volledige kuikenfase en die bovendien een vergelijking maakt tussen een groot aantal jaren (1992-1998). De studie bevestigt de uitgesproken gespecialiseerde voedselkeuze van deze soort. In de periode 1992-1998 bestond het menu van de Grote Sternenkuikens op Griend voor meer dan 99% uit haringachtigen en zandspieringen (**hoofdstuk 2**). Een kuiken kreeg dagelijks ongeveer 9 prooivissen aangeboden en dat aantal was onafhankelijk van de leeftijd van het kuiken. Om in de toenemende energiebehoefte van hun opgroeiende kuikens te voorzien, brachten de oudervogels steeds grotere prooien naar de kolonie. De verhouding tussen de beide prooisoorten (haringachtigen en zandspiering) fluctueerde sterk zowel op de lange termijn (van jaar tot jaar) als binnen kortere tijdsbestekken zoals een daglichtperiode. In sommige gevallen was de variatie in het menu te verklaren vanuit het gedrag van hun prooivissen. De dagritmiek in het kuikenmenu was bijvoorbeeld een afspiegeling van het cyclische verticale migratiegedrag van hun prooivissen. Andere veranderingen in het voedselaanbod konden worden verklaard uit een combinatie van fysische en biologische veranderingen. Wind had zeer sterke effecten op de frequentie van prooiaanvoer, op de menusamenstelling en ook op de lengte van de aangebrachte vissen. Wind veroorzaakt rimpelingen op het wateroppervlak en reduceert het doorzicht van het water waardoor prooivissen minder goed zichtbaar zijn voor de foeragerende oudervogels. Bovendien moeten de sterns bij harde wind meer moeite doen om biddend boven de prooi te blijven hangen, waardoor de vangstefficiëntie van de vis afneemt. Daarnaast beïnvloedt sterke wind de verticale verspreiding van hun prooivissen waardoor haringachtigen minder beschikbaar zijn voor stootduikende vogels. Ook waren er aanwijzingen dat Grote Sterns bij harde wind meer in de Waddenzee foerageren en minder in de ruwere Noordzee.

Wind beïnvloedde bovendien het roofgedrag van de Kokmeeuwen (**hoofdstuk 3**). Bij harde wind werden de sterns bij aankomst in de kolonie intensiever achtervolgd door kleptoparasiterende meeuwen. Onder die omstandigheden roofden de meeuwen zelfs heel kleine vissen van de sterns, die ze bij weinig wind ongemoeid lieten. Harde wind zorgt dus enerzijds voor een verminderde voedselaanvoer en anderzijds voor een toename van het kleptoparasitisme. De groei van de Grote Sternenkuikens op Griend was dan ook sterk afhankelijk van de heersende windsnelheid. Tijdens de eerste twee levensweken van de kuikens had harde wind relatief weinig effect op de groei (Fig. 1); enerzijds omdat de energiebehoefte van jonge kuikens nog relatief laag is en anderzijds omdat het roofgedrag van de meeuwen zich dan nog niet volledig ontwikkeld heeft. In de weken daarna (de kuikens vliegen uit als ze 30-35 dagen oud zijn) had wind een sterk negatief

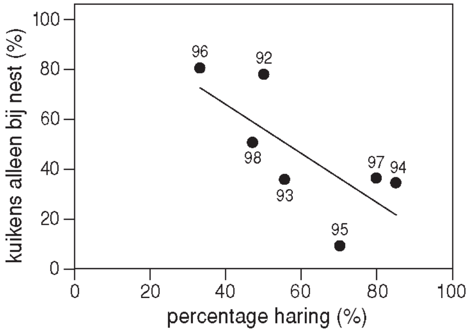


Figuur 1. Mathematisch model van het cumulatieve effect van wind en prooiverlies op de groei van Grote Sternenkuikens op Griend. De bovenste getrokken lijn geeft de theoretische groei van een kuiken bij zeer gunstige windomstandigheden (5 m/sec) en wanneer in het geheel geen prooiverlies zou optreden. De middelste lijn toont de groei bij aanhoudende harde wind (15 m/sec) maar eveneens zonder prooiverlies. Wanneer ook nog rekening wordt gehouden met het verlies van prooien o.a. aan rovende Kokmeeuwen (onderste lijn) dan blijft de groei sterk achter bij de werkelijke groei (witte stippen, gemiddelde gewichten ± SE). Bij aanhoudende harde wind zullen de kuikens het uiteindelijk niet overleven.

effect op de ontwikkeling van de kuikens. Langdurige harde wind kan het broedsucces van Grote Stern gevoelig reduceren omdat dan veel kuikens door verhongering om het leven komen.

Ook onder gunstige windomstandigheden werden lang niet alle prooien die de oudervogels naar de kolonie op Griend brachten daadwerkelijk gegeten door de kuikens. Maar liefst 29,3% van de aangebrachte prooien ging verloren, waarvan het grootste deel bij aankomst in de kolonie werd geroofd door Kokmeeuwen (18,0% van alle aangebrachte prooien). Ook de overige verliezen waren in veel gevallen gerelateerd aan het roofgedrag van de meeuwen. Wanneer een arriverende oudervogel werd achtervolgd door Kokmeeuwen, at de oudervogel de prooi soms zelf op (1,4%) of vloog weg uit de kolonie om vervolgens terug te keren zonder vis (7,7%). Slechts een klein gedeelte van het prooiverlies (2,2%) had niets te maken met roverij door meeuwen. De kans dat een prooi bij aankomst in de kolonie werd geroofd door een patrouillerende Kokmeeuw (ofwel op een andere manier verloren ging) was afhankelijk van de lengte van de vis (langere vissen werden vaker geroofd), maar niet van de soort vis (**hoofdstuk 4**). Een haringachtige van een bepaalde lengte had een even grote kans om uiteindelijk geconsumeerd te worden door het kuiken als een zandspiering van dezelfde lengte, hoewel haring een grotere energie-inhoud heeft. In theorie was het op Griend niet mogelijk om een kuiken op een menu van uitsluitend zandspiering groot te brengen; de grotere zandspieringen die daarvoor nodig zouden zijn worden te frequent geroofd. Men zou daarom verwachten dat de oudervogels hun opgroeiende kuikens meer en meer haringachtigen zouden aanbieden. In de praktijk bleek er echter geen eenduidig verband te zijn tussen de leeftijd van de kuikens en de samenstelling van hun menu. Er waren jaren dat het kuikenmenu gedomineerd werd door haring (1994, 1995 en 1998) en waarin de sterns nauwelijks in problemen kwamen. Er waren ook minder goede jaren (1992 en 1996) waarin het aandeel haring in het menu minder dan 50% bedroeg en dus relatief veel prooien verloren gingen aan kleptoparasiterende meeuwen. In die jaren dreigde er voedselschaarste te ontstaan wanneer de kuikens een bepaalde leeftijd hadden bereikt. De oudervogels reageerden daarop door tegelijkertijd te gaan foerageren en hun opgroeiende kuikens meer en meer alleen achter te laten bij het nest (Fig. 2). Op die manier werd de aanvoerfrequentie van prooivissen verhoogd en werd er gecompenseerd voor het prooiverlies aan rovende Kokmeeuwen.

Als semi-nestvlieders zijn Grote Sternenkuikens na enkele dagen in staat om de nestplaats zelfstandig te verlaten. Een dag of vijf na het uitkomen van de eieren verlaten de eerste kuikens het nest (meestal weggelokt door de ouders). Ze verschuilen zich in eerste instantie in de vegetatie in de directe omgeving van het nest, maar verwijderen zich daarna steeds verder van de oorspronkelijke nestplaats. Enkele weken na het uitkomen van de eerste eieren zijn Grote Sternenkolonies vaak volledig verlaten. In de literatuur wordt vermeld dat het verlaten van de kolonie vaak een gevolg is van verstoring door mensen (onderzoekers) en dat dergelijk gedrag functioneel is om infecties en ziektes te voorkomen (in Grote Sternenkolonies worden dikke pakketten feces afgezet die na verloop van tijd allerlei potentiële infectiebronnen herbergen). In **hoofdstuk 5** wordt



Figuur 2. Hoe minder haring in het menu van de sternenkuikens op Griend hoe vaker ze alleen werden achtergelaten door hun ouders.

getoetst of het weglopen van de oorspronkelijke nestplaats ook effectief zou kunnen zijn om rovende Kokmeeuwen te ontwijken. Daartoe werden enkele kuikens in een enclosure gedwongen om op hun geboorteplek te blijven tot aan het uitvliegen. Een andere groep kuikens van ongeveer twee weken oud werd verplaatst naar een enclosure die 15-50 m verderop was opgesteld. Inderdaad was de roverijdruk ten aanzien van de verplaatste groep kuikens veel lager dan de druk op de niet verplaatste groep. De verplaatste kuikens consumeerden tot 30% meer prooien dan de niet verplaatste kuikens en de tijd dat de oudervogels met een vis boven de kolonie vlogen in afwachting van een kans om bij hun kuiken te landen daalde significant. De verplaatste kuikens groeiden sneller en bereikten eerder het vliegvlugge stadium dan de niet verplaatste groep. Wanneer de verplaatste kuikens echter langer dan vijf dagen op dezelfde plaats werden gehouden, nam de roverijdruk ook daar sterk toe en werden de verschillen in groei weer tenietgedaan. Een tweede verplaatsing resulteerde wederom in een gewichtstoename ten opzichte van de niet verplaatste groep. Vrij levende kuikens zouden zich dus voortdurend moeten verplaatsen om het kleptoparasitisme tot een minimum te beperken. Op Griend werden de verplaatsingen vaak bemoeilijkt door de dichte vegetatie en aanvallen van soortgenoten en meeuwen.

In **hoofdstuk 6** wordt onderzocht in hoeverre de groei van de sternenkuikens hun overlevingskansen beïnvloedt. Men zou veronderstellen dat Grote Sterns een zeer flexibele groei vertonen vanwege de grote onvoorspelbaarheid van de beschikbaarheid van hun voedsel en het prooiverlies aan rovende meeuwen. Inderdaad waren er grote individuele verschillen in groeisnelheid en kon de lichaamsconditie van kuikens sterk variëren, maar wel nam de kans op uitvliegen toe met de groeisnelheid van de kuikens. Trage groeiers die het echter overleefden tot aan het vliegvlugge stadium waren bij het uitvliegen lichter, maar hun structurele maten (kop en vleugel) waren wel ongeveer hetzelfde als die van de snelle groeiers. De langzame groeiers hadden bij het uitvliegen dus minder lichaamsreserves. Toch beïnvloedde dat niet hun overlevingskansen na het uitvliegen.

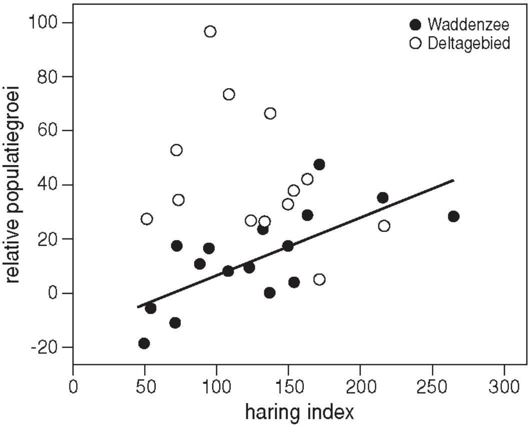
Kuikens met weinig lichaamsreserves bij het uitvliegen hadden een even grote kans om later als broedvogel in de kolonie gezien te worden als kuikens met veel reserves. Er wordt verondersteld dat de voedselomstandigheden na het uitvliegen zodanig verbeteren dat zelfs individuen in slechte conditie hun groeiachterstand snel weer inhalen. Na het uitvliegen brengen de oudervogels hun nakomelingen veel dichter bij de foerageergebieden, waardoor de tijd voor het transport van vis gevoelig afneemt en minder prooien worden verloren aan rovende Kokmeeuwen. Op die manier kan een groeiachterstand van enkele tientallen grammen binnen enkele dagen weer goed worden gemaakt. Wanneer een individu tijdens de kuikenfase een groeiachterstand had opgelopen, was dit niet meer meetbaar na rekrutering in de broedkolonie.

Tijdens de studieperiode op Griend kwam het nauwelijks voor dat een ouderpaar twee kuikens groot bracht. Ook bij een vergelijkende studie op het eiland Hirsholm in het noorden van Jutland, Denemarken, was geen van de ouders in staat twee kuikens groot te brengen. Dat was opmerkelijk omdat de meeste paren wel twee eieren legden (gemiddelde legselgrootte op Griend bedroeg 1,6 ei per nest). In **hoofdstuk 7** worden de voor- en nadelen van het leggen van twee eieren behandeld. Van alle broedparen die in eerste instantie twee kuikens hadden binnen de enclosures op Griend (1992-1999) en op Hirsholm (1997) was minder dan 2% in staat om beide kuikens groot te brengen. Doorgaans stierf het laatst uitgekomen kuiken voordat het vliegvlug was. In meer dan 50% van de gevallen stierf het tweede kuiken zelfs binnen vijf 5 dagen na het uitkomen. Het tweede, kleinere ei is waarschijnlijk vooral een verzekering voor het geval er iets mis gaat met het eerste ei (predatie, onbevrucht, etc.) of wanneer het eerste kuiken in een vroeg stadium sterft. Grote Sterns met een tweelegsel hadden een kleinere kans (6,1% lager) dat het legsel al in het eistadium volledig verloren ging. Omdat in sommige tweelegsels alleen het tweede ei uitkwam, was toch nog 7% van de kuikens uit tweelegsels afkomstig uit het tweede ei.

Ondervoeding was de belangrijkste doodsoorzaak van de kuikens op Griend en Hirsholm, wat duidt op een hoge mate van voedselstress in de noordelijke broedgebieden. Een vergelijkende studie in de winter van 1992/93 naar foeragerende sterns (Dwergstern *S. albifrons*, Grote Stern en Koningsstern *S. maxima*) in Guinee-Bissau (**hoofdstuk 8**) suggereert dat sterns in de overwinteringsgebieden mogelijk een veel gemakkelijker leven leiden. Vooral Grote Sterns hadden in Guinee-Bissau een zo efficiënte voedselopname dat men mag veronderstellen dat ze met enkele uren foerageertijd voldoende energie kunnen opnemen om in hun dagelijkse behoefte te voorzien. In het West-Afrikaanse overwinteringsgebied had het getij een veel groter effect op de foerageeractiviteit van de sterns dan in de broedgebieden in de Waddenzee. Ook wind en het doorzicht van het water hadden een significant effect op de voedselopname door sterns. In Guinee-Bissau vingen Grote Sterns voornamelijk rondvis van 8-15 cm, dus grotendeels overeenkomstig met hetgeen ze tijdens de broedperiode aan hun kuikens voeren.

In het recente verleden is het meerdere malen voorgekomen dat zeevogelpopulaties in enkele jaren tijd werden gedecimeerd als gevolg van het ineenstorten van een van hun voedselcomponenten. Vooral de kleinere zeevogels met een beperkte actieradius, met energetisch dure foerageertechnieken, afhankelijk van vis in de bovenste waterkolom en met snel groeiende kuikens blijken het meest gevoelig te zijn. Grote Sterns voldoen aan al deze criteria. Ze zijn bovendien zeer beperkt in hun voedselkeuze en hebben ook nog af te rekenen met een hoge predatiedruk door meeuwen. De onderhavige studie toont aan dat veranderingen in de menusamenstelling van Grote Sternenkuikens – die bij een voedselspecialist als deze waarschijnlijk een directe afspiegeling zijn van veranderingen in de beschikbaarheid van hun prooivissen – grote gevolgen hebben voor de groei van de kuikens en de inspanning die de oudervogels moeten leveren. Toch is het niet direct duidelijk hoe dat zich vertaalt in veranderingen op het niveau van de populatie. Immers in de onderhavige studie had de menusamenstelling geen invloed op de overleving van kuikens een ook niet op die van juveniele vogels. Mogelijk is er een verhoogde mortaliteit van adulte vogels in slechte haringjaren waarin ze harder moeten werken of brengen in ze in de daaropvolgende jaren minder jongen voort. Maar een meer voor de hand liggende verklaring is dat de heersende voedselsituatie rechtstreeks invloed heeft op het aantal broedparen. Bijvoorbeeld omdat sommige individuen onder slechte voedselomstandigheden een broedseizoen overslaan "intermittent breeding" of omdat ze dan op zoek gaan naar broedgebieden waar de omstandigheden beter zijn (emigratie). In **hoofdstuk 9** wordt onderzocht of en hoe schommelingen in de Nederlandse populatie zijn gerelateerd aan de voedselbeschikbaarheid. Er wordt een heel eenvoudig populatiedynamisch model opgesteld waarin de broedresultaten (gegevens uit lange termijnreeksen gemeten in de Waddenzee en in het Deltagebied) en overlevingskansen (afkomstig uit literatuur) worden gebruikt om het aantal broedparen in latere jaren te voorspellen. In jaren waarin volgens internationale surveys weinig haring en sprot aanwezig was in de zuidelijke Noordzee, broedden er minder Grote Sterns in de Waddenzee dan werd verwacht op basis van de uitkomsten van het populatiedynamische model en andersom was dat ook het geval. Dus de dynamiek van de populatie in de Waddenzee lijkt inderdaad afhankelijk te zijn van de voedselbeschikbaarheid (Fig. 3). Voor de populatie in het Deltagebied kon dit echter niet worden aangetoond.

Als de voedselbeschikbaarheid inderdaad zorgt voor zulke sterke schommelingen in de grootte van de broedpopulatie, kan men zich de vraag stellen waar dan in de "goede" jaren het surplus aan vogels vandaan komt en waar de vogels in de slechte jaren naar toe gaan. Uit ringonderzoek blijkt dat er nogal wat uitwisseling is tussen de verschillende kolonies in Europa; veel meer dan bij veel andere sternensoorten. Zo was een belangrijk deel van de Grote Sterns op Griend (~23%) in de jaren negentig afkomstig uit andere kolonies. De Griendse populatie stond in nauw contact met die in het Deltagebied, maar ook met kolonies in België, Groot-Brittannië en Denemarken. Tot nu toe is het nomadische karakter van de Grote Stern sterk onderschat. Aan het einde van de twintigste eeuw was de Europese populatie ongeveer even groot als 1950. De verspreiding over de verschillende landen was echter sterk veranderd en de Nederlandse populatie was beduidend minder dominant dan in de jaren vijftig. Uit de recente ontwikkeling (1969-heden) van de verschillende Europese populaties blijkt dat de populaties in de oostelijke en zuidelijke Noordzee (het Kanaal, België, Deltagebied, Nederlandse Waddenzee en Duitse



Figuur 3. Relatie tussen het aantal haringen en sprot gevangen tijdens IBTS (International Bottom Trawl Survey) in de zuidoostelijke Noordzee (hier uitgedrukt in een haring index) en de relatieve groei van de Grote Sternenpopulatie in de Waddenzee (1989-2003) en het Deltagebied (1992-2003).

Noordzee) sterk in omvang zijn toegenomen, maar dat het aantal broedparen in de Engelse en Ierse populaties veel minder is gestegen of zelfs is afgenomen. In elke deelpopulatie werd de aantalstoename onderbroken door enkele opeenvolgende jaren waarin de groei stagneerde, waardoor een stapsgewijs groeipatroon ontstond. Dergelijke patronen duiden mogelijk op zogenaamde "regime-shifts" waarbij vrij plotseling grote veranderingen plaatsvinden in het functioneren en de samenstelling van het ecosysteem. In de Noordzee waren zulke regime-shifts merkbaar op verschillende trofische niveaus (algen, vissen, vogels en zeezoogdieren) in 1988 en in 1998. Het Noordzee-ecosysteem is echter zeer complex en het functioneren ervan wordt slechts gedeeltelijk begrepen. De laatste jaren is vast komen te staan dat luchtdrukverschillen tussen de zuidelijke en de noordelijke Atlantische Oceaan (uitgedrukt in een zogenaamde NAO-index) een sterke invloed hebben op de ecologische processen in de Noordzee. De NAO beïnvloedt het windregime, de temperatuur en de saliniteit van het zeewater in de Noordzee. Daardoor hebben schommelingen in de NAO een sterk effect op allerlei organismen in de Noordzee zowel op lagere als hogere trofische niveaus. De NAO beïnvloedt onder andere de vispopulaties in de Noordzee en ook het transport van vislarven over de Noordzee en heeft dus grote effecten op piscivore zeevogels. Voor de Grote Stern is vooral het effect op het transport van haringlarven van belang. Haringlarven geboren in de Engelse kustwateren worden onder gunstige omstandigheden (positieve NAO) ongehinderd naar de kinderkamers in de Waddenzee en het Skagerrak/Kattegat getransporteerd. In het begin van de jaren zeventig – dus net na het ineenstorten van de Nederlandse populatie – bevond de NAO zich in een negatieve fase en werd het transport van haringlarven gehinderd. Samen met een sterke visserijdruk op haring zorgde dat voor een zeer lage haringstand, hetgeen een verklaring kan zijn voor het trage herstel van de Nederlandse Grote Sternenpopulatie.

Rond 1985 was er een ommekeer. De NAO kwam in een positieve fase en de haringstand in de Waddenzee, de oostelijke Noordzee en het Skagerrak/Kattegat verbeterde. Tegelijkertijd verslechterde de voedselsituatie in de Engelse kustwateren door een achteruitgang van de sprotstand.

In overeenstemming met het patroon in de NAO, kwam er rond 1985 een einde aan de stagnatie van de Duitse Noordzee populatie, terwijl de populatie langs de Engelse oostkust begon af te nemen. Er bestaat een positief verband tussen de NAO en het aantal broedparen van Grote Stern in de Nederlandse Waddenzee en in Duitse Noordzee in de periode 1969-2004. Voor de andere Europese populaties werd geen verband met de NAO gevonden. Er wordt geconcludeerd dat de NAO waarschijnlijk de drijvende kracht is die zorgt voor veranderingen in de verspreiding en samenstelling van prooivissen in de Noordzee die uiteindelijk de verspreiding van Grote Sterns bepaalt. De uiteindelijke grootte van de Europese populatie wordt waarschijnlijk niet bepaald door gebrek aan broedgelegenheid, maar eerder door beperkende factoren buiten de broedgebieden. Onder andere de vangst en het doden van sterns in de Afrikaanse overwinteringsgebieden heeft een grote invloed op de Grote Stern. In de laatste decennia vond bovendien een sterke intensivering plaats van de commerciële visserij voor de West-Afrikaanse kusten die mogelijk van grote invloed is op het prooiaanbod in de overwinteringsgebied.