

LIVING WITH GULLS – TRADING OF FOOD AND PREDATION IN THE SANDWICH TERN *STERNA SANDVICENSIS*

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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 the 1960s, the size of the Dutch population positively correlated with the amount of young herring present in the North Sea (Brenninkmeijer and 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 57ha 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 and 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 25km 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 (Brockmann 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 and 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 postfledging 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 and 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 Palearctic terns as well as local tern species. The different feeding strategies of Little Tern *S. albigrons*, 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.