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Temporal and spatial pattern of common tern (*Sterna hirundo*) foraging in the Wadden Sea

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Abstract. In 1989, 313 foraging flights of common terns in the Wadden Sea were radio-tracked. The feeding trips lasted on average 115 min covering about 30 km per flight. Completely tracked flights had a mean radius of 6.3 km. The terns preferred distinct foraging areas in the Wadden Sea. These were visited at site-specific phases of the tidal cycle resulting in a temporal and spatial pattern of foraging, caused by the site-specific and tide-related fluctuations of food availability.

Key words: *Sterna hirundo* – Foraging flights – Wadden Sea – Foraging areas – Tides.

In the Wadden Sea the tides are a dominating factor of life, periodically flooding or draining vast areas, mainly the tidal flats. The tides thus control the availability of food for many bird species feeding in the Wadden Sea, not only waterfowl and waders but also seabirds. In gulls feeding on tidal mudflats the timing of foraging flights and foraging activity, the numbers present at the colony site and the nest reliefs all depend on the tides (Drent 1970; Veen 1977; Gorke 1990; Noordhuis and Spaans 1992). The foraging of fish-eating species such as the common tern (*Sterna hirundo*) or the Arctic tern (*Sterna paradisaea*) is also related to the tides. Flight activities (Boecker 1967; Dunn 1972; Mes and Schuckard 1976; Becker et al. 1991a), nest reliefs (Frank and Becker 1992), feeding rates and food composition (Frank 1992) and the body condition of young and adults (Becker and Specht 1991; Frank and Becker 1992) show tidal rhythms.

As feeding seabirds are difficult to observe, however, information on the spatial pattern of foraging that shows its dependence on the tides is scarce. These methodological problems can be overcome by radiotracking which was used successfully for the common tern (Becker et al. 1991b). In this paper we present data on the temporal and spatial pattern of common tern foraging flights and their correlations with the tides in the Wadden Sea.

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Study area and methods

In 1989 we studied common terns nesting in about 2,000 pairs on the Wadden Sea island Minsener Oldeoog on the German North Sea coast (53.46° N, 8.01° E, Fig. 1). Twelve terns – only one of each pair – were caught during incubation and tagged with radiotransmitters weighing about 8 g. From 14 June to 4 July the tagged terns were radiolocated for an average of 10 days per bird from sunrise to sunset (the length of day is relatively constant during midsummer), resulting in 313 documented foraging flights. Bearings were taken from two towers 4 km apart (for methods see Becker et al. 1991b). The transmitters had no measurable effect on behaviour, food intake and body mass of common terns (Becker et al. 1991b; Klaassen et al. 1992).

To describe the foraging flights of the tagged birds, we distinguished (1) the time between departure and return to the colony, defined as "flight duration"; (2) the time spent at a distinct feeding area, defined as "presence" in this area; (3) any continuous visit at one area was defined as "occurrence" irrespective of its duration. In the course of one foraging flight various feeding areas could be visited.

The bearings were plotted on a map. To calculate the foraging radius we used 91 completely tracked flights. In some examples we also measured flight distance, which has to be regarded as minimum as all triangulations were made to an accuracy of $\pm 1°$ and shorter movements of about 50–100 m could not be detected. The average distance of the foraging flights was estimated using the minimum power flight speed (outgoing and return flight), calculated as 5.8 m/s (=21 km/h) after Pennycuick (1989) for 50% of the flight time, and half that speed (foraging) for the other 50%.

Most flights were documented during incubation or chick rearing. We pooled the data, however, as no differences were found between the stages in the preference for and in the presence at specific foraging areas or the tidal pattern of foraging. Non-parametric Wilcoxon or Wilcoxon-Wilcox tests were used to test for significant differences ($P \leq 0.05$, two-tailed tests for related samples).

Results

Foraging areas

The frequency of visits by common terns differed between the five areas in the vicinity of the colony site (Fig. 1,

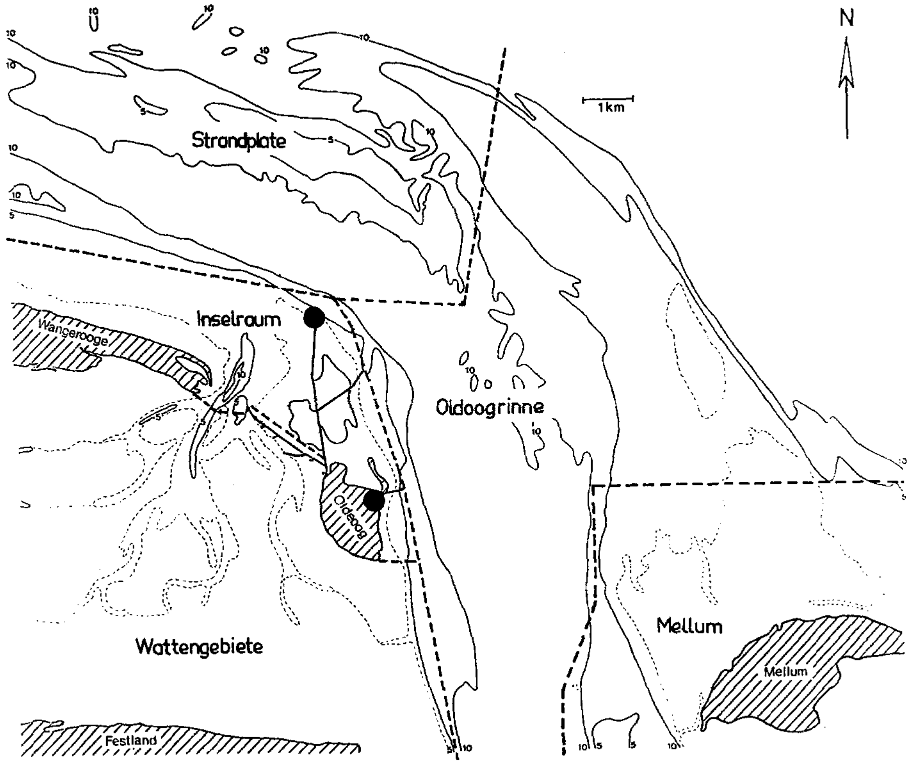

Fig. 1. Location of the five foraging areas in the vicinity of the common tern colony site Minsener Oldeoog, German Wadden Sea. The areas (*thick dashed lines*) are defined according to geographical and hydrogeological characteristics: two areas of mainly tidal flats (Wattengebiete, Mellum), one deep water area with a water depth of 20 m at maximum (Oldoogrinne), one area with water depth of 5 m at maximum (Strandplate) and one heterogeneous area including the islands (Inselraum). "*Festland*": mainland coast. *Lines*: 5 and 10 m water depth; *fine dashed line*: low water level. *Dots* mark the towers used for radiotracking. The colony was situated at the southern tower

Table 1). The areas Strandplate and Wattengebiete (tidal flats) were preferentially used for foraging. This is confirmed by the individual foraging flights of the tagged terns, which are given in Table 1 for birds during incubation, the stage with sufficient data for most individuals. Of the eight terns six predominantly used the Strandplate or the tidal flats. Five birds used both areas (together more than 58% of the flights). Nevertheless individual differences were obvious: e.g. compared to other terns some adults frequently flew to Mellum (most obviously # 22 and 91). On the way they possibly also used the southern part of the Oldoogrinne for foraging, thus increasing the share of use of this area.

Table 1. Use of the foraging areas (Fig. 1) by the radio-tagged terns during the breeding season 1989 (percent of total visits)

	n	Strand-plate	Oldoog-rinne	Insel-raum	Watten-gebiete	Mellum
Total	464	31.0	18.4	14.1	28.5	8.0
#01	46	12.0	13.0	15.2	**45.8**	13.0
#21	13	**38.5**	23.1	15.4	7.7	15.4
#22	17	23.5	**35.3**	11.8	5.9	23.5
#03	20	**50.0**	10.0	15.0	25.0	0.0
#05	31	25.8	9.7	22.6	**32.3**	9.7
#08	35	**44.4**	8.3	22.2	16.7	8.3
#91	27	25.9	25.9	3.7	14.8	**29.6**
#10	13	30.8	0.0	23.1	**46.2**	0.0

For incubation, data are individually presented in adults with ≥10 documented visits. The preferred areas are given in bold

Flight duration and presence at the foraging sites

The duration of 313 completely documented trips was from 10 to 563 min, on average 115±94 min (median 101 min). So the range covered very short flights as well as those lasting more than 9 h, which however were very rare. Foraging trips directed to only one feeding area show that flight durations to the Inselraum (islands) and Oldoogrinne were far shorter than those to other areas (Table 2). The greater distances to Mellum and Strandplate resulted in flights longer than those to the Wattengebiete nearby. Differences between the areas Strandplate and Oldoogrinne were significant ($P<0.05$, Wilcoxon-Wilcox test for 5 terns documented sufficiently, means 124 and 53 min, respectively). The presence at Strandplate and Wattenge-

Table 2. Duration (min) of flights to the five foraging areas (Fig. 1; n = number of flights)

	Strand-plate	Oldoog-rinne	Insel-raum	Watten-gebiete	Mellum
Mean ± SD	138±84	37±52	48±49	94±87	114±96
Min–Max	20–393	10–277	10–128	10–371	24–439
Median	119	21	20	57	94
n	70	29	10	77	19

Table 3. Presence (min) at the five foraging areas (Fig. 1; n = number of visits)

	Strand-plate	Oldoog-rinne	Insel-raum	Watten-gebiete	Mellum
Mean ± SD	59 ± 58	37 ± 11	23 ± 22	52 ± 52	88 ± 56
Min–Max	5–345	5–90	5–135	5–304	20–256
Median	38	14	15	35	82
n	116	75	59	110	22

biete was twice as long as at Oldoogrinne and Inselraum (Table 3). On Mellum the terns stayed twice as long as in the aforementioned regions (medians).

A total of 91 completely tracked foraging trips had a mean foraging radius of 6.3 ± 2.4 km. The real foraging radius should be somewhat greater, because in 38 flights (12% of all) contact was lost while the birds headed directly to areas too far away for triangulation. As they also returned from this direction we suppose that the foraging areas were also situated in this direction, but the birds were out of range of the receivers during the time when no signals were received.

On the shortest trips the terns covered a distance of 6 km, on the longest more than 70 km. Using the mean flight duration of 115 min and the estimated flight speed of 4.35 m/s (= 16 km/h), the average flight distance was about 30 km. In case of 15 selected well-documented flights the result of this calculation (29 ± 19 km during 110 ± 74 min) corresponded well to the measured flight distance (26 ± 16 km).

Relation to the tides

No diurnal pattern of the use of the foraging areas was found, but there was a distinct correlation with the tidal cycle. Figure 2 shows the preference for certain phases of the tidal cycle. It is obvious that the area Strandplate is visited some time later on each consecutive day, whereas the relation to the tide remains constant. The terns were foraging mainly during the flood in this area. On more extended foraging-trips the terns visited two or three foraging areas successively, each during the site-specific optimum of the tidal cycle.

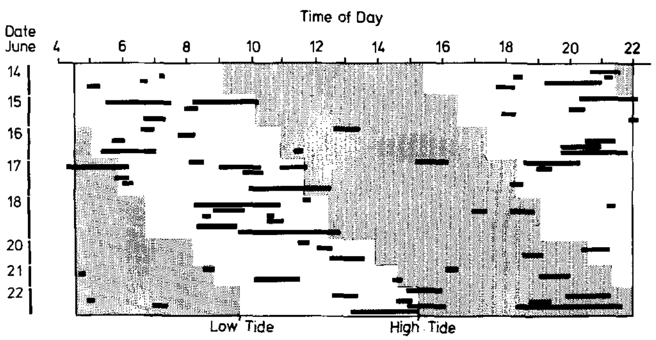

Fig. 2. Presence of tagged common terns at the foraging area Strandplate (Fig. 1) from 14 to 22 June 1989 during daylight (daytime = CEST; 19 June without data). Every *line per day* represents one radio-tagged tern. *Darker area* = ebb

In contrast to the Strandplate which was preferentially visited during flood (Fig. 3; hours +1 to −6 vs. others, Wilcoxon test: $Z = -2.223$, $n = 11$ birds, $P < 0.05$), the Wattengebiete were selected during the first 4 h of the outgoing tide (hours −6 to −3 vs. others, Wilcoxon test: $Z = -2.756$, $n = 11$, $P < 0.01$) and Mellum during ebb (hours −6 to +1 vs. others, Wilcoxon test: $Z = -2.666$, $n = 11$, $P < 0.01$). The two remaining areas both were frequented equally at all tidal stages. The tide-related pattern of use of the regions Strandplate and Wattengebiete differed conspicuously (Strandplate/Wattengebiete: hours +1 to −6, Wilcoxon-test: $Z = -2.134$, $n = 11$, $P < 0.05$; other hours: $Z = -1.689$, $n = 11$, $P > 0.05$; hours −6 to −3: $Z = -2.401$, $n = 11$, $P < 0.05$; other hours: $Z = 2.487$, $n = 11$, $P < 0.05$). The area Strandplate was visited most frequently during flood; after high tide nearly all terns left it. At the Wattengebiete most terns arrived in the hours 5 and 4 before low tide and the majority flew off an hour later. Immediately before high tide almost no terns could be found there. Mellum was not frequented at all during the hour before high tide.

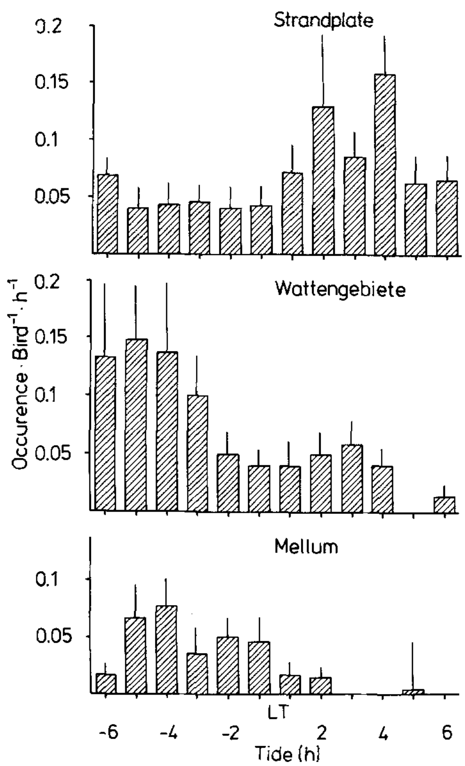

Fig. 3. Occurrence of the radio-tagged common terns at three foraging areas (Fig. 1). Given are the mean numbers of visits per bird and hour in relation to low tide. Only birds with at least 5 visits were considered

Discussion

In the course of a foraging trip the terns spent different amounts of time at the various feeding areas (Table 2, 3). Their presence at the regions of Oldoogrinne and Inselraum was shorter than at the mainly frequented regions Strandplate and Wattengebiete. Therefore these latter areas should be considered as the main foraging areas of the common terns, whereas both first-mentioned areas seemed to be transit areas, where less intense foraging took place. Here food was available only sporadically, e.g. when fish were eddied up by ships. The fifth feeding area, Mellum, was used less often, and the terns spent by far the most time there.The flight course to and especially back from a foraging area was rectilinear and performed at high speed (for examples see Becker et al. 1991b). The terns leave a foraging area immediately after catching food successfully to fly back to the colony site, where they have to relieve the incubating mate (Becker and Frank 1990; Frank and Becker 1992) or to feed their chicks. In this context the Wattengebiete, used before low water, were characterized by the terns' shortest flight duration and presence of all the feeding areas. This indicates that feeding at the tidal flats takes less time than at Strandplate or Mellum (see also below).

The feeding range of common terns in the Wadden Sea around Minsener Oldeoog corresponds to that documented at other sites (3–20 km: Bauer 1965; Boecker 1967; Pearson 1968; Erwin 1977; Nisbet 1983; Duffy 1986; Glasmacher 1987). As during incubation a common tern makes on average four feeding flights per day (Sudmann and Becker 1992), it flies a distance of about 120 km per day.

The timing of seabirds' daily foraging trips in the Wadden Sea may be influenced by two periodical processes. A diurnal rhythm with more frequent foraging flights in the morning and evening is described in the common tern e.g. by Mes and Schuckard (1976), Mes et al. (1978), Morris (1986), Frank (1992) and Frank and Becker (1992). Tidal periodicity has also been observed repeatedly, but the maximum of departures or arrivals was found by Mes and Schuckard (1976) and Frank and Becker (1992) during receding tide, whereas Boecker (1967) and Dunn (1972) observed maxima not only before but also after low tide. According to our study the tides mainly affect the choice of the foraging area, which causes a special flight activity pattern to appear at the nesting ground. The tides take effect by periodically producing certain environmental conditions at defined places, as distinct water levels, currents or turbidity (e.g. Boecker 1967; Becker and Specht 1991), which result in changes in the availability of prey organisms to the terns. The tidal dependence of the foraging conditions for common terns varies between the foraging areas, summing to a colony site-specific tidal rhythm of foraging activity, which might be different between various regions of the Wadden Sea and from year to year (Frank and Becker 1992).

The tide-induced choice of a specific feeding area results also in a tidal pattern of the diet composition (Becker et al. 1991a; Frank 1992). In 1986, sandeels *Hyperoplus lanceolatus* were fed more frequently to the chicks after low tide, whereas clupeids were fed most around high tide (Frank 1992). The preference for the deep water areas of Strandplate during flood in our study suggests that sandeels are caught especially here. Via the amount and quality of food taken, the tides also influence the terns' body condition. Frank and Becker (1992) found highest body mass of adult common terns during ebb, when the birds in 1989 came back mainly from the Wattengebiete (Fig. 3). The duration of absence for feeding and the body mass of adults and chicks are correlated also with the tide-dependent change in the daily span of time favourable for feeding (TFO-DH, Becker and Specht 1991; Frank and Becker 1992), so that the tides have effects on the terns reproductive output. Therefore, it is important to parent terns to reduce their dependence on the fluctuating food availability due to the tides, to keep the food intake and chick provisioning rates as constant as possible.

The tide-orientated foraging pattern in the Wadden Sea is the strategy of common terns to achieve this and to maximize feeding rate. It indicates a marked memory for the availability of food changing with site and time. Such knowledge is of great importance for reproductive output and fitness. The different quality of common tern breeders (Becker and Finck 1985; Frank 1990) and the significance of age and experience (Nisbet et al. 1984) may be the consequence of individual variation in the ability to gain experience of food availability under varying environmental conditions. The actual knowledge is the result of past and present experience (e.g. Kacelnik and Krebs 1985). The present experience of common terns may be achieved during the pre-laying and incubation period, when much time is available for foraging for both mates compared to the chick-rearing period, when feeding flights are more frequent and shortened in duration (Sudmann and Becker 1992) to achieve a high rate of feedings to the young. The past experience originates from gathering knowledge of the food situation over many breeding periods, possible in long-lived species like terns and other seabirds. The site-specific knowledge of food availability and of energetic consequences of different diets for body condition (Pierotti and Annett 1987; Massias and Becker 1990; Becker et al. 1991a) will be improved by using the same breeding area year by year which is the rule in terns (McNicholl 1975). Thus the advantage of enhanced knowledge of the food situation at one site might have been one of the factors for the evolution of site tenacity, which is common in many long-lived seabird species.

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References

Bauer K (1965) Zur Nahrungsökologie einer binnenländischen Population der Flußseeschwalbe (*Sterna hirundo*). Egretta 8: 35–51

Becker PH, Finck P (1985) Witterung und Ernährungssituation als entscheidende Faktoren des Bruterfolgs der Flußseeschwalbe (*Sterna hirundo*). J Ornithol 126: 393–404

Becker PH, Frank D (1990) Kontinuierliche Wägung brütender Seevögel zur Analyse der Ernährungssituation. In: Van den Elzen R, Schuchmann K-L, Schmidt-Koenig K (eds) Current

Topics in Avian Biology. Proc. Int. 100. DO-G Meeting Bonn 1988: 173–179

Becker PH, Specht R (1991) Body mass fluctuations and mortality in Common Tern *Sterna hirundo* chicks dependent on weather and tide in the Wadden Sea. Ardea 79: 45–56

Becker PH, Baum I, Marsh S-L (1991a) Warum wechseln Flußseeschwalben zwischen Nahrungsquellen im Wattenmeer und Binnenland? Verh Dtsch Zool Ges 84: 299–300

Becker PH, Frank D, Sudmann SR, Wagener M (1991b) Funkpeilung von Flußseeschwalben (*Sterna hirundo*) bei der Nahrungssuche im Wattenmeer. Seevögel 12: 52–61

Boecker M (1967) Vergleichende Untersuchungen zur Nahrungs- und Nistökologie der Flußseeschwalbe und der Küstenseeschwalbe. Bonn Zool Beitr 18: 15–126

Drent RH (1970) Functional aspects of incubation in the Herring Gull. In: Baerends GP, Drent RH (eds): The Herring Gull and its egg. Behaviour Suppl 17, pp 1–132

Duffy DC (1986) Foraging at patches: interactions between Common and Roseate Terns. Ornis Scand 17: 47–52

Dunn EK (1972) Studies on terns with particular reference to feeding ecology. D Phil thesis, University of Durham

Erwin RM (1977) Foraging and breeding adaptations to different food regimes in three seabirds: the Common Tern, *Sterna hirundo*, Royal Tern, *Sterna maxima*, and Black Skimmer, *Rynchops niger*. Ecology 58: 389–397

Frank D (1990) Fütterrate und Nahrungszusammensetzung von Flußseeschwalben (*Sterna hirundo*) anhand automatischer Registrierung am Nest. In: Van den Elzen R, Schuchmann K-L, Schmidt-Koenig K (eds) Current Topics in Avian Biology. Proc Int 100. DO-G Meeting Bonn 1988: 159–165

Frank D (1992) The influence of feeding conditions on food provisioning of chicks in Common Terns *Sterna hirundo* nesting in the German Wadden Sea. Ardea 80: 45–55

Frank D, Becker PH (1992) Body mass and nest reliefs in Common Terns *Sterna hirundo* exposed to different feeding conditions. Ardea 80: 57–69

Glasmacher M (1987) Nisthilfen für eine niederrheinische Flußseeschwalbenpopulation (*Sterna hirundo*). Charadrius 23: 183–199

Gorke M (1990) Die Lachmöwe (*Larus ridibundus*) in Wattenmeer und Binnenland. Seevögel 11: 1–48

Kacelnik A, Krebs JR (1985) Learning to exploit patchily distributed food. In: Sibly RM, Smith RH (eds) Behavioural Ecology. Blackwell, Oxford, pp 189–205

Klaassen M, Becker PH, Wagener M (1992) Transmitter loads do not affect the daily energy expenditure of nesting Common Terns. J Field Ornithol 63: 181–185

Massias A, Becker PH (1990) Nutritive value of food and growth in Common Tern (*Sterna hirundo*) chicks. Ornis Scand 21: 187–194

McNicholl MK (1975) Larid site tenacity and group adherence in relation to habitat. Auk 92: 98–104

Mes R, Schuckard R (1976) Een onderzoek naar verschillen in fourageeraktiviteit tussen Visdief *Sterna hirundo* en Noordse Stern *Sterna paradisaea* op de Engelsmanplaat (NL). (Report Nr. 11) Verslagen en Technische Gegevens Inst voor Taxon Zool, Amsterdam

Mes R, Schuckard R, Wattel J (1978) Visdieven *Sterna hirundo* zoeken koelte. Limosa 51: 64–68

Morris RD (1986) Seasonal differences in courtship feeding rates of male common terns. Can J Zool 64: 501–507

Nisbet ICT (1983) Territorial feeding by Common Terns. Colonial Waterbirds 6: 64–70

Nisbet ICT, Winchell JM, Heise AE (1984) Influence of age on the breeding biology of Common Terns. Colonial Waterbirds 7: 117–126

Noordhuis R, Spaans AL (1992) Interspecific competition for food between Herring *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus* in the Dutch Wadden Sea area. Ardea 80: 115–132

Pearson TH (1968) The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J Anim Ecol 37: 521–552

Pennycuick CJ (1989) Bird flight performance. Oxford University Press

Pierotti R, Annett C (1987) Reproductive consequences of dietary specialization and switching in an ecological generalist. In: Kamil AC, Krebs JR, Pulliam HR (eds) Foraging behavior. Plenum Press, New York London, pp 417–442

Sudmann SR, Becker PH (1992) Zeitaufwand für die Nahrungssuche von Flußseeschwalben (*Sterna hirundo*) während der Brut- und Huderphase. J Ornithol 133: 437–442

Veen J (1977) Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna s. sandvicensis Lath.*). Behaviour Suppl 20: 1–193