To eat or to feed? Prey utilization of Common Terns in the Wadden Sea

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ABSTRACT

Prey availability to seabirds has a profound influence on individual decisions about allocating somatic and reproductive investment. These decisions can be expressed in foraging behaviour and prey utilization and have consequences for establishing relationships between changes in the fish populations and responses in seabird breeding performance. We report here results of an unusual opportunity to investigate the relationships between fish abundance and at-sea foraging behaviour, prey utilization and food provisioning of partners and chicks of Common Terns *Sterna hirundo* breeding in the German Wadden Sea. High quality prey was carried out of the foraging area disproportionately often, while almost all low quality prey items were ingested by the foraging adult bird itself. Proportions of prey being used for provisioning were more similar to prey being carried out of the foraging area than to prey caught. The preferential utilization of high quality food for provisioning suggests that large proportions of low quality food being delivered to the colony may indicate a shortage of high quality food and, consequently, poor prospects of good breeding performance. Moreover, seabirds feeding whole, undigested prey items may indicate a higher abundance of high quality fish in the sea, due to selecting high quality prey for provisioning. This may result in overestimating the abundance of high quality prey fish when calculated from colony-based diet studies of single-loading seabird species such as terns alone.

Keywords: Foraging behaviour, prey utilization, central place foraging, Common Tern, Wadden Sea, prey quality, feeding observations

ZUSAMMENFASSUNG

Fressen oder verfüttern? Beutenutzung von Flussseeschwalben *Sterna hirundo* im Wattenmeer

Die Beuteverfügbarkeit für Seevögel hat eine zentrale Bedeutung für die individuelle Entscheidung, ob die verfügbare Energie in das eigene Überleben oder die Reproduktion investiert wird. Diese Entscheidungen werden u.a. in Jagdverhalten und Beutenutzung manifest, was sich wiederum auf die funktionelle Beziehung zwischen den Beutepopulationen, dem Brutverlauf und der Kükenaufzucht der Seevögel auswirken kann. Basierend auf direkten Beobachtungen beschreibt der vorliegende Artikel die Beziehung zwischen der Fischabundanz und dem Jagdverhalten auf See, der Beutenutzung sowie der Balz- und Kükenfütterung bei Flussseeschwalben *Sterna hirundo* im deutschen Wattenmeer. Qualitativ hochwertige Beute wurde überdurchschnittlich oft aus dem Jagdgebiet in die Kolonien getragen, während nahezu alle Beuteorganismen von geringer Qualität vom jagenden Altvogel selbst konsumiert wurden. Die relativen Anteile verschiedener Beutetiere an der Balz- und Kükennahrung stimmten besser mit der aus dem Jagdgebiet abtransportierten Beute überein als mit der Beute, die insgesamt gefangen wurde. Die bevorzugte Nutzung hochwertiger Beute für die Balz- und Kükenfütterung impliziert, dass große Anteile von qualitativ minderwertiger Beute in der Kolonie einen Mangel an hochwertiger Beute und somit schlechten Aussichten auf einen hohen Bruterfolg anzeigen können. Unsere Ergebnisse zeigen des weiteren, dass die Abundanz energetisch hochwertiger Fischarten im Meer überschätzt werden könnte, wenn diesen Abschätzungen koloniebasierte Fütterungsbeobachtungen von Seevögeln zugrunde liegen, die hochwertige Beutetiere bevorzugt an ihre Partner und Küken verfüttern.

INTRODUCTION

Seabirds have proven utility as indicators of change in their marine environment. This is due to their apical position in food webs and their colonial breeding, making it relatively easy to study their diet, demography, physiology and breeding performance (Cairns 1987; Montevecchi 1993; Becker 2003; Boyd et al. 2006; Piatt and Sydeman 2007). These favorable circumstances have stimulated a number of seabird diet studies drawing inferences about changes in fish populations (e. g. Aebischer et al. 1990; Davoren and Montevecchi 2003; Barrett 2007). Supplementing colony-based investigations (Duffy and Jackson 1986; Barrett et al. 2007) with information on fish abundance (e. g. Grémillet et al. 2004; Barrett 2007; Dänhardt and Becker 2008) is required to establish a link between seabird responses and their food supply. Seabird characteristics can be reliably calibrated with the spatial and temporal changes in their fish populations, when only one or few fish species are utilized and when there are only few prey alternatives. For example, the diet and breeding success of Black-legged kittiwakes *Rissa tridactyla* breeding in the northern North Sea is closely correlated with sandeel *Ammodytes marinus* abundance (Furness 2002, 2006; Frederiksen et al. 2004). This correlation is even the basis of the sandeel management rule in ICES sub-area IV, that the local fishery is closed when on average less than 0.5 kittiwake chicks fledge for three consecutive years (ICES 2002).

The trophic levels of the fish populations in the sea and the seabirds in the colony are linked via the actual process of foraging, which may not always be proportional to prey abundance as in the example above. Seabirds forage beyond the colonies, and they adjust their foraging behaviour immediately to a changed food situation (Walter and Becker 1998; Schwemmer et al. 2009), the presence of adequate prey alternatives provided. A behavioural response is thus regarded the most direct and useful indicator of food supply (Monaghan 1996). At the same time, foraging behaviour is most difficult to study, because it requires predictable foraging events that can be accessed by the observer. These conditions are usually not met due to the foraging range of most seabird species being too large to be systematically surveyed. To meet these methodological challenges, techniques to obtain *indirect* measures of seabird behaviour while away from the colony have been developed and applied (Becker et al. 1993; Burness et al. 1994; Weimerskirch, 1998; Daunt et al., 2003; Elliott et al., 2008), whereas *direct* observations (Walter and Becker 1998) of foraging behaviour at sea are still very rare (Davoren and Burger 1999), especially in surface-feeding seabird species (Taylor 1979).

To maximize energetic investment in reproduction, colony-breeding single loaders such as terns are predicted to bring only large and energy-rich prey items to their partners or chicks. This concept, known as the central place foraging theory (Orians and Pearson 1979), implies that the relationship between prey abundance and a given seabird characteristic measured inside the colony may be biased due to individual decisions during foraging. This has been demonstrated by means of direct observations of Roseate Terns *Sterna dougallii* (Shealer 1998) and Common Terns *Sterna hirundo* during courtship (Taylor 1979). Terns are among the few seabird species that allow for direct observations at sea due to their limited foraging range around their breeding colonies (Taylor 1979; Becker et al. 1993; Schwemmer et al. 2009).

Using the framework of the central place foraging theory (Orians and Pearson 1979), we present an integrated analysis of local fish abundance, foraging behaviour and prey utilization of Common Terns in their foraging areas at sea and, eventually, of the prey organisms being fed to partners or chicks in one of the largest breeding colonies in the German Wadden Sea.

MATERIAL & METHODS

Between May and July 2007 foraging behaviour of Common Terns was observed around the island Minsener Oog (53° 45'N 008° 01'E) in the National Park Lower Saxon Wadden Sea in northern Germany. Minsener Oog is one of the most important breeding sites of terns and larid gulls in the German Wadden Sea, hosting 197 breeding pairs of Common Terns in 2007. Feedings of partners and chicks were observed in the breeding area in synchrony with the foraging observations. To provide information on the prey composition and abundance, stow net catches (Dänhardt & Becker 2010) were carried out close to the island (Fig. 1).

→ Figure 1

Observations of feeding flocks and foraging behaviour

In order to ensure successful foraging observations, the foraging locations of the terns had to be identified. Feeding aggregations were located from two elevated observation sites in the north and in the south of the island, respectively, using binoculars (Minox 10 x 42) and a scope (Leica 20 x 80). Feeding flocks could be reliably tracked within a range of ≤ 3 km around each observation point. Two locations close to the island turned out to be recurrently and predictably utilized for foraging by the Common Terns for at least 30 minutes: One at the southeast end at the confluence of two tidal channels, and another off the northwest shore of the island, being confined to the north by a stony breakwater (Fig. 1). Common Terns breeding on Minsener Oog utilize a wide range of foraging areas, but these two locations represented one of two main foraging sites that had earlier been identified by means of radio-telemetry ("Wattengebiete", Becker et al. 1993). The feeding areas were easily accessed either walking or by boat and could be approached close enough for reliable identification of behaviour and prey items (≤ 30m). Feeding flocks consisted of 15 individuals on average, below a minimum of 5 individuals observations were discontinued.

To ensure correct and consistent identification of prey items during the foraging and feeding observations at Minsener Oog, observers were trained at another Common Tern colony (Banter See, Wilhelmshaven, for details see Becker 1996) with convenient observation conditions and with breeding phenology being two weeks ahead of Minsener Oog. At Minsener Oog, observations of foraging behaviour were carried out weekdays five times a week, using binoculars (Minox 10 x 42). Individual Common Terns were randomly selected from the foraging flock and their behaviour was tracked for exactly one minute. On any given observation day 25 observations of one minute each were carried out in each of the two foraging areas, unless weather conditions or breakup of foraging flocks terminated the observations before 25 minutes of individual tracking were completed. Between May 3rd and July 28th the observation effort amounted to 597 minutes and 935 minutes in the foraging areas northwest and southeast of Minsener Oog, respectively (Fig. 1).

During both foraging and feeding observations, prey items were identified to the lowest possible taxonomic level. Herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and twaite shad (*Alosa fallax*) could not be distinguished and were thus summarized as clupeids. Plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and sole (*Solea solea*) were noted as flatfish. Whiting (*Merlangius merlangius*) and cod (*Gadus morhua*) were recorded as gadids; identification of squid, gobies (*Pomatoschistus spec*.), pipefish (*Syngnathus spec*.) and sandeel (*Ammodytes spec*. or *Hyperoplus spec*.) was also not possible down to species level. Judging from the stow net catches, where species identification was always carried out except for gobies, clupeids were mainly herring, flatfish were mainly plaice, gadids were mainly whiting, pipefish were mainly Nilsson's pipefish (*Syngnathus rostellatus*) and sandeel were mainly lesser sandeel (*Ammodytes tobianus*). Brown shrimp (*Crangon crangon*), eelpout (*Zoarces viviparus*), hooknose (*Agonus cataphractus*) and smelt (*Osmerus eperlanus*) could be identified to species level. If identification was not possible, prey items were recorded as 'unidentified'. In addition to the identification of the prey it was noted if the item was consumed by the successful forager itself or if the prey was carried away.

Prey group-specific length differences, as examined in earlier studies (e. g. Taylor 1979), were not considered, because the length range of the majority of prey items observed was smaller than the potential bias inherent to length comparisons based on average bill length (Duffy and Jackson 1986; Barrett et al. 2007).

Observations in the colony

Starting in the middle of May, clutches and eggs were counted every other day in a colony in the north of Minsener Oog, representing the majority of Common Tern breeding pairs on the island (Fig. 1). From the beginning of June chicks were regularly counted. Feeding observations were carried out during a total of 47 hours in May, 63 hours in June and 44 hours in July. Feeding observations were synchronized with the foraging observations described above. Feedings of partners and chicks were observed in units of two hours. Prey eaten by partners or chicks was identified as described above. Courtship feedings were observed between May 13^{th} and June 13^{th}. Eggs were present after May 22^{nd}; first chicks were observed on June 11^{th}. All chicks died during a storm flood on June $27^{th}/28^{th}$. After that, partner feedings were again observed. Accordingly, observations of foraging (May 3^{rd} – June 13^{th}) and partner feedings (May 13^{th} – June 13^{th}) are subsequently referred to as “courtship 1”, referring to both courtship feedings in the colony and provisioning of incubating females. The category courtship 1 also included prey caught and delivered to partners before colony formation. Prey captured and fed between June 14^{th} and June 27^{th} is labeled “chicks”; foraging and feeding observations were noted as “courtship 2” from June 28^{th} until July 28^{th}.

Stow net fisheries

To account for the terns’ prey supply, stow net catches were conducted at a fixed sampling station located in the immediate vicinity of both foraging areas and breeding sites of the Common Terns (Fig. 1). Stow nets are passive catching gear operated from an anchoring vessel, utilizing the water movement as encountered in rivers or in tidally influenced marine areas such as the Wadden Sea. This gear is largely unselective and thus representative especially of pelagic fish (Breckling and Neudecker 1994; Dänhardt and Becker 2010), the terns’ main prey. Stow net catches were timed to represent prey composition during the breeding periods described above. The fishing campaigns took place on May 23^{rd}, June 19^{th} and July $9^{th}/10^{th}$ and were assumed to represent prey availability during the different periods within the terns’ breeding season (see results section). Haul duration was 45 ± 5 minutes. The stretched mesh size decreased from 40 mm close to the mouth to 10 mm in the cod end. Water flow was recorded by means of four propeller flow meters (Hydrobios, Kiel). Absolute catch numbers were normalized to individuals caught per 10 000 m^3 filtered water volume by

$$No_{10000}=No_{absolute} / (FC_{End} - FC_{Start} \times 0.3 \times Net_{Height} \times Net_{Width}) \times 10000$$

with No_{10000} = Fish numbers per 10000m³ fished water volume, $No_{absolute}$=Absolute fish numbers, FC_{End} = Flowmeter count at the end of a haul, FC_{Start} = Flowmeter count at the start of a haul, 0.3 = meters per rotation of the propeller flowmeter (value provided by manufacturer), Net_{Height} = Net height in m (varying with the current pressure), Net_{Width}= Net width in m (constant). The catches were sorted by species and individuals were counted. Species that occurred in the stow net catches but were not utilized by the terns were excluded from subsequent analyses.

Statistics

The approach of the present paper mostly required comparisons of proportions. Thus, only non-parametric tests were applied. The similarity between the composition of stow net catches, the prey items caught, eaten and carried away by the foraging terns and the feeding observations was quantified using Renkonen's percentage similarity coefficient (Renkonen 1938; Wolda 1981; Krebs 1999), ranging from 0 (no similarity) to 100 (complete similarity). The index is expressed in percent (Krebs 1999).

Prey items were classified to be of high or low quality according to their potential energy yield per unit foraging effort to the terns. This classification was based on information on specific energy content (Massias and Becker 1990; Hislop et al. 1991; Pedersen and Hislop 2001; Harris et al. 2008; Fischer unpublished data), determining whether a prey item can be profitably utilized by the terns. Clupeids, gadids, gobies, sandeel and squid were classified high quality items, brown shrimp, pipefish, flatfish and hooknose were classified low quality items. Smelt and eelpout were not considered, because only single individuals were recorded. Differences in the distribution of proportions of high and low quality prey items were tested for significance using cross tables and subsequent chi²-tests. Test results were not considered, if more than 20% of the cells of the respective cross table were allocated an expected frequency of less than 5. A sequential Bonferroni test was performed to adjust significance levels according to an assumed experimentwise type I error rate of 5% (Sokal and Rohlf 1995).

All tests were carried out two-sided and were considered significant at $p<0.05$.

RESULTS

Composition of stow net catches and tern prey

In the stow net samples all prey items could be identified. Herring was by far the most numerous species in all months, followed by Nilsson's pipefish in May and brown shrimp and gadids in July. All other items, including sandeel, were present in proportions of 1% or less. Eleven classes of tern prey were identified. In order of decreasing percentage, clupeids, pipefish, brown shrimp, gadids and gobies were dominant integrated over the whole season but with variable weighting within the single breeding periods (Table 1). Despite their numerical dominance in the stow net catches, only one half to one third of prey caught by the terns was clupeids. Sandeel was not observed to be caught, but appeared in the feeding observations. The remaining five prey classes eelpout, flatfish, hooknose, smelt and squid were caught by the terns only occasionally and in low numbers. They were thus summarized as 'others'. Of all prey items caught 3–10% could not be identified (Table 1).

→ Table 1

Prey utilization

The different prey classes were consumed in the same proportions as they were caught, both during the single breeding periods and integrated over the whole season. Of all consumed prey items 3–8% could not be identified (Table 1).

Prey items carried away were made up mainly of clupeids, gadids and gobies. The exception was courtship 2, when no clupeids were carried away. The percentage of both caught and ingested clupeids decreased over the course of the breeding period from 44% in courtship 1 to 8–9% during the courtship 2 period. However, clupeids made up the largest part of the partner and chick feedings. Even though gadids were not among the most numerous species in the stow net catches, their share of prey caught, consumed and carried away increased over the course of the breeding period. This development was also seen in the feeding observations. Gobies were neither caught with the stow net in considerable numbers nor were they fed to partners (courtship) or chicks. They were observed to be caught, consumed and also carried away during both courtship periods, but not during the chick period.

In all three periods, the percentage of both pipefish and brown shrimp utilized by the terns was higher than in the stow net catches. These two prey species were mostly eaten by the adult terns themselves, even during courtship 1 and chick rearing, when pipefish and brown shrimp, respectively, were caught by the terns in highest proportions of all prey (Table 1). During courtship 1, 20% of the prey class ‘others’ was carried away. This was attributed to squid, of which 70% were carried away, even though this prey class was among the least numerous species in the stow net catches. Of all prey items carried away 7–33% were not identified (Table 1).

Among all prey items recorded in the feeding observations, clupeids, gadids and sandeel were fed in highest proportions to both partners and chicks. Clupeids and gadids were also caught, ingested and carried away by the terns from the foraging areas observed, whereas sandeels were never seen during the foraging observations and only rarely caught by the stow net. Pipefish and brown shrimp were hardly recorded in the feeding observations, which is in agreement with these species being hardly carried away from the foraging area. ‘Other’ prey items were usually not seen in the feeding observations, except for squid, which made up 4% of prey fed to partners during courtship 1. The percentage of unidentified prey ranged from 10 to 25% (Table 1).

Selection rates

Integrated over the whole season, gobies, gadids and clupeids were transported off the foraging area most often, whereas brown shrimp and pipefish were hardly ever seen to be carried away, both within the single breeding periods and integrated over the whole season. Among the three prey items carried away most often, only the share of gadids remained relatively constant throughout the season. In gobies and clupeids there were marked fluctuations in selection rates with periods when they were not carried out of the foraging area at all. Of all unidentified prey items, 17–29% were carried away (Table 2).

→ Table 2

Similarity in prey composition

Stow net catches did not match the composition of prey caught by the terns very closely, which was the case in all three periods and integrated over the entire breeding season (Fig. 2a). The terns consumed prey in the same proportions as they caught it, being expressed in > 90% similarity. This very high agreement remained constant throughout the breeding season (Fig. 2b). In contrast, similarity coefficients of prey caught vs. prey carried away were decreasing as the season progressed (Fig. 2c). A decline over the course of the season was also noted in the similarity between prey consumed and prey carried away, reaching a minimum of less than 20% during the courtship 2 period (Fig. 2d). The composition of prey carried away vs. prey fed to partners and chicks revealed the second-best match of all comparisons (Fig. 2e). The similarity between prey caught in the foraging areas and fed to partners and chicks decreased from 50% during courtship 1 to 30% during courtship 2 (Fig. 2f). In four out of six comparisons there was a tendency towards lower similarity as the season progressed with lowest similarity coefficients during the courtship 2 period (Fig. 2).

→ Figure 2

Proportion of high and low quality food

The share of high quality food was significantly greater in the stow net catches than in the prey caught by the terns in all breeding periods examined (Table 3). This was mainly attributed to the large proportion of herring (Table 1). The relative contribution of high and low quality items to prey caught and prey consumed did not differ.

A significantly greater percentage of high quality prey organisms was carried out of the foraging area compared to both prey caught and prey consumed by the forager itself (Table 3). As already indicated by the comparatively large proportions of high quality prey being carried out of the foraging area (Tables 1 and 2), prey fed to partners and chicks contained significantly more high quality items than prey caught in the foraging area (Table 3). The composition of prey carried out of the foraging area did not match that of prey fed to partners and chicks. During courtship 1, slightly less high quality items were fed than carried away and almost one quarter of all prey items fed was not identified. During the chicks and courtship 2 periods, statistical comparisons were not possible due to the low number of observations of prey being carried out of the foraging area (Table 3).

Throughout the season, the share of high quality items remained fairly constant in the stow net catches, the prey carried away and fed to partners and chicks. In contrast, there was a seasonal decline in the proportions of high quality prey caught and consumed (Table 3).

The impact of unidentified prey items on chi²-test results was subtle. After leaving them out (not shown), the expected frequency in the cells of the cross tables 'stow net vs. prey caught' and 'prey caught vs. prey consumed' did not go below 5 anymore (see Material and Methods section) and the tests revealed highly significant differences in the respective proportions of high and low quality food. In all other test results, significance patterns did not change.

→ Table 3

DISCUSSION

Methodological aspects

The division of the study period into courtship 1, chicks and courtship 2 was more or less arbitrary, because the foraging and feeding observations were not individual-based, e. g. by marking birds or by direct and uninterrupted observations between prey capture and subsequent feeding to partners (Taylor 1979) or chicks. Thus, it could not be decided, if a prey item carried away from the foraging area would be fed to the mate or to a chick. However, towards the end of courtship 1, there was only a short temporal overlap in which prey carried out of the foraging areas could have been fed to both incubating partners and chicks. Moreover, due to the abrupt termination of the chick rearing period on June 27th/28th, the periods chicks and courtship 2 could be reliably distinguished. The actual recipients of food carried out of the foraging area were thus likely to be correctly represented by the classification of the breeding periods.

The percentage of unidentified items was usually < 10%, except for those carried away during the periods chicks and courtship 2 and during the feeding observations (Table 1). The high proportions of unidentified prey being carried away suggest that it may have been mostly high quality items. Moreover, low quality prey items, such as brown shrimp and pipefish, would have been more easily identified. Nevertheless, the uncertainty about the bias brought about by unidentified prey organisms remains, which is one major disadvantage of foraging and feeding observations in the field (Barrett et al. 2007).

Foraging observations

The finding of the present study that profitable prey is carried away and fed to partners or chicks at much higher rates than low quality prey items agrees both with the literature (Taylor 1979; Shealer 1998; McLeay et al. 2009) and the predictions of the central place foraging theory (Orians and Pearson 1979). Even though fish being caught could not be followed to its final destination e. g. in the colony, there is support for assuming that fish seen being carried away was indeed brought into the colony to be fed to chicks or mates: Following radio-tracked Common Terns revealed that their flight course to and especially from the foraging areas was rectilinear and performed at high speed (Becker et al. 1991, 1993), indicating that the birds fly straight back to the colony. This is further supported by own observations during the field work of the present study (Fresemann, unpublished data), that terns left the foraging area in the majority of cases in the direction of the breeding colony. Those terns not leaving towards the colony on Minsener Oog headed either west or east, where other small colonies are located on neighboring islands (Wangerooge and Mellum). These birds may use the same foraging areas as their conspecifics breeding on Minsener Oog.

The rate at which prey was carried away during the periods chicks and courtship 2 must be interpreted with caution, since only six observations were available during each period (Table 1). However, the results matched those of the courtship 1 period as well as the literature (e. g. Taylor 1979; McLeay et al. 2009).

The two foraging locations examined in the present study represent two out of five foraging sites identified by means of radio-telemetry: "Wattengebiete" and "Oldeoogrinne", which have been the destination of 28.5% and 18.4% of foraging flights, respectively (Becker et al. 1991, 1993). Nevertheless, Common Terns have been found to utilize a wide variety of habitats within their foraging range around Minsener Oog which were located outside the area of investigation (Becker et al. 1991, 1993). However, the key finding that Common Terns select high quality prey for provisioning and tend to eat low quality prey themselves is largely independent of the overall relevance of a given foraging site. Thus it remains valid even if an area is only secondarily used for foraging. Delivering high quality prey to partners or chicks appears to be a general behavioural pattern in the Common Tern not confined to a single breeding period such as courtship (Taylor 1979), as indicated by high quality items preferentially being carried away in all three periods (Table 1). Similar results have been reported for auks (Davoren and Burger 1999) and other tern species (Shealer 1998; McLeay et al. 2009). Even when utilizing anthropogenic food sources, this pattern becomes evident, as reported by Dänhardt and Becker (2008), who found that Common Terns foraging at a cooling water outlet of a power plant carried away 28% of clupeids, 50% of smelt and 17% of gobies (high quality food; Massias and Becker 1990) as compared to 0% of flatfish, pipefish and brown shrimp, respectively (low quality food; Massias and Becker 1990).

Individual decisions what to do with a given prey item after having caught it are a trade-off between somatic (eating the prey) and reproductive (feeding the prey to partners or chicks) investment (Swihart and Johnson 1986). Despite the relatively large proportions of high quality food being carried away and fed to partners or chicks, the bulk of both high and low quality prey was eaten by the foraging tern itself (Table 1). This may have been indicative of a favorable food situation in 2007, providing a surplus of profitable food items also to the adult forager. Nevertheless, clupeids were not utilized in proportions similar to those found in the stow net catches. This may be due to prey species-specific availability changing with the tide (e. g. Becker and Specht 1991; Becker et al. 1993; Wendeln et al. 1994). Unfortunately, this aspect could not be covered by the stow net fisheries. The proportions of clupeids decreased after the courtship 1 period despite consistently high herring abundance throughout the whole breeding season (Table 1). Starting in the last quarter of June, average wind speed increased causing turbulent water surfaces, most likely exacerbating foraging conditions. In addition to a hampered visibility brought about by turbulent water surfaces (Dunn 1973), pelagic schooling fish such as clupeids may avoid turbulent water strata. Accordingly, the foraging success of the Common Terns was highest at low wind speeds with e. g. 74% of clupeids being caught at wind speeds of 1–2 Beaufort, but reduced at > 6 Beaufort (Frank 1992; Fresemann, unpublished data).

During the study period, high quality prey species were more abundant than low quality prey (Table 1), but large proportions of low quality food were caught and consumed by the foraging terns in all three periods. As with the proportions of clupeids described above, this may also be due to prey species-specific availability changing within the tidal cycle. However, the most abundant low quality prey, the pipefish, is a pelagic species and its availability to the terns is probably equal to that of clupeids. Still 10 to 60% of tern prey was pipefish (Table 1). Alternatively, utilizing low quality prey when high quality prey is available could indicate that selective foraging does not occur. Following the idea that foraging should generally be aimed at maximizing energy yield per unit foraging effort (Pyke 1984; Ydenberg et al. 1994), choosing to consume low quality prey in the presence of high quality prey suggests that Common Terns do not select prey items prior to catching them. A certain amount of energy available for foraging would go into catching low quality food, which may be energetically justified given the lower effort required to self-feed. The probability of catching high quality food could be increased by choosing foraging sites where encounter with high quality food is more likely (e. g. Becker et al. 1993; Camphuysen and Webb 1999), but the catch frequency of low quality prey may provide information to the foraging tern about the overall food situation and, as a consequence, influence its partitioning between somatic and reproductive investment.

Feeding observations

In years of poor food supply foraging trips may be longer due to lower rates of successful foraging attempts or lower rates of catching high quality food being worthwhile delivering to partners or chicks (Frank and Becker 1992; Monaghan 1996). Based on our results, it can be assumed that high quality prey will be used for provisioning disproportionately often, suggesting that the share of low quality food ending up the colony is in turn indicative of the availability of high quality food in the sea. In 2007, the overall food situation was obviously sufficient for low quality food not to be used for provisioning (Table 1). In other years, even low quality food was utilized to provision mates or chicks (Becker et al. 1987; Frick and Becker 1995; Schreiber unpublished).

The prey being used for provisioning was best reflected by the prey being carried out of the foraging area (Fig. 2e). Prey compositions would have been even more similar when sandeel was not considered. Sandeel was frequently noted in the feeding observations, but it was not caught with the stow net and it was also not observed to be caught in the foraging areas (Table 1). Sandeel inhabits the shallow sandbanks north of Minsener Oog that were neither covered by the stow net catches nor by the foraging observations. These areas are however frequented for foraging by the Common Terns (Becker et al. 1991, 1993). The increase in gadid proportions in the courtship 2 period was attributed to a whiting invasion into the Wadden Sea, reaching its maximum in the beginning of July when partner feedings were again observed (Dänhardt and Becker 2008).

Conclusions

The data presented here support the framework of the central place foraging theory. Below an (unknown) threshold when adult survival would be compromised, individual decisions by the adult terns can be viewed as a mechanism to buffer their reproductive success against environmental variability, including varying food supplies and impaired prey availability. The finding that high quality prey items are preferentially carried out of the foraging area suggests that in turn large proportions of low quality food items such as pipefish or brown shrimp being observed to be fed to partners or chicks may indicate a confined availability of high quality food and, consequently, poor prospects of good breeding performance.

The terns' phenotypic plasticity may also be a crucial aspect to consider when colony-based diet data are to be used to draw inferences about the state and abundance of fish populations being utilized by a given seabird species. Given the preferential delivery of high quality items to partners and chicks, the abundance of high quality fish in the sea would be overestimated when calculated from colony-based seabird diet studies. However, this bias due to preferring high quality prey for provisioning applies only to seabird species delivering whole and undigested prey to partners and chicks, but not to species swallowing their prey at sea and regurgitating stomach contents to partners and chicks at the colony. In these species, bias may emerge from differential digestion of body parts and tissue (Barrett et al. 2007) and prey selecting prey before catching it.

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The authors declare that they have no conflict of interest.

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FIGURE CAPTIONS:

Figure 1: Study areas on and around the island of Minsener Oog in the Lower Saxon Wadden Sea, Northern Germany. The black circle denotes the colony location where feeding observations and egg and chick counts were carried out. White circles denote two preferred foraging areas of the Common Terns breeding on Minsener Oog. The white cross denotes the location were stow net catches were obtained.

Figure 2: Percentage similarity index of prey proportions in the stow net catches (stow net), of prey caught by the terns in the foraging areas (prey caught), prey eaten by the successful forager itself (prey consumed), prey carried out of the foraging area (prey carried away) and prey fed to partners or chicks. Values range from 0 (no similarity) to 100 (complete similarity). For definitions of breeding phases see text. A) stow net vs. prey caught, b) prey caught vs. prey consumed, c) prey caught vs. prey carried away, d) prey consumed vs. prey carried away, e) prey carried away vs. prey fed to chicks and partners, f) prey caught vs. prey fed to chicks and partners.

TABLE CAPTIONS:

Table 1: Proportions (%) of the Common Terns' dominant prey items. Results from the stow net catches, the foraging observations in the feeding areas (highlighted in grey) and the feeding observations in the colonies are given. All prey proportions are presented both by breeding period (courtship 1: May 3rd – June 13th, chicks: June 14th –June 27th, courtship 2: June 28th – July 28th) and integrated over the whole breeding season. The top four prey classes represent high quality food, the bottom two prey species represent low quality food. For definition of breeding periods and food quality see material and methods section. *Feeding observations.

Table 2: Number of prey items selected to be carried away expressed as percentage of prey caught. The selection rates are presented both by breeding period (courtship 1, chicks and courtship 2) and integrated over the whole breeding season. The top three prey classes represent high quality food, the bottom two prey species represent low quality food. For definition of breeding periods and food quality see material and methods section. Note that sandeel, though present in courtship and chick feedings, has not been observed to be caught in the foraging areas.

Table 3: Relative contribution of high quality food (clupeids, gadids, gobies, sandeel and squid), low quality food (brown shrimp, flatfish, hooknose and pipefish) and unidentified prey (unid.) to prey composition during courtship and chick periods. Percentage of high quality, low quality and unidentified prey and sample size are given. Largest proportions are highlighted in bold. Results of chi^2-tests (chi^2-values and Bonferroni-corrected significance levels) are given. n. s. = not significant, *** = $p < 0.001$ (bold). Degrees of freedom = 2 in all cases. [a]Results were not considered in cross tables where the expected frequency was less than 5 in more than 20% of the cells (indicated as e. g. 33.3%<5).

Table 1

Prey class (%)	Courtship 1					Chicks					Courtship 2					Whole season				
	Stow net catches, May 23rd	Caught	Consumed	Carried away	Feed. obs.*, May 13th- June 13th	Stow net catches, June 8th & 19th	Caught	Consumed	Carried away	Feed. obs.*, June 13th - 28th	Stow net catches, July 9th/10th	Caught	Consumed	Carried away	Feed. obs.*, June 29th - July 28th	Stow net catches, all dates	Caught	Consumed	Carried away	Feed. obs.*, whole season
Clupeids	84	44	44	49	36	97	23	20	50	70	84	8	9	0	46	86	34	33	44	50
Gadids	1	3	2	11	12	0	4	3	17	15	4	12	9	67	36	3	5	4	18	20
Gobies	0	3	2	9	3	0	0	0	0	0	0	1	0	17	0	0	2	1	9	1
Sandeel	1	0	0	0	19	0	0	0	0	3	0	0	0	0	2	0	0	0	0	9
Brown shrimp	0	14	16	0	1	0	10	11	0	0	8	62	65	0	0	6	23	26	0	0
Pipefish	13	28	32	4	0	2	52	57	0	1	3	10	11	0	0	4	28	31	4	0
others	2	3	1	20	5	1	1	2	0	0	2	2	2	0	0	1	3	1	16	2
unidentified	0	3	3	7	25	0	10	8	33	10	0	5	5	17	14	0	5	4	11	17
n	**533**	**344**	**299**	**45**	**530**	**726**	**71**	**65**	**6**	**430**	**3086**	**110**	**104**	**6**	**412**	**4345**	**525**	**468**	**57**	**1372**

Table 2

	Courtship 1	Chicks	Courtship 2	Whole season
Clupeids	14	19	0	14
Gadids	42	33	31	36
Gobies	44	0	100	50
Brown shrimp	0	0	0	0
Pipefish	2	0	0	1
unidentified	25	29	17	24

Table 3

	Courtship 1	Chicks	Courtship 2	Whole season
high/low/ unid. (n)	**high/low/ unid. (n)**	**high/low/ unid. (n)**	**high/low/ unid. (n)**	**high/low/ unid. (n)**
Stow net	**87.2**/12.8/0.0 *(533)*	**97.9**/2.1/0.0 *(726)*	**89.0**/11.0/0.0 *(3055)*	**90.3**/9.7/0.0 *(8690)*
vs. caught	**52.9**/43.6/3.5 *(344)*	26.8/**63.4**/9.9 *(71)*	22.2/**74.1**/3.7 *(108)*	42.9/**52.4**/4.8 *(525)*
Chi²/p	132.03/***	430.32/***	3.3%<5[a]	1285.48/***
Caught	**52.9**/43.6/3.5 *(344)*	26.8/**63.4**/9.9 *(71)*	22.2/**74.1**/3.7 *(108)*	42.9/**52.4**/4.8 *(525)*
vs. consumed	48.2/**48.8**/3.0 *(299)*	23.1/**69.2**/7.7 *(65)*	18.6/**78.4**/2.9 *(102)*	38.0/**57.9**/4.1 *(468)*
Chi²/p	1.77/n.s.	0.54/n.s	33.3%<5[a]	3.07/n.s.
Caught	**52.9**/43.6/3.5 *(344)*	26.8/**63.4**/9.9 *(71)*	22.2/**74.1**/3.7 *(108)*	42.9/**52.4**/4.8 *(525)*
vs. carried away	**84.4**/8.9/6.7 *(45)*	**66.7**/0.0/33.3 *(6)*	**83.3**/0.0/16.7 *(6)*	**82.5**/7.0/10.5 *(57)*
Chi²/p	20.16/***	50%<5[a]	67%<5[a]	42.53/***
Consumed	48.2/**48.8**/3.0 *(299)*	23.1/**69.2**/7.7 *(65*	18.6/**78.4**/2.9 *(102)*	38.0/**57.9**/4.1 *(468)*
vs. carried away	**84.4**/8.9/6.7 *(45)*	**66.7**/0.0/33.3 *(6)*	**83.3**/0.0/16.7 *(6)*	**82.5**/7.0/10.5 *(57)*
Chi²/p	25.54/***	50%<5[a]	67%<5[a]	52.98/***
Caught	**52.9**/43.6/3.5 *(344)*	26.8/**63.4**/9.9 *(71)*	22.2/**74.1**/3.7 *(108)*	42.9/**52.4**/4.8 *(525)*
vs. fed	**74.3**/1.1/24.5 *(530)*	**89.1**/1.2/9.8 *(430)*	**85.2**/0.7/14.1 *(412)*	**82.2**/1.0/16.8 *(1372)*
Chi²/p	282.20/***	265.85/***	343.18/***	780.63/***
Carried away	**84.4**/8.9/6.7 *(45)*	**66.7**/0.0/33.3 *(6)*	**83.3**/0.0/16.7 *(6)*	**82.5**/7.0/10.5 *(57)*
vs. fed	**74.3**/1.1/24.5 *(530)*	**89.1**/1.2/9.8 *(430*	**85.2**/0.7/14.1 *(412)*	**82.2**/1.0/16.8 *(1372)*
Chi²/p	20.63/***	50%<5[a]	50%<5[a]	16.92/***

Figure 1 (made in MS Power Point formatted as jpeg)

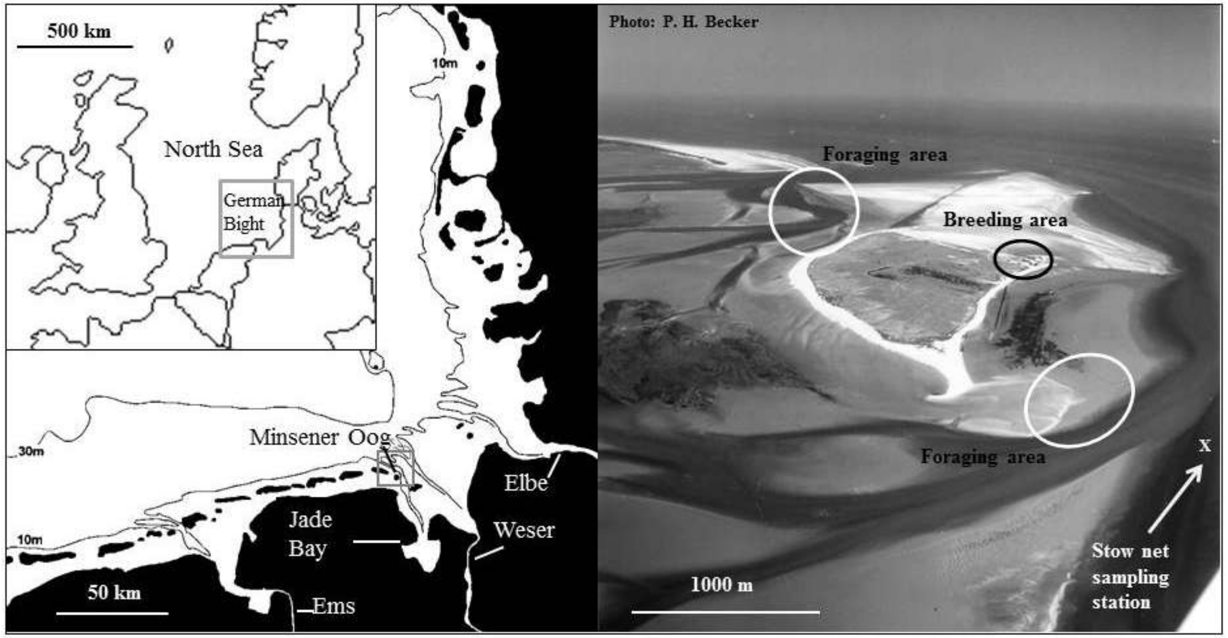
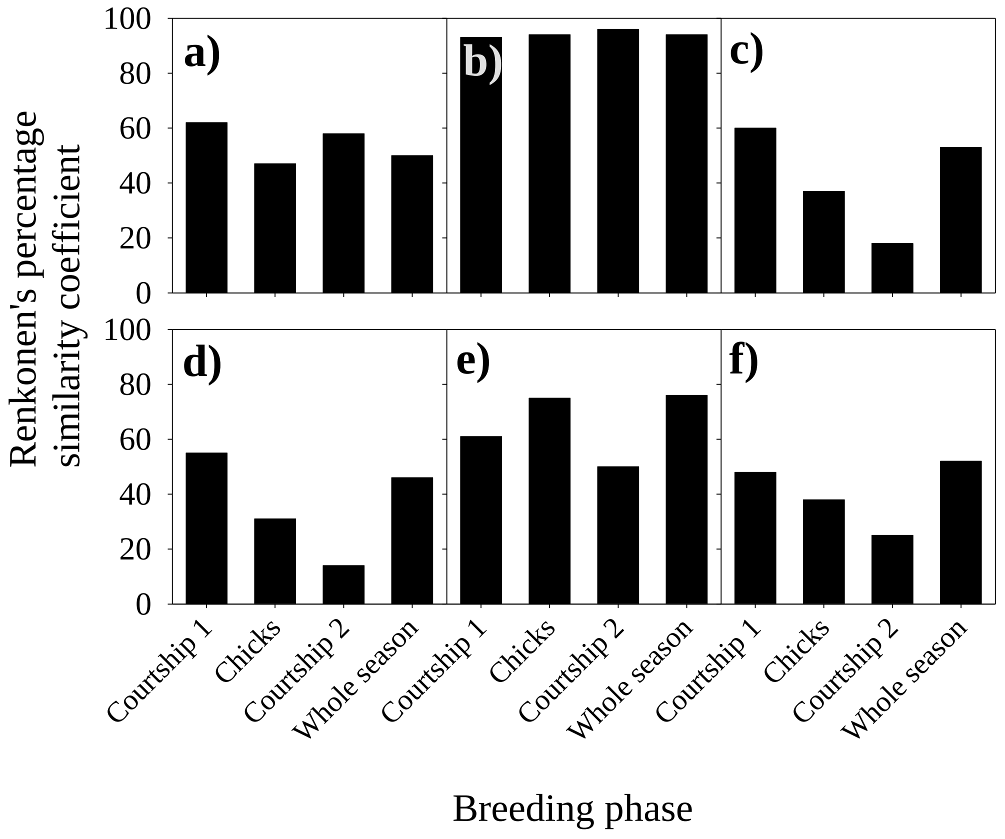


Figure 2 (made in Sigma Plot)


a)
b)
c)
d)
e)
f)
Renkonen's percentage similarity coefficient
0
20
40
60
80
100
Courtship 1
Chicks
Courtship 2
Whole season
Breeding phase

756

757