



HAL
open science

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

Andreas Dänhardt, Tido Freseman, Peter H. Becker

► **To cite this version:**

Andreas Dänhardt, Tido Freseman, Peter H. Becker. To eat or to feed? Prey utilization of Common Terns in the Wadden Sea. *Journal für Ornithologie = Journal of Ornithology*, 2010, 152 (2), pp.347-357. 10.1007/s10336-010-0590-0 . hal-00634352

HAL Id: hal-00634352

<https://hal.science/hal-00634352>

Submitted on 21 Oct 2011

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 To eat or to feed? Prey utilization of Common Terns *Sterna hirundo* in the
2 Wadden Sea

3
4 Andreas Dänhardt^{1,2*}, Tido Fresemann³ and Peter H. Becker¹

5
6 ¹Institute of Avian Research, An der Vogelwarte 21, 26386 Wilhelmshaven, Germany.

7 E-mail: peter.becker@ifv-vogelwarte.de, +49 (0) 44 21 96 89 0

8 *corresponding author

9 present address:

10 ²Suerhoper Brunnenweg 13 a, 21244 Buchholz/ Nordheide, Germany.

11 E-mail: andreas@daenhardt.com, Phone: + 49 (0) 1 79 5 17 15 36

12 ³Loitzer Straße 48, 17489 Greifswald, Germany,

13 E-mail: tido.fresemann@gmx.de, +49 (0) 38 34 35 16 77

14

15 ABSTRACT

16

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

34

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

37

38

39 ZUSAMMENFASSUNG

40

41 **Fressen oder verfüttern? Beutenutzung von Flusseeeschwalben *Sterna hirundo* im** 42 **Wattenmeer**

43

44 Die Beuteverfügbarkeit für Seevögel hat eine zentrale Bedeutung für die individuelle
45 Entscheidung, ob die verfügbare Energie in das eigene Überleben oder die Reproduktion
46 investiert wird. Diese Entscheidungen werden u.a. in Jagdverhalten und Beutenutzung
47 manifest, was sich wiederum auf die funktionelle Beziehung zwischen den
48 Beutepopulationen, dem Brutverlauf und der Kükenaufzucht der Seevögel auswirken kann.

49 Basierend auf direkten Beobachtungen beschreibt der vorliegende Artikel die Beziehung
50 zwischen der Fischabundanz und dem Jagdverhalten auf See, der Beutenutzung sowie der
51 Balz- und Kükenfütterung bei Flusseeeschwalben *Sterna hirundo* im deutschen Wattenmeer.
52 Qualitativ hochwertige Beute wurde überdurchschnittlich oft aus dem Jagdgebiet in die
53 Kolonien getragen, während nahezu alle Beuteorganismen von geringer Qualität vom
54 jagenden Altvogel selbst konsumiert wurden. Die relativen Anteile verschiedener Beutetiere
55 an der Balz- und Kükennahrung stimmten besser mit der aus dem Jagdgebiet abtransportierten
56 Beute überein als mit der Beute, die insgesamt gefangen wurde. Die bevorzugte Nutzung
57 hochwertiger Beute für die Balz- und Kükenfütterung impliziert, dass große Anteile von
58 qualitativ minderwertiger Beute in der Kolonie einen Mangel an hochwertiger Beute und
59 somit schlechten Aussichten auf einen hohen Bruterfolg anzeigen können. Unsere Ergebnisse
60 zeigen des weiteren, dass die Abundanz energetisch hochwertiger Fischarten im Meer
61 überschätzt werden könnte, wenn diesen Abschätzungen koloniebasierte
62 Fütterungsbeobachtungen von Seevögeln zugrunde liegen, die hochwertige Beutetiere
63 bevorzugt an ihre Partner und Küken verfüttern.

64

65 INTRODUCTION

66

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

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

98 To maximize energetic investment in reproduction, colony-breeding single loaders such as
99 terns are predicted to bring only large and energy-rich prey items to their partners or chicks.
100 This concept, known as the central place foraging theory (Orians and Pearson 1979), implies
101 that the relationship between prey abundance and a given seabird characteristic measured
102 inside the colony may be biased due to individual decisions during foraging. This has been
103 demonstrated by means of direct observations of Roseate Terns *Sterna dougallii* (Shealer
104 1998) and Common Terns *Sterna hirundo* during courtship (Taylor 1979). Terns are among
105 the few seabird species that allow for direct observations at sea due to their limited foraging
106 range around their breeding colonies (Taylor 1979; Becker et al. 1993; Schwemmer et al.
107 2009).

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

112 MATERIAL & METHODS

113

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

121

122 → Figure 1

123

124 *Observations of feeding flocks and foraging behaviour*

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

139 To ensure correct and consistent identification of prey items during the foraging and feeding
140 observations at Minsener Oog, observers were trained at another Common Tern colony
141 (Banter See, Wilhelmshaven, for details see Becker 1996) with convenient observation
142 conditions and with breeding phenology being two weeks ahead of Minsener Oog. At
143 Minsener Oog, observations of foraging behaviour were carried out weekdays five times a
144 week, using binoculars (Minox 10 x 42). Individual Common Terns were randomly selected
145 from the foraging flock and their behaviour was tracked for exactly one minute. On any given

146 observation day 25 observations of one minute each were carried out in each of the two
147 foraging areas, unless weather conditions or breakup of foraging flocks terminated the
148 observations before 25 minutes of individual tracking were completed. Between May 3rd and
149 July 28th the observation effort amounted to 597 minutes and 935 minutes in the foraging
150 areas northwest and southeast of Minsener Oog, respectively (Fig. 1).

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

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

170

171 *Observations in the colony*

172

173 Starting in the middle of May, clutches and eggs were counted every other day in a colony in
174 the north of Minsener Oog, representing the majority of Common Tern breeding pairs on the
175 island (Fig. 1). From the beginning of June chicks were regularly counted. Feeding
176 observations were carried out during a total of 47 hours in May, 63 hours in June and 44
177 hours in July. Feeding observations were synchronized with the foraging observations
178 described above. Feedings of partners and chicks were observed in units of two hours. Prey
179 eaten by partners or chicks was identified as described above. Courtship feedings were

180 observed between May 13th and June 13th. Eggs were present after May 22nd; first chicks were
181 observed on June 11th. All chicks died during a storm flood on June 27th/28th. After that,
182 partner feedings were again observed. Accordingly, observations of foraging (May 3rd – June
183 13th) and partner feedings (May 13th – June 13th) are subsequently referred to as “courtship 1”,
184 referring to both courtship feedings in the colony and provisioning of incubating females. The
185 category courtship 1 also included prey caught and delivered to partners before colony
186 formation. Prey captured and fed between June 14th and June 27th is labeled “chicks”;
187 foraging and feeding observations were noted as “courtship 2” from June 28th until July 28th.

188

189 *Stow net fisheries*

190 To account for the terns’ prey supply, stow net catches were conducted at a fixed sampling
191 station located in the immediate vicinity of both foraging areas and breeding sites of the
192 Common Terns (Fig. 1). Stow nets are passive catching gear operated from an anchoring
193 vessel, utilizing the water movement as encountered in rivers or in tidally influenced marine
194 areas such as the Wadden Sea. This gear is largely unselective and thus representative
195 especially of pelagic fish (Breckling and Neudecker 1994; Dänhardt and Becker 2010), the
196 terns’ main prey. Stow net catches were timed to represent prey composition during the
197 breeding periods described above. The fishing campaigns took place on May 23rd, June 19th
198 and July 9th/10th and were assumed to represent prey availability during the different periods
199 within the terns’ breeding season (see results section). Haul duration was 45 ± 5 minutes. The
200 stretched mesh size decreased from 40 mm close to the mouth to 10 mm in the cod end. Water
201 flow was recorded by means of four propeller flow meters (Hydrobios, Kiel). Absolute catch
202 numbers were normalized to individuals caught per 10 000 m³ filtered water volume by

203

$$204 \text{No}_{10000} = \text{No}_{\text{absolute}} / (\text{FC}_{\text{End}} - \text{FC}_{\text{Start}} \times 0.3 \times \text{Net}_{\text{Height}} \times \text{Net}_{\text{Width}}) \times 10000$$

205

206 with No_{10000} = Fish numbers per 10000m³ fished water volume, $\text{No}_{\text{absolute}}$ =Absolute fish
207 numbers, FC_{End} = Flowmeter count at the end of a haul, FC_{Start} = Flowmeter count at the start
208 of a haul, 0.3 = meters per rotation of the propeller flowmeter (value provided by
209 manufacturer), $\text{Net}_{\text{Height}}$ = Net height in m (varying with the current pressure), $\text{Net}_{\text{Width}}$ = Net
210 width in m (constant). The catches were sorted by species and individuals were counted.
211 Species that occurred in the stow net catches but were not utilized by the terns were excluded
212 from subsequent analyses.

213

214 *Statistics*

215 The approach of the present paper mostly required comparisons of proportions. Thus, only
216 non-parametric tests were applied. The similarity between the composition of stow net
217 catches, the prey items caught, eaten and carried away by the foraging terns and the feeding
218 observations was quantified using Renkonen's percentage similarity coefficient (Renkonen
219 1938; Wolda 1981; Krebs 1999), ranging from 0 (no similarity) to 100 (complete similarity).
220 The index is expressed in percent (Krebs 1999).

221 Prey items were classified to be of high or low quality according to their potential energy
222 yield per unit foraging effort to the terns. This classification was based on information on
223 specific energy content (Massias and Becker 1990; Hislop et al. 1991; Pedersen and Hislop
224 2001; Harris et al. 2008; Fischer unpublished data), determining whether a prey item can be
225 profitably utilized by the terns. Clupeids, gadids, gobies, sandeel and squid were classified
226 high quality items, brown shrimp, pipefish, flatfish and hooknose were classified low quality
227 items. Smelt and eelpout were not considered, because only single individuals were recorded.
228 Differences in the distribution of proportions of high and low quality prey items were tested
229 for significance using cross tables and subsequent chi²-tests. Test results were not considered,
230 if more than 20% of the cells of the respective cross table were allocated an expected
231 frequency of less than 5. A sequential Bonferroni test was performed to adjust significance
232 levels according to an assumed experimentwise type I error rate of 5% (Sokal and Rohlf
233 1995).

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

235

236 RESULTS

237

238 *Composition of stow net catches and tern prey*

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

250

251 → Table 1

252

253 *Prey utilization*

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

257 Prey items carried away were made up mainly of clupeids, gadids and gobies. The exception
258 was courtship 2, when no clupeids were carried away. The percentage of both caught and
259 ingested clupeids decreased over the course of the breeding period from 44% in courtship 1 to
260 8–9% during the courtship 2 period. However, clupeids made up the largest part of the partner
261 and chick feedings. Even though gadids were not among the most numerous species in the
262 stow net catches, their share of prey caught, consumed and carried away increased over the
263 course of the breeding period. This development was also seen in the feeding observations.
264 Gobies were neither caught with the stow net in considerable numbers nor were they fed to
265 partners (courtship) or chicks. They were observed to be caught, consumed and also carried
266 away during both courtship periods, but not during the chick period.

267 In all three periods, the percentage of both pipefish and brown shrimp utilized by the terns
268 was higher than in the stow net catches. These two prey species were mostly eaten by the

269 adult terns themselves, even during courtship 1 and chick rearing, when pipefish and brown
270 shrimp, respectively, were caught by the terns in highest proportions of all prey (Table 1).

271 During courtship 1, 20% of the prey class ‘others’ was carried away. This was attributed to
272 squid, of which 70% were carried away, even though this prey class was among the least
273 numerous species in the stow net catches. Of all prey items carried away 7–33% were not
274 identified (Table 1).

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

284

285 *Selection rates*

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

293

294 → Table 2

295

296 *Similarity in prey composition*

297 Stow net catches did not match the composition of prey caught by the terns very closely,
298 which was the case in all three periods and integrated over the entire breeding season (Fig.
299 2a). The terns consumed prey in the same proportions as they caught it, being expressed in >
300 90% similarity. This very high agreement remained constant throughout the breeding season
301 (Fig. 2b). In contrast, similarity coefficients of prey caught vs. prey carried away were
302 decreasing as the season progressed (Fig. 2c). A decline over the course of the season was

303 also noted in the similarity between prey consumed and prey carried away, reaching a
304 minimum of less than 20% during the courtship 2 period (Fig. 2d). The composition of prey
305 carried away vs. prey fed to partners and chicks revealed the second-best match of all
306 comparisons (Fig. 2e). The similarity between prey caught in the foraging areas and fed to
307 partners and chicks decreased from 50% during courtship 1 to 30% during courtship 2 (Fig.
308 2f). In four out of six comparisons there was a tendency towards lower similarity as the
309 season progressed with lowest similarity coefficients during the courtship 2 period (Fig. 2).

310

311 → Figure 2

312

313 *Proportion of high and low quality food*

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

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

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

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

336

337 → Table 3

338

339 DISCUSSION

340

341 *Methodological aspects*

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

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

360

361 *Foraging observations*

362 The finding of the present study that profitable prey is carried away and fed to partners or
363 chicks at much higher rates than low quality prey items agrees both with the literature (Taylor
364 1979; Shealer 1998; McLeay et al. 2009) and the predictions of the central place foraging
365 theory (Orians and Pearson 1979). Even though fish being caught could not be followed to its
366 final destination e. g. in the colony, there is support for assuming that fish seen being carried
367 away was indeed brought into the colony to be fed to chicks or mates: Following radio-
368 tracked Common Terns revealed that their flight course to and especially from the foraging
369 areas was rectilinear and performed at high speed (Becker et al. 1991, 1993), indicating that
370 the birds fly straight back to the colony. This is further supported by own observations during

371 the field work of the present study (Fresemann, unpublished data), that terns left the foraging
372 area in the majority of cases in the direction of the breeding colony. Those terns not leaving
373 towards the colony on Minsener Oog headed either west or east, where other small colonies
374 are located on neighboring islands (Wangerooge and Mellum). These birds may use the same
375 foraging areas as their conspecifics breeding on Minsener Oog.

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

380 The two foraging locations examined in the present study represent two out of five foraging
381 sites identified by means of radio-telemetry: “Wattengebiete” and “Oldeogrinne”, which
382 have been the destination of 28.5% and 18.4% of foraging flights, respectively (Becker et al.
383 1991, 1993). Nevertheless, Common Terns have been found to utilize a wide variety of
384 habitats within their foraging range around Minsener Oog which were located outside the area
385 of investigation (Becker et al. 1991, 1993). However, the key finding that Common Terns
386 select high quality prey for provisioning and tend to eat low quality prey themselves is largely
387 independent of the overall relevance of a given foraging site. Thus it remains valid even if an
388 area is only secondarily used for foraging. Delivering high quality prey to partners or chicks
389 appears to be a general behavioural pattern in the Common Tern not confined to a single
390 breeding period such as courtship (Taylor 1979), as indicated by high quality items
391 preferentially being carried away in all three periods (Table 1). Similar results have been
392 reported for auks (Davoren and Burger 1999) and other tern species (Shealer 1998; McLeay et
393 al. 2009). Even when utilizing anthropogenic food sources, this pattern becomes evident, as
394 reported by Dänhardt and Becker (2008), who found that Common Terns foraging at a
395 cooling water outlet of a power plant carried away 28% of clupeids, 50% of smelt and 17% of
396 gobies (high quality food; Massias and Becker 1990) as compared to 0% of flatfish, pipefish
397 and brown shrimp, respectively (low quality food; Massias and Becker 1990).

398 Individual decisions what to do with a given prey item after having caught it are a trade-off
399 between somatic (eating the prey) and reproductive (feeding the prey to partners or chicks)
400 investment (Swihart and Johnson 1986). Despite the relatively large proportions of high
401 quality food being carried away and fed to partners or chicks, the bulk of both high and low
402 quality prey was eaten by the foraging tern itself (Table 1). This may have been indicative of
403 a favorable food situation in 2007, providing a surplus of profitable food items also to the
404 adult forager. Nevertheless, clupeids were not utilized in proportions similar to those found in

405 the stow net catches. This may be due to prey species-specific availability changing with the
406 tide (e. g. Becker and Specht 1991; Becker et al. 1993; Wendeln et al. 1994). Unfortunately,
407 this aspect could not be covered by the stow net fisheries. The proportions of clupeids
408 decreased after the courtship 1 period despite consistently high herring abundance throughout
409 the whole breeding season (Table 1). Starting in the last quarter of June, average wind speed
410 increased causing turbulent water surfaces, most likely exacerbating foraging conditions. In
411 addition to a hampered visibility brought about by turbulent water surfaces (Dunn 1973),
412 pelagic schooling fish such as clupeids may avoid turbulent water strata. Accordingly, the
413 foraging success of the Common Terns was highest at low wind speeds with e. g. 74% of
414 clupeids being caught at wind speeds of 1–2 Beaufort, but reduced at > 6 Beaufort (Frank
415 1992; Fresemann, unpublished data).

416 During the study period, high quality prey species were more abundant than low quality prey
417 (Table 1), but large proportions of low quality food were caught and consumed by the
418 foraging terns in all three periods. As with the proportions of clupeids described above, this
419 may also be due to prey species-specific availability changing within the tidal cycle.
420 However, the most abundant low quality prey, the pipefish, is a pelagic species and its
421 availability to the terns is probably equal to that of clupeids. Still 10 to 60% of tern prey was
422 pipefish (Table 1). Alternatively, utilizing low quality prey when high quality prey is
423 available could indicate that selective foraging does not occur. Following the idea that
424 foraging should generally be aimed at maximizing energy yield per unit foraging effort (Pyke
425 1984; Ydenberg et al. 1994), choosing to consume low quality prey in the presence of high
426 quality prey suggests that Common Terns do not select prey items prior to catching them. A
427 certain amount of energy available for foraging would go into catching low quality food,
428 which may be energetically justified given the lower effort required to self-feed. The
429 probability of catching high quality food could be increased by choosing foraging sites where
430 encounter with high quality food is more likely (e. g. Becker et al. 1993; Camphuysen and
431 Webb 1999), but the catch frequency of low quality prey may provide information to the
432 foraging tern about the overall food situation and, as a consequence, influence its partitioning
433 between somatic and reproductive investment.

434

435 *Feeding observations*

436 In years of poor food supply foraging trips may be longer due to lower rates of successful
437 foraging attempts or lower rates of catching high quality food being worthwhile delivering to
438 partners or chicks (Frank and Becker 1992; Monaghan 1996). Based on our results, it can be

439 assumed that high quality prey will be used for provisioning disproportionately often,
440 suggesting that the share of low quality food ending up the colony is in turn indicative of the
441 availability of high quality food in the sea. In 2007, the overall food situation was obviously
442 sufficient for low quality food not to be used for provisioning (Table 1). In other years, even
443 low quality food was utilized to provision mates or chicks (Becker et al. 1987; Frick and
444 Becker 1995; Schreiber unpublished).

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

455

456 *Conclusions*

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

465 The terns' phenotypic plasticity may also be a crucial aspect to consider when colony-based
466 diet data are to be used to draw inferences about the state and abundance of fish populations
467 being utilized by a given seabird species. Given the preferential delivery of high quality items
468 to partners and chicks, the abundance of high quality fish in the sea would be overestimated
469 when calculated from colony-based seabird diet studies. However, this bias due to preferring
470 high quality prey for provisioning applies only to seabird species delivering whole and
471 undigested prey to partners and chicks, but not to species swallowing their prey at sea and
472 regurgitating stomach contents to partners and chicks at the colony. In these species, bias may

473 emerge from differential digestion of body parts and tissue (Barrett et al. 2007) and prey
474 selecting prey before catching it.

475

476

477 ACKNOWLEDGMENTS

478

479 We wish to thank Mellumrat e. V. and Wasser- und Schifffahrtsamt Wilhelmshaven for
480 supporting field work on Minsener Oog and Captain K.-H. Rostek and his crew for their
481 professionalism during the fish sampling. We also thank H. Mühlichen for carrying out the
482 feeding observations, G. Wagenknecht for his support in collecting the data on breeding
483 performance of the Common Terns and J. Schreiber for providing additional information on
484 food quality used for provisioning in 2006. The project received financial support from the
485 Niedersächsische Wattenmeerstiftung (53-NWS-41/04).

486

487 The authors declare that they have no conflict of interest.

488

489 REFERENCES

490

491 Aebischer, N. J., Coulson, J. C. and Colebrooke, J. M. (1990) Parallel long-term trends across
492 four marine trophic levels and weather. *Nature*, 347: 753–755.

493

494 Barrett, R. T. (2007) Food web interactions in the southwestern barents sea: Black-legged
495 kittiwakes *Rissa tridactyla* respond negatively to an increase in herring *Clupea harengus*.
496 *Mar Ecol Prog Ser*, 349: 269–276.

497

498 Barrett, R. T., Camphuysen, C. J., Anker-Nilssen, T., Chardine, J. W., Furness, R. W., Garthe,
499 S., Hüppop, O., Leopold, M. F., Montevecchi, W. A. and Veit, R. R. (2007) Diet studies of
500 seabirds: A review and recommendations. *ICES J Mar Sci*, 64: 1675–1691.

501

502 Becker, P. H. (2003) Biomonitoring with birds. *In* Markert, B., Breure, T. and H.
503 Zechmeister, H. (Eds.) *Bioindicators & biomonitors – principles, concepts and applications*
504 (trace metals and other contaminants in the environment), pp. 677–737. Elsevier, Amsterdam.

505

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

508

509 Becker, P. H., Frank, D. and Walter, U. (1987) Geografische und jährliche Variation der
510 Ernährung der Flusseeeschwalbe (*Sterna hirundo*) an der Nordseeküste. *J Ornithol* 128:
511 457–475.

512

513 Becker, P. H., Frank, D. and Sudmann, S. R. (1993) Temporal and spatial pattern of Common
514 Tern (*Sterna hirundo*) foraging in the Wadden Sea. *Oecologia* 93: 389–393.

515

516 Becker, P. H., Frank, D., Sudmann, S. R., Wagener, M. (1991) Funkpeilung von
517 Flusseeeschwalben (*Sterna hirundo*) bei der Nahrungssuche im Wattenmeer. *Seevögel* 12 (3):
518 52-61.

519

520 Boyd, I. L., Wanless, S. and Camphuysen, C. J. (2006) *Top predators in marine ecosystems*.
521 Cambridge University Press, Cambridge. 378 p.

522

523 Breckling, P. and Neudecker, T. (1994) Monitoring the fish fauna in the Wadden Sea with
524 stow nets (part 1): A comparison of demersal and pelagic fish fauna in a deep channel. Arch
525 Fish Mar Res 42: 3–15.
526

527 Burness, G. P., Morris, R. D. and Bruce, J. P. (1994) Seasonal and annual variation in brood
528 attendance, prey type delivered to chicks, and foraging patterns of male Common Terns
529 *Sterna hirundo*). Can J Zool 72: 1243–1251.
530

531 Cairns, D. K. (1987) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:
532 261–271.
533

534 Camphuysen, C. J. and Webb, A. (1999) Multi-species feeding associations in North Sea
535 seabirds: Jointly exploiting a patchy environment. Ardea 87: 177–197.
536

537 Dänhardt, A. and Becker, P. H. (2008) Die Bedeutung umweltbedingter Verteilungsmuster
538 von Schwarmfischen für Seevögel im Ökosystem Niedersächsisches Wattenmeer. Institute of
539 Avian Research, Wilhelmshaven., Final project report, 248 p. (in German).
540

541 Dänhardt, A. and Becker, P. H. (2010) Does small-scale vertical distribution of juvenile
542 schooling fish affect prey availability to surface-feeding seabirds in the Wadden Sea?
543 Submitted to J Sea Res.
544

545 Daunt, F., Peters, G., Scott, B., Grémillet, D. and Wanless, S. 2003. Rapid-reponse recorders
546 reveal interplay between marine physics and seabird behaviour. Mar Ecol Prog Ser 55: 283–
547 288.
548

549 Davoren, G. K. and Burger, A. E. (1999) Differences in prey selection and behaviour during
550 self-feeding and chick provisioning in rhinoceros auklets Anim Behav 58: 853–863.
551

552 Davoren, G. K. and Montevecchi, W. A. (2003) Signals from seabirds indicate changing
553 biology of capelin stocks. Mar Ecol Prog Ser 258: 253–261.
554

555 Duffy, D. C. and Jackson, S. (1986) Diet studies of seabirds: A review of methods. Col
556 Waterbirds, 9: 1–17.

557
558 Dunn, E. K. (1973) Changes in fishing ability of terns associated with windspeed and sea
559 surface conditions. *Nature*, 244: 520–521.
560
561 Einoder, L. D. (2009) A review of the use of seabirds as indicators in fisheries and ecosystem
562 management. *Fish Res* 95: 6–13.
563
564 Elliott, K. H., Woo, K., Gaston, A. J., Benvenuti, S., Dall'antonia, L. and Davoren, G. K.
565 (2008) Seabird foraging behaviour indicates prey type. *Mar Ecol Prog Ser* 354: 289–303.
566
567 Frank, D. (1992) The influence of feeding conditions on food provisioning of chicks in
568 Common Terns *Sterna hirundo* nesting in the German Wadden Sea. *Ardea* 80: 45–55.
569
570 Frank, D. and Becker, P. H. (1992) Body mass and nest reliefs in Common Terns *Sterna*
571 *hirundo* exposed to different feeding conditions. *Ardea*, 80: 57–69.
572
573 Frederiksen, M., Wanless, S., Harris, M. P., Rothery, P. and Wilson, L. J. (2004) The role of
574 industrial fisheries and oceanographic change in the decline of North Sea black-legged
575 kittiwakes. *J Appl Ecol* 41: 1129–1139.
576
577 Frick, S. and Becker, P. H. (1995) Unterschiedliche Ernährungsstrategien von Fluss- und
578 Küstenseeschwalbe (*Sterna hirundo* und *S. paradisaea*) im Wattenmeer. *J Ornithol* 136: 47–
579 63.
580
581 Furness, R. W. (2002) Management implications of interactions between fisheries and
582 sandeel-dependent seabirds and seals in the North Sea. *ICES J Mar Sci* 59: 261–269.
583
584 Furness, R. W. (2006) Responses of seabirds to depletion of food fish stocks. *J Ornithol* 148
585 (Supplement 2): 247–252.
586
587 Garthe, S., Grémillet, D. and Furness, R. W. (1999) At-sea activity and foraging efficiency in
588 chick-rearing northern gannets *Sula bassana*: A case study in shetland. *Mar Ecol Prog Ser*
589 185: 93–99.
590

591 Greenstreet, S. P. R., Becker, P. H., Barrett, R. T., Fossum, P. & Leopold, M. F. (1999)
592 Consumption of pre-recruit fish by seabirds and the possible use of this as an indicator of
593 fish stock recruitment. *In*: Furness, R. W. & Tasker, M. L. (Eds.): Diets of seabirds and
594 consequences of changes in food supply. ICES Coop Res Rep 232: 6–17.
595
596 Grémillet, D., Kuntz, G., Delbart, F., Mellet, M., Kato, A., Robin, J.-P., Chaillon, P.-E.,
597 Gendner, J.-P., Lorentsen, S.-H. and Le Mayo, Y. (2004) Linking the foraging performance of
598 a marine predator to local prey abundance. *Function Ecol*, 18: 793–801.
599
600 Hamer, K. C., Humphreys, E. M., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Phillips,
601 R. A., Harris, M. P. and Wanless, S. (2007) Annual variation in diets, feeding locations and
602 foraging behaviour of gannets in the North Sea: Flexibility, consistency and constraint. *Mar*
603 *Ecol Prog Ser* 338: 295–305.
604
605 Harris, M. P., Newell, M., Daunt, F. and Spe, J. R. (2008) Snake pipefish *Entelurus*
606 *aequoreus* are poor food for seabirds. *Ibis* 150: 413–415.
607
608 Hislop, J. R. G., Harris, M. P. and Smith, J. G. M. (1991) Variation in the calorific value and
609 total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by
610 seabirds. *J Zool* 224: 501–517.
611
612 ICES (2002) Report of the ICES advisory committee on ecosystems. ICES Coop Res Rep
613 254. 129 pp.
614
615 Krebs, C. J. (1999) *Ecological methodology*, Addison Wesley Longman, Menlo Park,
616 Reading, New York, Harlow, Don Mills, Amsterdam, Madrid, Sidney, Mexico City.
617
618 Massias, A. and Becker, P. H. (1990) Nutritive value of food and growth in Common Tern
619 (*Sterna hirundo*) chicks. *Ornis Scand* 21: 187–194.
620
621 Mcleay, L. J., Page, B., Goldsworthy, S. D., Ward, T. M. and Paton, D. C. (2009) Size
622 matters: Variation in the diet of chick and adult crested terns. *Mar. Biol.* 156: 1765-1780.
623

624 Monaghan, P. (1996) Relevance of the behaviour of seabirds to the conservation of marine
625 environments. *Oikos* 77: 227–237.

626

627 Montevecchi, W. A. (1993) Birds as indicators of change in marine prey stocks. *In* Furness,
628 R. W. and Greenwood, J. J. D. (Eds): *Birds as monitors of environmental change*, p. 217–266,
629 Chapman & Hall, London.

630

631 Orians, G. H. and Pearson, N. E. (1979) On the theory of central place foraging. *In* Horn, D.
632 J., Mitchell, R. D. and Stairs, G. R. (Eds.): *Analysis of Ecological Systems*, pp. 154–177.
633 Ohio State University Press., Columbus, Ohio.

634

635 Pedersen, J. and Hislop, J. R. G. (2001) Seasonal variations in the energy density of fishes in
636 the North Sea. *J Fish Biol* 59: 380–389.

637

638 Piatt, J. F. and Sydeman, W. J. (2007) Seabirds as indicators of marine ecosystems. *Mar Ecol*
639 *Prog Ser* 352: 199–309.

640

641 Pyke, G. H. (1984) Optimal foraging theory: A critical review. *Ann Rev Ecol System* 15:
642 523–575.

643

644 Renkonen, O. (1938) Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt
645 der finnischen Bruchmoore. *Ann Zoo Soc Fenn Vanamo*, 6: 1–231.

646

647 Schwemmer, P., Adler, S., Guse, N., Markones, N. and Garthe, S. (2009) Influence of water
648 flow velocity, water depth and colony distance on distribution and foraging patterns of terns
649 in the Wadden Sea. *Fish Oceanogr* 18: 161–172.

650

651 Shealer, D. A. (1998) Size-selective predation by a specialist forager, the Roseate tern. *Auk*,
652 115: 519–525.

653

654 Sokal, R. R. and Rohlf, F. J. (1995) *Biometry*, WH Freeman, New York.

655

656 Swihart, R. K. and Johnson, S. G. (1986) Foraging decision of American robins: Somatic and
657 reproductive tradeoffs. *Behav Ecol Sociobiol* 19: 275–282.

658
659 Taylor, I (1979) Prey selection during courtship feeding in the Common Tern. *Ornis Scand.*
660 10: 142–144.
661
662 Walter, U. and Becker, P. H. (1998) Influence of physical factors and fishing activity on the
663 occurrence of seabirds scavenging around shrimpers in the Wadden Sea. *Senckenbergiana*
664 *maritima*, 29: 155–162.
665
666 Weimerskirch, H. (1998) Can a pelagic seabird provision its chick when relying on a distant
667 food resource? Cyclic attendance at the colony, foraging decision and body condition in
668 sooty shearwaters. *J Anim Ecol* 67: 99–109.
669
670 Weimerskirch, H., Mougey, T. and Hindermeier, X. (1997) Foraging and provisioning
671 strategies of black-browed albatrosses in relation to the requirements of the chick: Natural
672 variation and experimental study. *Behav Ecol* 8: 635–643.
673
674 Wendeln, H., Mickstein, S. and Becker, P. H. (1994) Auswirkungen individueller
675 Ernährungsstrategien von Flusseeeschwalben (*Sterna hirundo*) auf die Anwesenheit am
676 Koloniestandort. *Vogelwarte* 37: 290–303.
677
678 Wolda, H. (1981) Similarity indices, sample size and diversity. *Oecologia* 50: 296–302.
679
680 Ydenberg, R. C., Welham, C. V. J., Schmid-Hempel, R., Schmid-Hempel, P. and
681 Beauchamp, G. (1994) Time and energy constraints and the relationships between currencies
682 in foraging theory. *Behav Ecol* 5: 28–34.
683

684 FIGURE CAPTIONS:

685

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

691

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

700

701 TABLE CAPTIONS:

702

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

711

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

719

720 Table 3: Relative contribution of high quality food (clupeids, gadids, gobies, sandeel and
721 squid), low quality food (brown shrimp, flatfish, hooknose and pipefish) and unidentified prey
722 (unid.) to prey composition during courtship and chick periods. Percentage of high quality,
723 low quality and unidentified prey and sample size are given. Largest proportions are
724 highlighted in bold. Results of chi²-tests (chi²-values and Bonferroni-corrected significance
725 levels) are given. n. s. = not significant, *** = p < 0.001 (bold). Degrees of freedom = 2 in all
726 cases. ^aResults were not considered in cross tables where the expected frequency was less
727 than 5 in more than 20% of the cells (indicated as e. g. 33.3%<5).

728 Table 1

Prey class (%)	Courtship 1					Chicks					Courtship 2					Whole season				
	Stow net catches, May 23 rd	Caught	Consumed	Carried away	Feed. obs. *, May 13 th - June 13 th	Stow net catches, June 8 th & 19 th	Caught	Consumed	Carried away	Feed. obs. *, June 13 th - 28 th	Stow net catches, July 9 th /10 th	Caught	Consumed	Carried away	Feed. obs. *, June 29 th - July 28 th	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

729
730
731
732
733

734 Table 2

735

	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

736

737

738

739

740

741

742

743

744

745

746

747

748

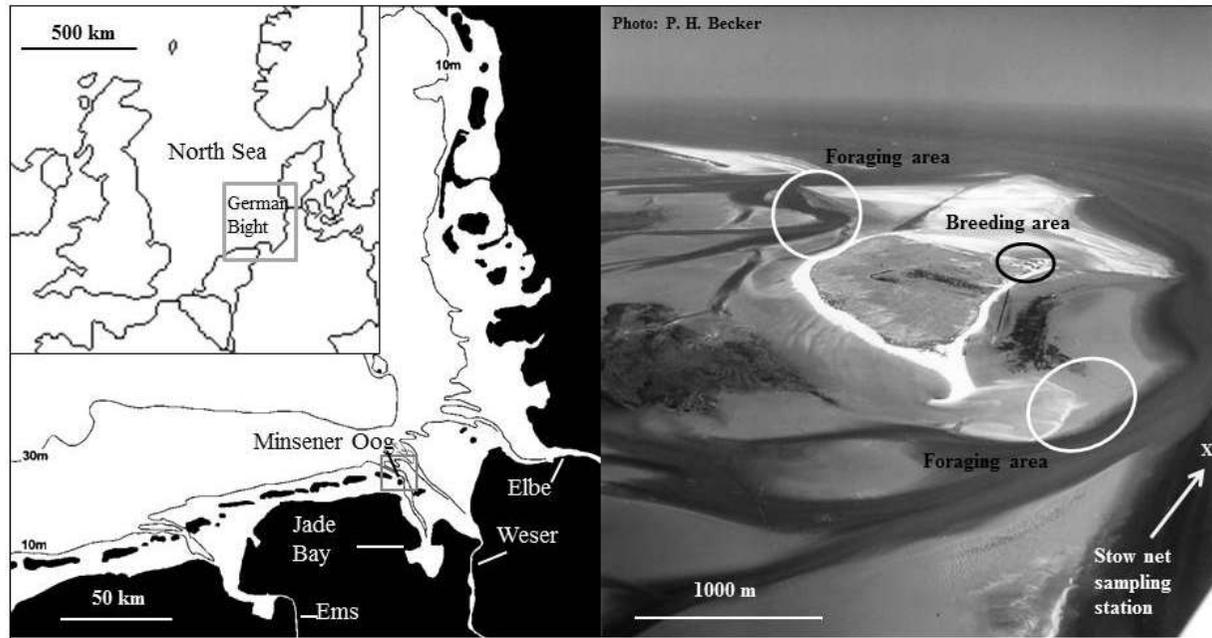
749

750 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)
Chi ² /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)
Chi ² /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)
Chi ² /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)
Chi ² /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)
Chi ² /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)
Chi ² /p	20.63/***	50%<5 ^a	50%<5 ^a	16.92/***

751

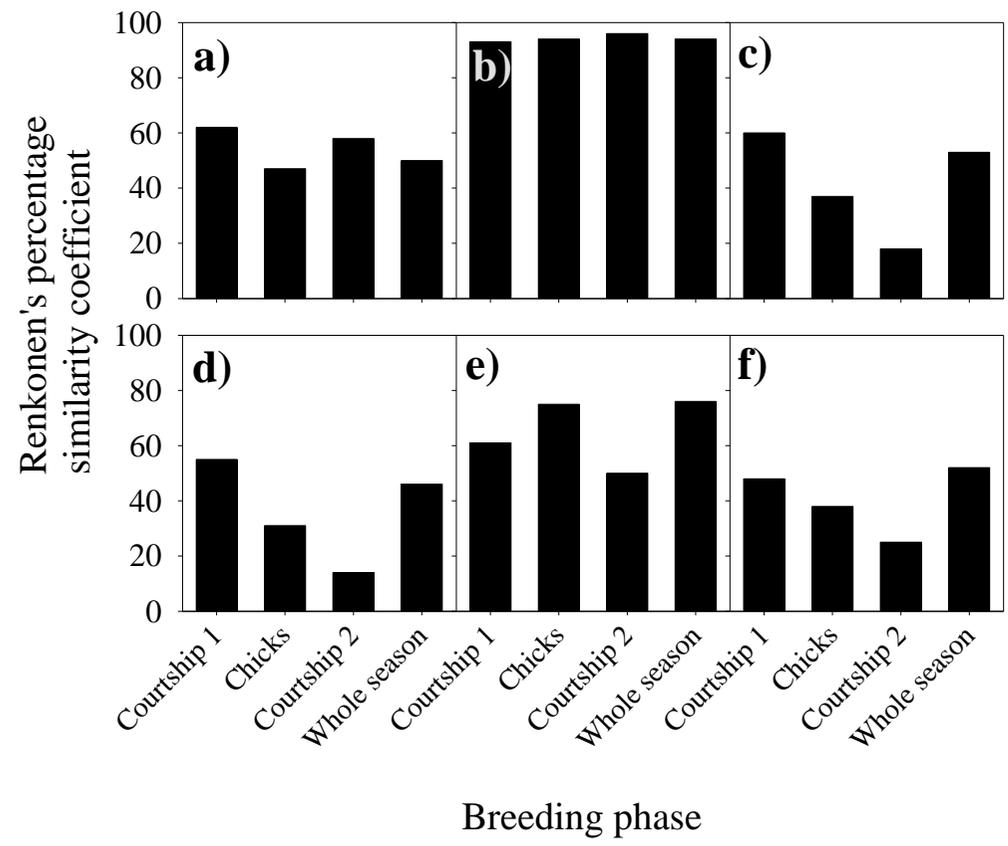
752 Figure 1 (made in MS Power Point formatted as jpeg)



753

754

755 Figure 2 (made in Sigma Plot)



756

757