Feeding ecology of wintering terns in Guinea-Bissau

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

During the last century, some populations of marine tern species in Europe, Central America and Asia have shown large fluctuations in numbers (Cramp 1985, del Hoyo *et al*. 1996). Besides hunting (Mead 1978, Meininger 1988) and poisoning (Koeman & Van Genderen 1966), crashes have been caused by decreases in prey fish availability (Heubeck 1988, Monaghan *et al*. 1992, Wright 1996, Suddaby & Ratcliffe 1997). Fish stock size and abiotic factors, such as water clarity (Eriksson 1985, Haney & Stone 1988), wind speed (Dunn 1973, Veen 1977), water temperature, salinity and water current (Hunt & Schneider

1987), have been suggested to influence fish availability by affecting the behaviour of fish as well as the behaviour of their potential avian predators. Crashes were not always followed by a complete recovery, which may have been due to problems in the wintering as well as in the breeding areas (Brenninkmeijer & Stienen 1992, Stienen & Brenninkmeijer 1992).

We studied the feeding ecology of wintering Little Terns *Sterna albifrons*, Sandwich Terns *S. sandvicensis* and Royal Terns *S. maxima* in the coastal waters of Guinea-Bissau. The total number of terns wintering in 1992/93 in these waters has been estimated at 62 000 (S. Asbirk unpubl. data, J.S. Salvig unpubl. data). Most of the Royal Terns in Guinea-Bissau probably breed in Senegal or Mauritania (Keijl *et al*. 2000), whereas the Little and Sandwich Terns originate from European breeding colonies (Cramp 1985). The coastal waters of Guinea-Bissau are of great international importance to terns, since more than 25% (10 000) of the

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40 000 Western Palearctic Little Terns, 5% (7500) of the 150 000 Western Palearctic Sandwich Terns and 10% (7500) of the 75 000 West African Royal Terns spend the northern winter in the area (J.S. Salvig unpubl. data, Rose & Scott 1997, Keijl *et al.* 2000).

In this paper, relationships between the foraging behaviour of the three tern species and abiotic factors, such as time, tide and water clarity, are discussed. Furthermore, a simple model shows the energetic consequences of the differences in feeding behaviour of the three species.

METHODS

Study site

Fieldwork was carried out on 32 days between 15 November 1992 and 7 February 1993, at 12 sites in the Archipélago dos Bijagós (11°40′N, 15°45′W), a group of islands and intertidal mudflats off the coast of Guinea-Bissau (Fig. 1). Each site was visited by boat for a period of 1–8 days. The sites holding the highest tern densities were chosen for study, although not all sites were accessible by boat or provided suitable observation opportunities. Site selection was based on the following considerations. The lowest density of foraging terns was measured in the harbour of Bissau (1 tern/km^2), while high densities were found around the Isle of Orangozinho (197 terns/km^2, Brenninkmeijer *et al.* 1998). The maximum density of foraging terns at the 12 study sites averaged 46.9 ± 47.1 (sd) terns/km^2, which is close to the average density of terns in the entire area (62 000 terns at 1570 km^2 of tidal area, J.S. Salvig unpubl. data). However, at the study sites even more terns were present, as some were always roosting on the beaches or on the tidal flats, suggesting that the sites chosen for study held relatively high numbers of terns.
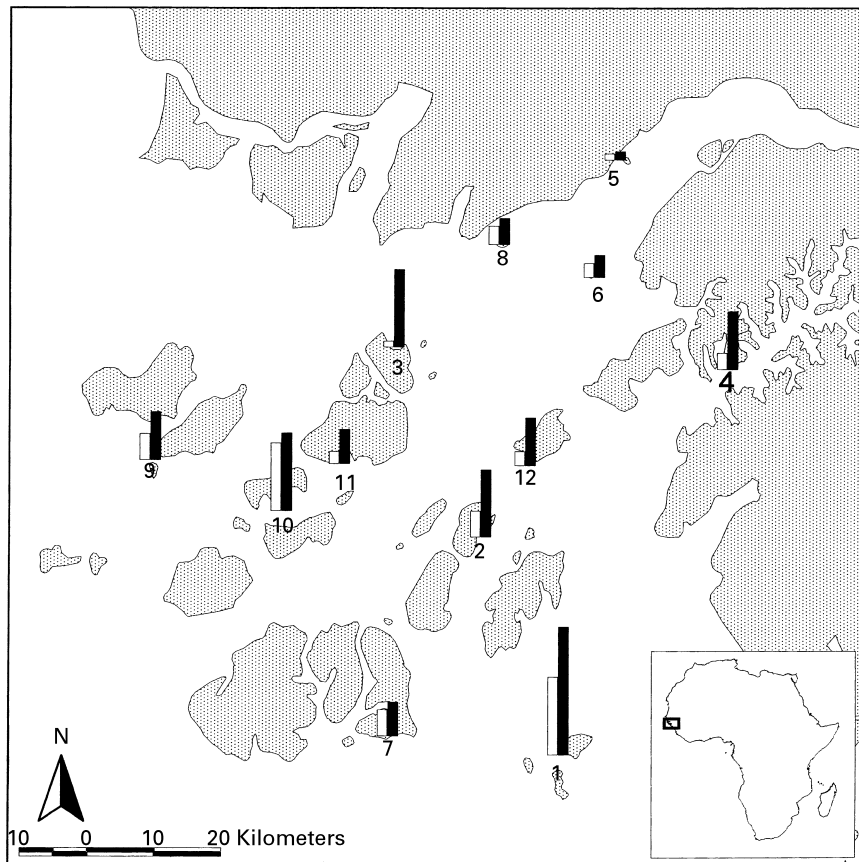
Figure 1. Study area in Guinea-Bissau with average water clarities (m) per study site (1: Cavalos 2.00–3.25 m, 2: Rubane 0.70–1.75 m, 3: Maio 0.20–2.00 m, 4: Bolama 0.45–1.50 m, 5: Bissau 0.20–0.25 m, 6: Areias 0.40–0.60 m, 7: Orangozinho 0.70–0.90 m, 8: Prabis 0.50–0.70 m, 9: Porcos 0.70–1.25 m, 10: Enu 1.75–2.00 m, 11: Egumbane 0.35–0.90 m, 12: Galinhas 0.40–1.25 m).

Study on fish

For logistic and technical reasons (most sites were not suitable for hauling a net over the bottom), species composition was measured at only two sites in the centre of the Archipélago (Maio and Rubane). Nevertheless, 236 beam trawl catches at 31 different sites in the Archipélago showed that species composition of roundfish was essentially the same at all sites except Bissau (Van der Veer 1998). Species composition was measured by hauling a beach seine net (length 22 m, depth 1 m, mesh width 10 × 10 mm) over the bottom towards the shore over a distance of *c.* 500 m. These observations were made at the same time as our tern investigations, on 11 (Maio), 25 (Rubane), 30 December 1992 (Maio) and 18 January 1993 (Maio). In total, 22 catches were conducted at regular intervals over a full tidal cycle. The total length of each fish caught was measured in 0.5-cm classes.

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

Behavioural observations on birds

Foraging terns were observed between 07:00 h and 19:00 h on 32 observation days for a total of 214 h. The number of terns using the observation area, measuring *c.* 12 500 m^2 (taking a semicircular area of about 90 m in radius), was counted at least once per hour by telescope (magnification 20–60 times). Of all terns flying in the observation area, one was selected randomly to study its feeding behaviour for as long as possible. Flying immatures were not distinguished from adults, since their winter plumages are very similar. Although terns sometimes foraged in flocks, most observations refer to terns foraging alone. Observations stopped when the tern flew out of the observation area, since prey size could not be estimated accurately from a distance greater than 90 m. Terns that did not dive for fish during the observation period were omitted from further analysis. Because of the method used, individual foraging periods were highly variable and lasted between 19 and 2280 s (average 299 ± 280 (sd) s). Foraging behaviour was observed for 16.8 h in Little Terns,

11.9 h in Sandwich Terns and 7.8 h in Royal Terns. Prey size (total length, cm) was estimated with reference to the tern's bill length (this culmen length, from tip to feathers, is for Little Tern: 2.9 cm; Sandwich Tern: 5.4 cm; Royal Tern: 6.2 cm; Cramp 1985) and classified in 3-cm length classes. Prior to data collection, fish size estimates of each observer were calibrated by holding fishes of various sizes in front of a stuffed tern. Nevertheless, it was sometimes impossible to estimate prey length in the field. Afterwards, these unknown prey were given the average fish length per category of the known prey. Capture rate (the number of prey per hour foraging) was determined for each bird observed. Data on prey size were pooled per tern species and per category (flock or solitary foraging, water clarity, phase of the tidal cycle). Food intake rate (g/h foraging) was calculated for each category by multiplying capture rate with the average prey mass.

Abiotic measurements

For the analyses of foraging behaviour, four tidal phases were distinguished: high tide (HT) (from 45 min before HT until 45 min after HT), receding tide (RT) (from 45 min after HT until 05:15 hours after HT), low tide (LT) (from 45 min before LT until 45 min after LT), and incoming tide IT (from 05:15 hours before HT until 45 min before HT); data from Admiralty Tide Tables. The daylight period (07:00–19:00 h) was divided into five periods (before 10:00, 10:01–12:00, 12:01–14:00, 14:01–16:00, after 16:00 h).

Water clarity was measured with a Secchi disk at hourly intervals during most foraging observations and beach seine days. Water clarity generally increased gradually from the beach towards the channel. To obtain a characteristic water clarity value per site per hour, water clarity was measured every 25 m along a transect approximately 250 m perpendicular to the shoreline, and the average taken. No significant day-to-day variation in water clarity was observed at any site when tidal phase was considered. Therefore, for each site and tidal phase an average clarity value was used in the statistical analyses of foraging behaviour.

Statistics

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

RESULTS

Water clarity

Water clarity varied from 0.2 m in the shallow, brackish waters near the capital of Bissau to 3.25 m in the very south of the Archipélago dos Bijagós (Fig. 1). Corrected for place, there was no relationship between water clarity and time of day (ANCOVA, $F_{4,154} = 0.385$, $P = 0.819$), nor between water clarity and tide (ANCOVA, $F_{3,155} = 4.068$, $P = 0.077$).

Prey selection

More than 95% of the 263 observed prey items taken by terns were roundfish, but these could not be identified at the species level.

In total, 3645 roundfish were captured in beach seine samples. Roundfish accounted for more than 85% of all prey items that we caught, the remainder being stingrays, flatfish and crabs (Table 1). Mullets (*Mugil* spp., *Liza* spp.) occurred in all but one sample, representing almost 25% of all roundfish caught. Another potentially important prey species for terns was *Ilisha africana*. However, this species had a very patchy distribution: virtually all 1046 individuals occurred in a single catch.

About 80% of the roundfish captured in the beach seine samples measured between 7.5 and 16.5 cm (Fig. 2). The size of prey items taken by Royal and Sandwich Terns roughly resembled the distribution in beach seine samples, although prey larger than 13.5 cm were rarely caught by the terns. Little Terns clearly selected smaller prey. Fish smaller than

Table 1. The occurrence of roundfish in 22 samples between 11 December 1992 and 18 January 1993 in the central part of the Archipélago dos Bijagós. Four different species of mullets (*Liza ramada, L. grandisquamis, Mugil cephalus* and *M. curema*) were grouped together.

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

[a]Nomenclature after Sanches (1991).
[b]All but six individuals occurred in one haul.
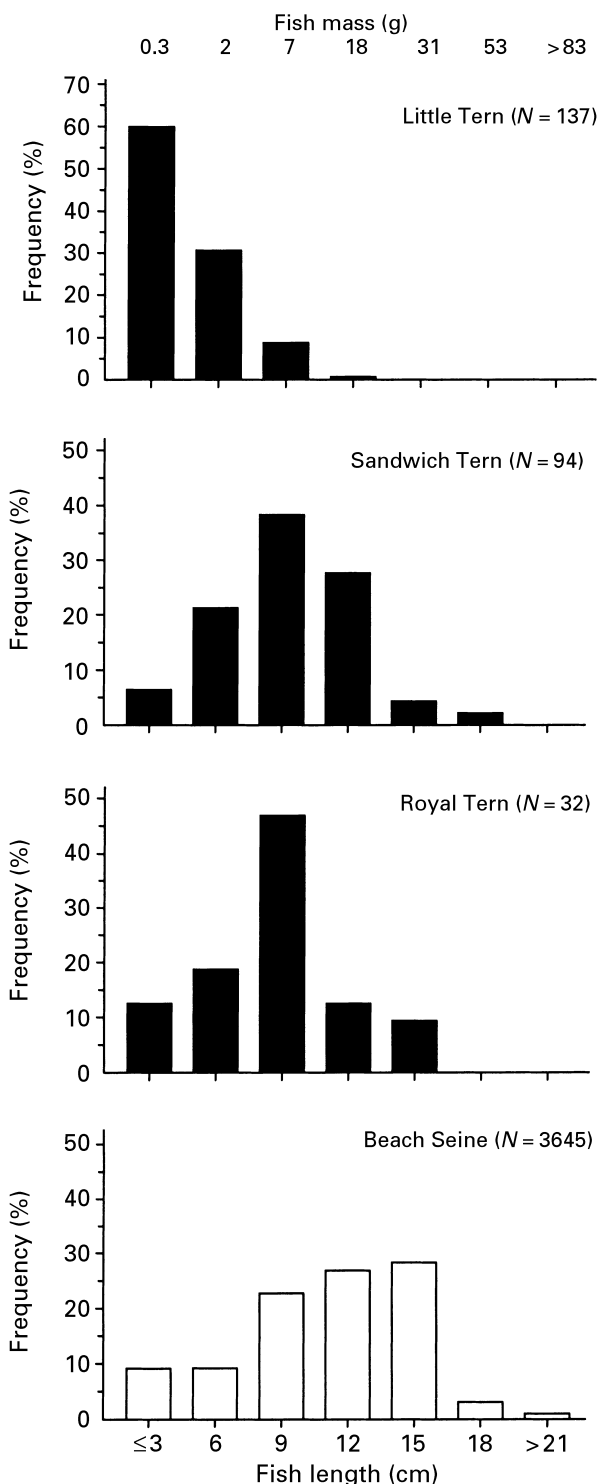
Figure 2. Frequency distribution of fish size (length and mass) caught by Little Tern (LT), Sandwich Tern (ST), and Royal Tern (RT) and by beach seine (BS). Mann–Whitney *U* tests LT – BS: $Z = -2.51$, $P = 0.012$; ST – BS: $Z = -1.25$, $P = 0.212$; RT – BS: $Z = -1.29$, $P = 0.196$.
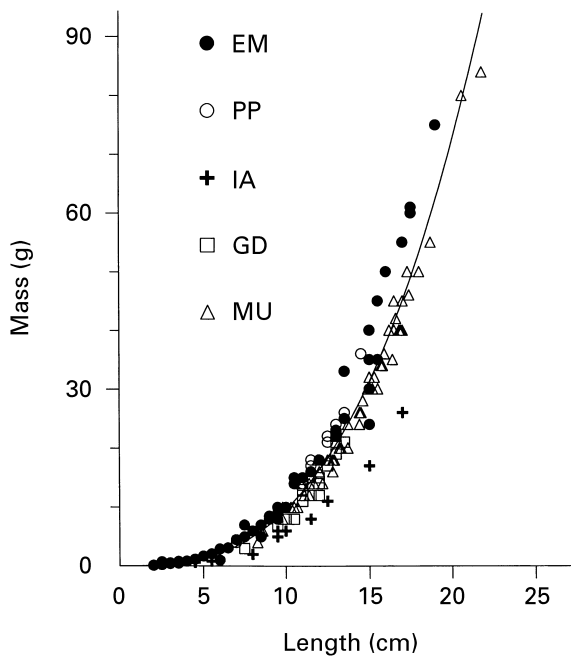
Figure 3. Relationship between mass (g) and total length (cm) of roundfish, caught in different places in the Archipélago dos Bijagós from October to December 1992 by beam trawls by H. Witte. Mass (g) = 0.01167 × Length (cm)$^{2.915}$, r^2 = 0.94, n = 184; EM = *Eucinostomus melanopterus*, GD = *Galeiodes decadactylus*, IA = *Ilisha africana*, MU = mullet (*Liza grandisquamis, L. ramada, Mugil cephalus* or *M. curema*) and PP = *Pomadasys peroteti*.

7.5 cm were significantly more abundant in their diet (90%) than in the beach seine samples (18%) (X_1^2 = 13.69, P < 0.001).

The fresh mass of roundfish increased exponentially with length (Fig. 3). Since we were unable to identify which species were captured, we had no better option than to use the overall regression equation to estimate the mass of prey taken by the terns:

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

Fortunately, fish longer than 16.5 cm were only occasionally taken and within this size range most species fell on the same curve (Fig. 3). Only the patchily distributed *Ilisha africana* had prey masses 39–47% lower than predicted by the curve, while the masses of *Eucinostomus melanopterus* were 16–28% higher.

Food intake rate

Food intake rate per hour foraging averaged 8 g in Little Terns, 60 g in Sandwich Terns and 45 g in

Royal Terns (Table 2). Despite large samples, the standard errors amounted to 16–29% of the average values, indicating large variation in the underlying data. Some of this variation may be of environmental origin due to differences related to phase of the tidal cycle, water clarity and whether birds foraged in flocks or alone. These issues are addressed below.

Occasionally, terns foraged in mixed-species flocks consisting of 15–200 individuals. Fish capture rate in flocks was always higher than that of birds foraging alone, but this did not translate into a higher food intake rate, since birds foraging in flocks caught smaller fish (Table 2). Because food intake rate did not differ between birds foraging individually and those in flocks, we decided to combine all data.

Terns spent most of the high water period at their roosts, while food was collected throughout the remainder of the tidal cycle. Foraging terns were observed for only 2.5% of 15.8 h of observations during high tide. Foraging terns were observed about six times more frequently during the other phases of the tidal cycle (receding tide: 16.6% of 93.1 h; low tide: 17.5% of 37.5 h; incoming tide: 14.7% of 67.3 h). These percentages cannot be used to calculate the amount of time that the terns spent foraging because, during this observation time, we not only followed foraging terns, but also counted the terns and made regular measurements of water clarity. Nevertheless, these figures give a fair indication of the large differences in foraging during the tidal cycle. Food intake rate was highest during a receding tide and low tide, and declined during an incoming tide (Table 3). This reduction amounted to 50%, but the average food intake rate, pooled for receding and low tides, differed significantly from an incoming tide only for Little Tern (Student's paired t-test: t_{198} = 2.939, P < 0.01) and Royal Tern (Student's paired t-test: t_{41} = 2.325, P < 0.05).

Capture rate increased with water clarity in all three species (Fig. 4, middle column), but this was only significant in the Royal Tern (Student's paired t-test: clarity < 50 cm vs. ≥ 50 cm: t_{41} = 3.62, P < 0.05). Water clarity showed a quadratic relationship with the size of the fish taken (Fig. 4, left column), since the largest fish were captured at a water clarity of only 0.5–0.9 m. For Little Tern and Sandwich Tern, food intake rate was lower in the most turbid waters (visibility < 50 cm) than in clearer waters (≥ 50 cm) (Student's paired t-test: Little Tern: t_{198} = 2.03, P < 0.05, Sandwich Tern: t_{136} = 3.41, P < 0.001) (Fig. 4, right column).

Table 2. Foraging success and calculated food intake rate of terns foraging individually or in flocks during the winter of 1992/1993 in Guinea-Bissau. For all three species, the average food intake rate was calculated combining all the data irrespective of time of day, tidal phase, water clarity or whether the bird foraged individually or in a flock (Student's paired *t*-test: Little Tern $t_{198} = 0.793$, $P > 0.20$, Sandwich Tern $t_{136} = 0.985$, $P > 0.15$, Royal Tern $t_{41} = 0.013$, $P > 0.40$).

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

Table 3. Foraging observations and the calculation of food intake rate of wintering terns in Guinea-Bissau during different phases of the tidal cycle.

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

Foraging time

From a nutritional perspective, the quality of a wintering area can be expressed as the time required to meet the daily food requirements. We assume that wintering terns in Guinea-Bissau have to at least maintain an energetic equilibrium (energy income = expenditure). Energy income (kJ/day) is calculated as the product of the time spent foraging (t_{for}) (h/day) and the rate of energy acquisition (REA) (kJ/h) while foraging:
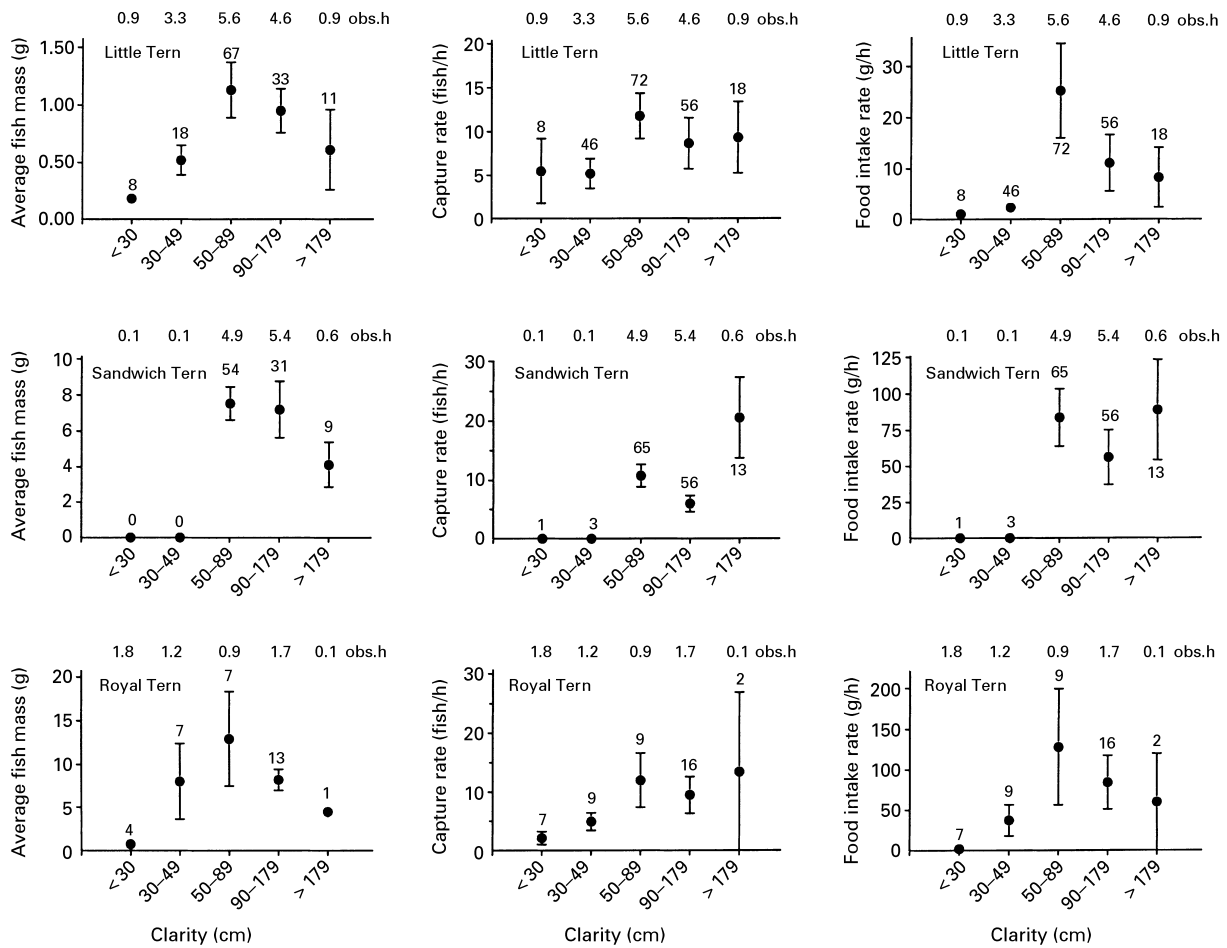
Figure 4. Relationship between water clarity and capture rate (fish/h) (middle column), average fish mass (g) (left column) and food intake rate (g/h) (right column, Student's paired *t*-test: Little Tern $t_{198} = 2.0316$, $P < 0.05$, Sandwich Tern $t_{136} = 3.4099$, $P < 0.001$, Royal Tern $t_{41} = 1.4156$, $P > 0.05$) with standard error and the number of fish caught or the number of terns of Little Tern (upper panel), Sandwich Tern (middle panel) and Royal Tern (lower panel). Clarity is divided logarithmically into five categories: < 30 cm, 30−49 cm, 50−89 cm, 90−179 cm, and > 179 cm. At the upper *x*-axis stands the observation time (in h).

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

Energy expenditure under thermoneutral conditions is largely determined by the proportions of time spent in flying and non-flying activities. The rate of energy expenditure during flight in the tropical Sooty Tern *Sterna fuscata* was estimated at 4.77 × BMR from doubly labelled water measurements, whereas metabolism averaged 1.62 × BMR during the remainder of the time (Flint & Nagy 1984). Adopting these values for the tern species in Guinea-Bissau, we estimate daily energy expenditure as

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

So, when income equals expenditure

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

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

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

Table 4. Fish length (cm), body composition (%), energy content (of wet weight, kJ/g) and digestibility Q (%) of small (sub) tropical roundfish.

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

[a]Cooper (1977).
[b]Cooper (1978).
[c]Batchelor and Ross (1984).
[d]Tollan (1988).

Table 5. The rate of energy acquisition of wintering Little Terns, Sandwich Terns and Royal Terns in Guinea-Bissau.

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

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

The rate of energy acquisition is the product of food intake rate, energy content of food and its digestibility. Several authors provide data on the energy content of tropical roundfish and their digestibility (Table 4). We used the average values of 6.37 kJ/g and 76.8%, in combination with the average food intake rate of all our measurements (Table 2), to calculate the rate of energy acquisition of each tern species (Table 5).

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

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

The effect of latitude on BMR in birds is a well-known phenomenon (e.g. Ellis 1984, Klaassen 1994, 1995b). The inclusion of latitude L (in °N or °S) in this relationship appeared to have a significant effect (Fig. 5):

$$BMR = [0.617\,(\pm 0.313) + 0.029\,(\pm 0.012)L] \times M^{0.833(\pm 0.075)}, \quad r^2 = 0.963. \quad (6)$$
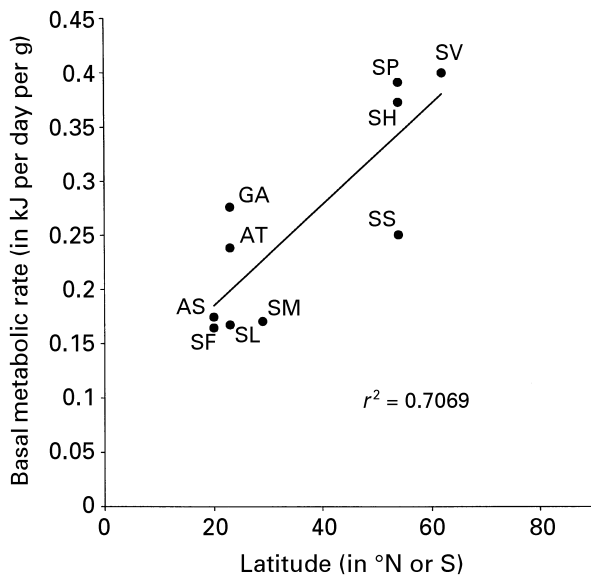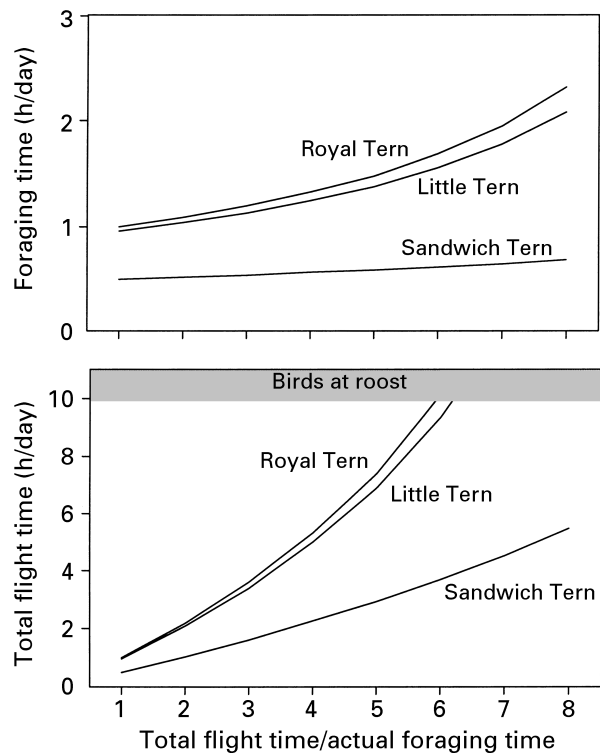
Figure 5. Basal metabolic rate (BMR, in kJ per day per g$^{1.21}$) of different terns (*Sterna lundata* (SL), *S. fuscata* (SF), *S. maxima* (SM), *Anous stolidus* (AS), *A. tenuirostris* (AT), *Gygis alba* (GA), *S. vittata* (SV), *S. paradisaea* (SP), *S. hirundo* (SH), *S. sandvicensis* (SS)) on various latitudes *L* (in °N or °S).

Figure 6. Foraging time (top) and total flight time (bottom) required to meet daily energy requirements of three species wintering in Guinea-Bissau in relation to the ratio between total flight time and actual foraging time (*m* in Equation 4, see text). Total flight time consists of foraging time plus time spent on the wing in order to find patchily distributed prey.

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

Daily food requirements can be met in a remarkably short time (1–4 h), as long as the time required to locate exploitable patches is short relative to actual foraging time (*m* < 3). When the time on the wing spent searching for exploitable food patches increases, actual foraging time increases more rapidly in Royal Terns and Little Terns than in Sandwich Terns. The results indicate that wintering terns in Guinea-Bissau should be able to meet their daily food requirements in a couple of hours foraging. However, terns may become time restricted when it takes a long time to find exploitable food patches. Terns are essentially diurnal and spend about 2 h inactive at the roost around high tide. Consequently, the time available for finding and collecting food is about 10 h. This seriously limits the range of *m* values over which terns are able to meet their daily

food requirements (Fig. 6, bottom). In order to survive, *m* should not exceed 5.9 for Royal Terns, or 6.2 for Little Terns. Sandwich Terns can deal with much more patchily distributed food; *m* values up to 8.0 are acceptable for them.

DISCUSSION

Food intake rate

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

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

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

Surprisingly, water clarity had a more pronounced effect on the size of fish captured than on capture rate. Average fish mass was highest at water clarity between 50 and 90 cm. We have no idea why the average fish mass declined when water clarity improved beyond 90 cm. Fish captured in clear water were considerably larger than those captured in the most turbid waters, but few very large individuals were captured. Recently, Mous (2000) reported on the vertical distribution of fish in relation to water clarity in Lake IJsselmeer, the Netherlands. He showed that larger fish move towards the surface as water turbidity increases. This suggests that changes in fish availability rather than visibility might be responsible for the fact that fewer large fish were captured in the clearest waters. Consequently, food intake rate increased with water clarity up to 50–90 cm, but not beyond. In general, water clarity increased with distance from the mainland, which is where most tern concentrations were also encountered. The most turbid waters occurred at the river mouth of the Rio Geba, around Bissau, Areias and Prabis (localities 5, 6 and 8, Fig. 1). With the exception of Areias (6), which is an important roost area for terns, only small numbers of terns were observed on these sites.

Wintering area quality

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

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

In our model, daily energy expenditure was calculated as the sum of energies expended during flight and non-flight activities. Daily energy expenditure increases linearly with flight time, because the presumed rate of energy expenditure was almost three times as high during flight (4.77BMR) as during 'non-flight' (1.62BMR). When food becomes more patchily distributed, terns need more time to locate exploitable patches and flight time increases until a maximum of 10 h per day. Consequently, daily energy expenditure will reach its maximum under these circumstances. This maximum rate of daily energy expenditure can be estimated provisionally for terns wintering in the tropics: DEE = (10 × 4.77BMR + 14 × 1.62BMR)/24 = about 3 × BMR (kJ/h).

This is a rather moderate value, given that sustainable rates of energy expenditure in other bird species are in the order of 4–5 × BMR (Drent & Daan 1980).

Actual rates of daily energy expenditure are almost certainly lower, since terns are not likely to

forage all day. Therefore, from an energetic point of view, wintering terns in Guinea-Bissau seem to have an easy living. Since the observed rates of food intake while foraging are high (Table 5), the crucial factor determining whether terns are able to meet their food requirements is the time required to locate exploitable food patches. With respect to this parameter, Sandwich Terns are better off than either Little Terns or Royal Terns. Sandwich Terns can afford to search for more than 1 h to find a patch, which they can exploit for 10 min. Little Terns and Royal Terns must find a similar patch within 30 min.

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

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