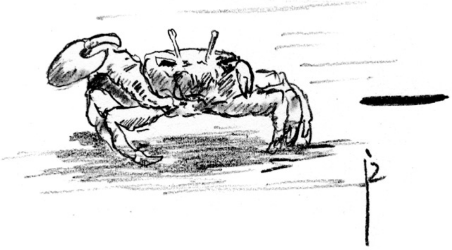
Why do Gull-billed Terns *Gelochelidon nilotica* feed on fiddler crabs *Uca tangeri* in Guinea-Bissau?

Eric W.M. Stienen[1,*], **Allix Brenninkmeijer**[2] **& Marcel Klaassen**[3]

Stienen E.W.M., Brenninkmeijer A. & Klaassen M. 2008. Why do Gull-billed Terns *Gelochelidon nilotica* feed on fiddler crabs *Uca tangeri* in Guinea-Bissau? Ardea 96(2): 243–250.

Gull-billed Terns *Gelochelidon nilotica* wintering in Guinea Bissau mainly fed on fiddler crabs *Uca tangeri* and were occasionally seen feeding on fish and locusts. As fiddler crabs have a low energy content, terns need a large gross intake to meet daily energy demands. Fiddler crabs also have a low ratio of digestible flesh to exoskeleton, and therefore tern food intake may be limited by gut capacity. Activity budgets of Gull-billed Terns feeding on fiddler crabs showed that a considerable part of the time was spent resting. The duration of resting intervals increased with energy intake and was positively correlated with the metabolisable energy content of the crab eaten, suggesting that resting periods were required for a proper digestion. The poor quality of fiddler crabs was offset by high capture rates. So daily energy expenditure of the terns could easily be met by feeding on fiddler crabs. Even when resting pauses were included in foraging time, foraging for only 1.5 hours on fiddler crabs satisfied the terns' daily energy demands. Instead, feeding on energy-rich fish would require about 2.5 hours to satisfy daily energy demands. Compared to the more specialised piscivorous Little Tern *Sternula albifrons* and Sandwich Tern *Sterna sandvicensis*, capture rate of fish was poor in Gull-billed Terns. From an energetic point of view, wintering Gull-billed Terns feeding on fiddler crabs seem to have an easy living in Guinea Bissau.

Key words: foraging behaviour, diet selection, digestive constraint, daily energy requirements, energetics, wintering, Africa



[1]Research Institute for Nature and Forest, Kliniekstraat 25, 1070 Brussels, Belgium; [2]Altenburg & Wymenga ecological consultants, P.O.Box 32, 9269 ZR Veenwouden, The Netherlands;
[3]Netherlands Institute of Ecology (NIOO-KNAW), Centre for Limnology (CL), P.O. Box 1299, 3600 BG Maarssen, The Netherlands;
*corresponding author (eric.stienen@inbo.be)

INTRODUCTION

Guinea-Bissau, notably the Archipélago dos Bijagós, is an important area for wintering waders and terns (Altenburg *et al.* 1992) among which 10 000 – 15 000 Gull-billed Terns *Gelochelidon nilotica* (Salvig *et al.* 1997). Typically, the diet of this species consists of a wide range of vertebrates and invertebrates (Gloe 1974, 1976, Møller 1977, Cramp 1985). However, on the Banc d'Arguin (Mauritania) and in the Archipélago dos Bijagós, Gull-billed Terns feed on fiddler crabs *Uca tangeri* mainly (Altenburg *et al.* 1982, 1992, Ens *et al.* 1993). Given the Gull-billed Tern's dietary spectrum including energy rich roundfish, fiddler crabs have a relatively low metabolisable energy content and a low ratio of digestible flesh to exoskeleton (Zwarts & Blomert 1990), which means that relatively large amounts must be eaten to fulfil energetic demands. In birds feeding on such poor-quality prey (Zwarts & Wanink 1991, Visser *et al.* 2000), the rate of food intake is limited by the capacity of the digestive tract (e.g. Levey & Karasov 1989, Zwarts & Blomert 1990, Zwarts & Dirksen 1990, Kersten & Visser 1996, van Gils *et al.* 2003, 2005). If digestive capacity limits food intake rate, setting a maximum to the daily amount of food that can be processed, this also limits an animal's sustained energy expenditure. In this study, we investigated if food intake rate of Gull-billed Terns foraging on fiddler crabs is limited by a digestive bottleneck and if switching to other prey species would alleviate this constraint. In the light of these results we subsequently evaluate the suitability of the coastal waters of Guinea-Bissau for Gull-billed Terns.

METHODS

Observations

Observations on foraging Gull-billed Terns were conducted at six different sites in the Archipélago dos Bijagós, Guinea-Bissau, from 15 November 1992 – 7 February 1993 (for a detailed description of the study area see Salvig *et al.* 1994, Brenninkmeijer *et al.* 2002). Observations were done by the three authors who had intercalibrated observation methods with a stuffed tern during the breeding season. Foraging terns were observed from the coast with a telescope (magnification 15–60x) between 7:00 and 19:00. Food intake rate (scored as number of items per hour, N h^{-1}), prey species (crab, fish, locust), prey size and foraging success were recorded. We estimated prey size as prey length in case of fish and locusts and carapace width in case of fiddler crabs, using the bill of the foraging tern as a reference (bill length = 38.8 mm; Cramp 1985); prey sizes were estimated to the nearest quarter bill length. Birds were only observed when off their roosting sites. Nevertheless, not all of this time was dedicated to foraging only. Whenever a tern was spotted (regardless whether it was flying without searching for food, feeding or resting), time was noted and the tern was followed until it flew out of sight. We distinguished three foraging dive classes: successful dives, failed dives and interrupted dives. Of the total observation time of 494 min, 44 min were allocated to foraging on fish, 428 min to foraging on fiddler crabs and 22 min to foraging on locusts. We observed 4, 75 and 13 successful catches of fish, fiddler crabs and locusts, respectively, during 12, 53 and 6 observation bouts that lasted on average 3.6, 8.1 and 3.7 min. During observations individual terns did not switch between prey types.

We distinguished four different rates of food consumption: *food intake rate* (N h^{-1} feeding), *crude food intake rate* (N h^{-1} foraging time; foraging time combines feeding and associated non-feeding time spent to flying and loafing), *metabolisable energy intake rate* (kJ h^{-1} feeding time) and *crude metabolisable energy intake rate* (kJ h^{-1} foraging time).

Energy content

Gull-billed Terns dived at larger crabs (>20 mm), apparently immobilising the prey by a hard peck on its carapace. After this dive the tern made a loop and landed on top of the prey. Extremities of large crabs were shaken off before swallowing the prey's carapace. Quite often, we subsequently observed the tern eating the previously removed extremities. Small crabs (≤ 20 mm) were often picked from the mudflats and swallowed as a whole in flight. Disregarding sex differences, we used allometric relationships provided by Zwarts & Blomert (1990) to convert carapace width (*cw*, mm) to gross energy content (E, kJ) of the fiddler crabs using:

$$E = 0.\,021 \times \exp\,(2.97 \times \ln(cw) - 3.10) \qquad (1)$$

We assumed a digestibility of 65%, as was found in Whimbrels *Numenius phaeopus* feeding on fiddler crabs (Zwarts & Blomert 1990). Similarly to Gull-billed Terns, Whimbrels swallowed the smaller crabs as a whole, often discarding extremities of larger crabs. Since both species preyed on the same size of crabs, we assumed a comparable proportion of leftovers in both species. Following Zwarts & Blomert (1990), we assumed a linear increase of the proportion of energy left over (0.5% increase per mm cw) for crabs with a carapace width of over 10 mm. For different sized crabs the calculation of metabolisable energy intake from gross energy content of the fiddler crabs (Eq. 1) thus was:

$$\begin{aligned} ME &= 0.65 \times E \quad \text{if } cw \leq 10\text{ mm} \qquad (2)\\ ME &= 0.65 \times E \times (1-(cw-10) \times 0.005) \quad \text{if } cw > 10\text{ mm} \end{aligned}$$

Brenninkmeijer *et al.* (2002) sampled roundfish in Guinea-Bissau and recorded the following relationship between fish length (L, mm) and mass (M, g):

$$M = 0.001419 \times L^{2.915} \qquad (3)$$

Average energy content of fish is 21.3 kJ g^{-1} dry mass (range 16.8–23.9), water content is 76.7% (82.7–69.8) and digestibility is 82.5% (81.1–84.9) (Dunn 1975, Barrett *et al.* 1987, Tollan 1988, Massias & Becker 1990, Klaassen *et al.* 1992) resulting in the following relationship for metabolisable energy content of captured fish:

$$ME = 4.09 \text{ kJ g}^{-1} \times M \qquad (4)$$

Fat and protein contents of the locust *Locusta migratoria* are variable, depending on stage in the life cycle and phase (*gregaria* or *solitaria*, Matthée 1945, Cheu 1952). We used mean values of fat and protein content of the *gregaria* phase of 2–7 weeks old locusts (154.9 mg fat and 494.3 mg protein per locust; Cheu 1952) yielding an energy content of 17.8 kJ per locust using energy equivalents of 39.5 kJ g^{-1} and 23.6 kJ g^{-1} for fat and protein respectively (Brody 1945). Employing the digestibility of 72% as was found in American Robins *Turdus migratorius* and European Starlings *Sturnus vulgaris* feeding on crickets (Levey & Karasov 1989) and disregarding differences in length, metabolisable energy content of a locust was estimated at:

$$ME = 12.8 \text{ kJ} \qquad (5)$$

Predictive energy budget

Based on estimates of crude metabolisable energy intake rates we predicted the amount of time to satisfy daily energy requirements. In the model we assumed basal metabolic costs of Gull-billed Terns at 2.3 $g^{0.774}$ (kJ day^{-1}) following Bryant & Furness (1995). For body mass (g), the average of Gull-billed Terns caught in Guinea-Bissau was used (198.3 ± 23.5 g, $n = 48$). Field Metabolic Rates (FMR) at rest and during flight were estimated using 1.6 x BMR and 4.77 x BMR, respectively, following a study on Sooty Terns *Sterna fuscata* by Flint & Nagy (1984). We assumed that the terns were resting when not foraging.

Statistical analysis

Data handling and statistics were conducted using SPSS (Norusis 1990) and GENSTAT (Genstat 5 Committee 1993). Mean values (including SDs) as shown in the figures and tables were computed by averaging all observations falling within a specific category (e.g. hour during the tidal cycle) after weighting for the duration of the observation within that category.

RESULTS

Gull-billed Terns were observed feeding on locusts on one occasion only. After a night with strong offshore winds, thousands of mostly dead locusts floated on the water surface. Diving success on locusts was highest, followed by fiddler crabs and roundfish (Fig. 1).

Nevertheless, food intake rate while feeding on fiddler crabs was highest, directly followed by locusts, with roundfish being lowest. Time spent in other behaviours but feeding highly depended on the species preyed upon (Fig. 1). When foraging

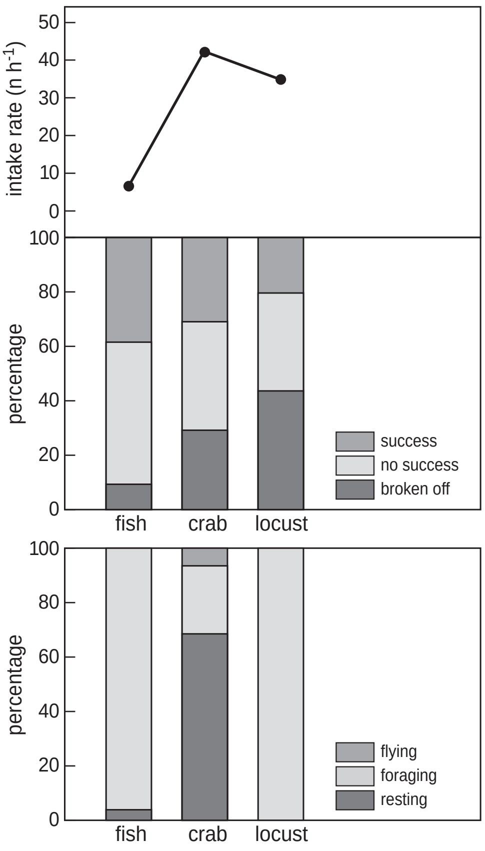


Figure 1. Average food intake rate (n h^{-1}), diving success (%) and activity budget (i.e. time dedicated to feeding, resting and flying as % of time) of Gull-billed Terns foraging on roundfish, fiddler crabs or locusts. The dives are divided in successful, unsuccessful and interrupted dives (i.e. dives broken off without touching the surface).

on fiddler crabs, the proportion of time dedicated to resting was very high compared to periods when foraging on fish or locusts. Taking the time spent in other behaviours but feeding (i.e. loafing and flying without searching for food) into account, crude food intake rates and crude metabolisable energy intake rates were lowest when feeding on fish, intermediate on fiddler crabs and highest when feeding on locusts (Table 1). Given the crude metabolisable energy intake rates the terns would balance their daily energy requirements by foraging for about 2.5 hours per day on fish (feeding and non-feeding time combined, Fig. 2), while foraging on crabs would take about 1.5 hours per day. Foraging on locusts would take less than 1 hour to acquire the daily amount of metabolisable energy needed.

Activity budgets of Gull-billed Terns foraging on fiddler crab were strongly dependent on tide (Fig. 3). Around high tide no foraging terns were present in the area. Gull-billed Terns were observed flying to the roosting areas just before high tide and returned to the feeding areas one hour after high tide. Feeding started three hours prior to low tide increasing to a maximum of 80% of the observed time two hours after low tide. However, metabolisable energy intake rate showed a maximum well before low tide and gradually decreased in the hours after low tide (Fig. 3), whereas crude metabolisable energy intake was highest from low tide to two hours after low tide. Feeding activity was therefore poorly correlated with metabolisable energy intake rate (logistic regression, $R^2 = 0.009$,

Table 1. Weighted means (±SD) of food intake rate, crude food intake rate, metabolisable energy intake rate and crude metabolisable energy intake rates of Gull-billed Terns feeding on roundfish, fiddler crab or locust. Numbers between brackets denote number of foraging /feeding bouts.

Variable	Roundfish	Fiddler crab	Locust
Food intake rate (N h^{-1} feeding)	5.9 ± 12.0 (12)	41.7 ± 38.2 (36)	34.8 ± 25.6 (6)
Crude food intake rate (N h^{-1} foraging)	5.6 ± 10.7 (12)	10.5 ± 13.3 (53)	34.8 ± 25.6 (6)
Metabolisable energy intake rate (kJ h^{-1} feeding)	116.7 ± 335.1 (12)	617.3 ± 656.0 (36)	446.0 ± 328.1 (6)
Crude metabolisable energy intake rate (kJ h^{-1} foraging)	111.7 ± 328.2 (12)	164.7 ± 189.9 (53)	446.0 ± 328.1 (6)

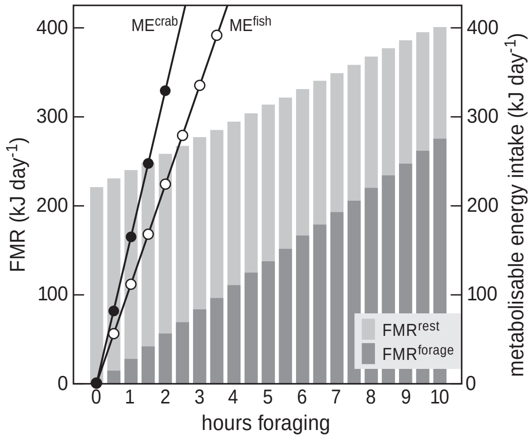


Figure 2. Model predicting the required foraging time for Gull-billed Terns when foraging on either fiddler crabs (ME^{crab}) or roundfish (ME^{fish}). The bars are predictions of the field metabolic rate (FMR) at rest and at flight.

$P > 0.05$, $n = 53$), proportion of time spent in resting intervals paralleling metabolisable energy intake considerably better (logistic regression, $R^2 = 0.23$, $P < 0.001$, $n = 53$). The latter suggests that gut processing rate may be limiting metabolisable energy intake rate in Gull-billed Tern foraging on fiddler crabs. More direct proof for this hypothesis is obtained from comparing the duration of the recorded resting intervals after a crab was eaten with the energy content of the ingested fiddler crab (Pearson regression, $R^2 = 0.44$, $P < 0.001$, $n = 73$; Fig. 4).

We did not measure fiddler crab availability in Guinea Bissau, but Ens *et al.* (1993) showed that the number of surfacing fiddler crabs was highest at low tide on the Banc d'Arguin in Mauritania. Using their data on the number of surfacing fiddler crabs in relation to tide, we found that metabolisable energy intake rate correlated positively with the tide-specific abundance of fiddler crabs (Pearson regression, $R^2 = 0.11$, $P = 0.01$, $n = 53$). Also a logistic regression of the proportion of time spent resting yielded a significant contribution of tide-specific fiddler crab abundance (Table 2). The subsequent inclusion of metabolisable energy

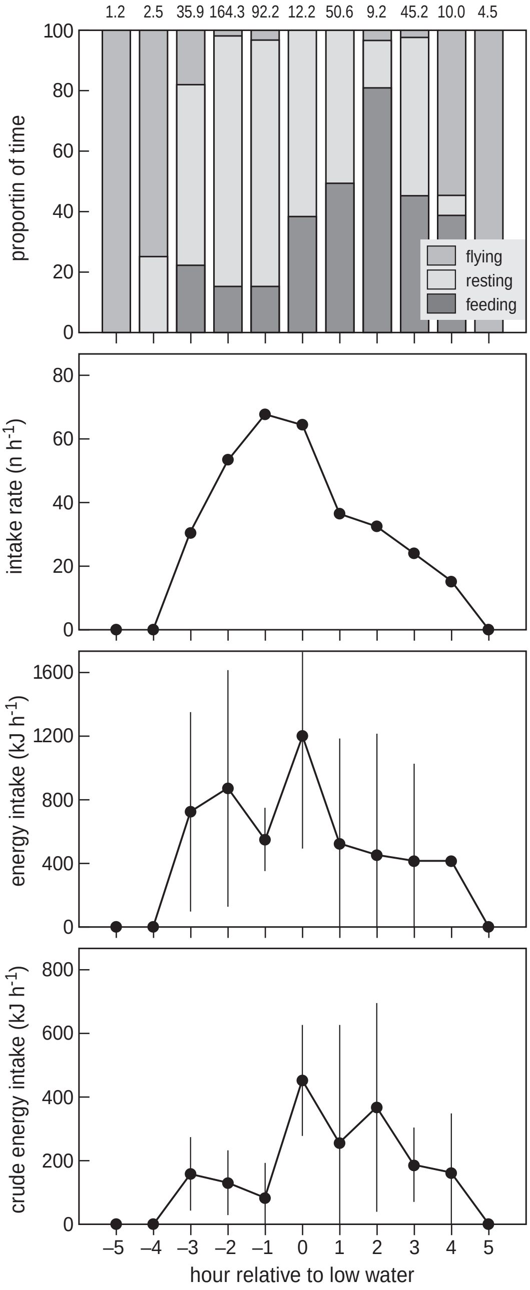


Figure 3. Time budget, food intake rate, energy intake rate and crude energy intake rate as a function of the moment in the tidal cycle. Numbers above the top-panel depict total observation time per period in minutes. Error bars denote SDs.

Table 2. Stepwise logistic regression analysis examining variation in proportion of time spent resting by Gull-billed Terns in relation to expected tide-specific fiddler crab abundance (from Ens *et al.* 1993) and metabolisable energy intake rate.

Variable	Estimate (SE)	R^2 change	P
Fiddler crab abundance	0.3880 (0.203)	0.122	< 0.001
Metabolisable energy intake rate	0.0010 (0.0004)	0.172	< 0.001
Constant	–2.3300 (0.635)		

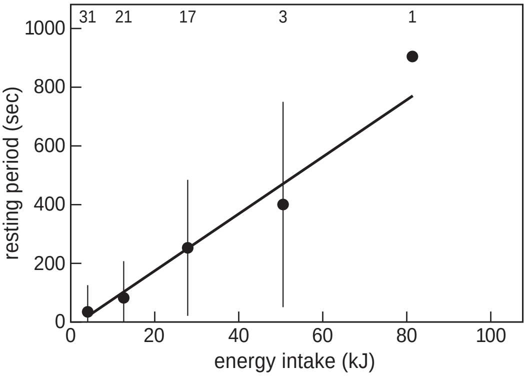


Figure 4. Relationship between the metabolisable energy content of the crab eaten and the duration of the subsequent resting interval. The regression line is based on all data. Numbers above the figure denote sample sizes.

intake rate in this model significantly improved the explained variance. The proportion of non-feeding time (i.e. resting and flying without searching for food combined) decreased with fiddler crab abundance (logistic regression, R^2 change = 0.82, $P < 0.001$, $n = 53$).

DISCUSSION

Food intake rates of Gull-billed Terns feeding on fiddler crabs were somewhat higher than those found by Ens *et al.* (1993) on the Banc d'Arguin in Mauritania. In Mauritania food intake rates ranged between 19.3–32.1 crabs h^{-1}, with highest intake rates when foraging on flocking fiddler crabs. However, foraging on flocking fiddler crabs rarely occurred in both Mauritania and Guinea-Bissau. Terns foremost foraged on the beach where the on average smaller crabs can be found feeding near their burrows (Ens *et al.* 1993). Studying Whimbrel foraging in Guinea-Bissau, Zwarts (1985) also found that fiddler crabs of 20–30 mm, which typically do not occur in flocks but typically forage near their burrows, suffered the highest predation risk.

Around high tide, when no fiddler crabs were available, the terns had two options. The first option was switching to other prey types, the only alternative prey type available being fish. However, as Brenninkmeijer *et al.* (2002) showed, the numbers of specialised fish-feeding terns in the area, like Little Tern *Sternula albifrons*, Sandwich Tern *Sterna sandvicensis* and Royal Tern S. maxima, were lowest during high tide. This suggests that fish availability is lowest during the high water period. It is thus unlikely that a non-specialist like the Gull-billed Tern would switch to foraging on fish during high tide. The remaining option was to cease foraging altogether during high tide. This makes it conceivable that time allocated to behaviours other than feeding (resting and flying without searching for food) is highest when crab availability is at a minimum. However, if food intake rate is constrained by gut processing capacity, one should at the same time expect that time spent resting is positively related to food intake rate. We indeed found that the time allocated to resting increased with metabolisable energy intake rate. Although we do not provide conclusive evidence, the observations can be explained by a limiting capacity of the digestive tract. Moreover, the duration of the resting intervals increased with crab size, supporting the hypothesis that resting periods were digestive pauses, thus reflecting digestive limitations.

Apparently, Gull-billed Terns encountered the same digestive problems as Whimbrels foraging on fiddler crabs (Zwarts & Blomert 1990, Zwarts & Dirksen 1990). Although energy intake rates matched crab abundance, foraging activity did not; despite increasing crab abundance in the hours prior to low tide, foraging activity of the terns was more or less stable at a low level. Only from low tide onwards, foraging activity was relatively high with concomitantly high crude metabolisable energy intake rates. We suggest that in the hours following high tide, the terns' motivation to feed was high after roosting for some hours. At this moment in time their guts must also have been empty, allowing for the initial ingestion of relatively large amounts of food in a short time, though at the expense of long resting pauses.

If the capacity of the gut limited intake rates, as we suggest, Gull-billed Terns should be able to increase energy intake by changing to other prey with less non-digestible matter. However, our calculations indicated that switching to fish feeding would be even less profitable (Table 1). Fish intake rate of 5.9 fish h^{-1} in Gull-billed Terns was much lower than that in specialised fish-feeders like Little Tern (8.9 fish h^{-1}) and Sandwich Tern (8.4 fish h^{-1}) in the same area (Brenninkmeijer *et al.* 2002). Locust-feeding forms a good alternative in terms of crude metabolisable energy intake rate, yet they are available only occasionally. This leaves fiddler crabs as the best alternative for Gull-billed Terns in Guinea-Bissau. Although we provide indications that food intake rate might be limited by a digestive constraint when feeding on fiddler crabs, daily energy requirements are easily met. In fact, foraging for less than two hours (crude foraging time) would satisfy the terns' daily energy demands. From this point of view, Guinea-Bissau is clearly a very suitable habitat for wintering Gull-billed Terns.

ACKNOWLEDGEMENTS

We thank the crew of the research vessel "Knud W." and all participants of the Guinea-Bissau expedition for their pleasant company and help in the field. The Ministry of Agriculture, Fishery, Education and Science, and the Swedish Embassy, the Foundation Dutch Volunteers (SNV) and the IUCN Biosphere Project (Bubaque), all in Guinea-Bissau, gave permissions or supported the expedition otherwise. The manuscript benefited from the comments by Marcel Kersten, Leo Zwarts, Arie L. Spaans, Hans Schekkerman and two anonymous reviewers. This is publication 4317 of the Netherlands Institute of Ecology (NIOO-KNAW). The publication was partly written under the support of Belgian Science Policy (WEST-BANKS SD/BN/01A).

REFERENCES

Altenburg W., Engelmoer M., Mes R. & Piersma T. 1982. Wintering waders at the Banc d'Arguin, Mauritania. Comm. 6 Wadden Sea Working Group, Leiden.

Altenburg W., Wymenga E. & Zwarts L. 1992. Ornithological importance of the coastal wetlands of Guinea-Bissau. WIWO-report 26, Zeist.

Barrett R.T., Anker-Nilssen T., Rikardsen F., Valde K., Røø N. & Vader W. 1987. The food, growth and fledging success of Norwegian Puffin chicks *Fratercula arctica* in 1980–1983. Ornis Scand. 18: 73–83.

Brenninkmeijer A., Stienen E.W.M., Klaassen M. & Kersten M. 2002. Feeding ecology of wintering terns in Guinea-Bissau. Ibis 144: 602–613.

Brody S. 1945. Bioenergetics and growth. Reinhold Publishing Company, New York.

Bryant D.M. & Furness R.W. 1995. Basal metabolic rates of North Atlantic seabirds. Ibis 137: 219–226.

Cheu S.P. 1952. Changes in the fat and protein content of the African migratory locust, *Locusta migratoria migratorioides* (R. & F.). Bull. Entomol. Res. 43: 101–109.

Cramp S. 1985. The birds of the western Palearctic, 4. Oxford University Press, Oxford.

Dunn E.H. 1975. Caloric intake of nestling Double-crested Cormorants. Auk 92: 553–565.

Ens B.J., Klaassen M. & Zwarts L. 1993. Flocking and feeding in the fiddler crab (*Uca tangeri*): prey availability as risk-taking behaviour. Neth. J. Sea Res. 31: 477–494.

Flint E.N. & Nagy K.A. 1984. Flight energetics of free-living Sooty Terns. Auk 101: 288–294.

Genstat 5 Committee 1993. Genstat 5 Release 3 Reference Manual. Clarendon Press, Oxford.

Gloe P. 1974. Die Lachseeschwalbe (*Gelochelidon nilotica*) in Dithmarschen. Orn. Mitt. 26: 47–51.

Gloe P. 1976. Nahrung und Zug der Lachseeschwalbe (*Gelochelidon n. nilotica*) im Wattenmeer. Orn. Mitt. 28: 117–123.

Kersten M. & Visser W. 1996. The rate of food processing in the Oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. Funct. Ecol. 10: 440–448.

Klaassen M., Zwaan B., Heslenfeld P., Lucas P. & Luijckx B. 1992. Growth rate associated changes in the energy requirements of tern chicks. Ardea 80: 19–28.

Levey D.J. & Karasov W.H. 1989. Digestive responses of temperate birds switched to fruit or insect diets. Auk 106: 675–686.

Massias A. & Becker P.H. 1990. Nutritive value of food and growth in Common Tern *Sterna hirundo* chicks. Ornis Scand. 21: 187–194.

Matthée J.J. 1945. Biochemical differences between the solitary and gregarious phases of locusts and noctuids. Bull. Entomol. Res. 36: 343–371.

Møller A.P. 1977. Sandternens *Gelochelidon n. nilotica* Gmel. fode i yngletiden i Nordjylland og Camarque, Frankrig, med en oversigt over fodeemner i andre dele af artens udbredelsesområde. Dansk orn. Foren. Tidskr. 71: 103–111.

Norusis M.J. 1990. SPSS/PC+ 4.0 Base Manual. SPSS Inc., Chicago.

Salvig J.C., Asbirk S., Kjeldsen J.P. & Rasmussen P.A.F. 1994. Wintering waders in the Bijagós Archipélago, Guinea-Bissau 1992–1993. Ardea 82: 137–142.

Salvig J.C., Asbirk S., Kjeldsen J.P., Rasmussen P.A.F., Quade A., Frikke J. & Christophersen E. 1997. Wintering Terns in the Coastal Zone of Guinea-Bissau. In: Asbirk S. & Petersen I.K. 1997. Waterbirds in Guinea-Bissau: Report on the Activities of the Work Program 1995–1997. Unpubl. report to the Trilateral Cooperation on the Protection of the Wadden Sea.

Tollan A.M. 1988. Maintenance energy requirements and energy assimilation efficiency of the Australasian Harrier. Ardea 76: 181–186.

van Gils J.A., Schenk I.W., Bos O. & Piersma T. 2003. Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. Am. Nat. 161: 777–793.

van Gils J.A., De Rooij S.M., van Belle J., van der Meer J., Dekinga A., Piersma T. & Drent R. 2005. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. I. Prey choice. J. Anim. Ecol. 74: 105–119.

Zwarts L. 1985. The winter exploitation of fiddler crabs *Uca tangeri* by waders in Guinea-Bissau. Ardea 73: 3–12.

Zwarts L. 1990. Increased prey availability drives premigration hyperphagia in Whimbrels and allows them to leave the Banc d'Arguin, Mauritania, in time. Ardea 78: 279–300.

Zwarts L. & Blomert A-M. 1990. Selectivity of Whimbrels feeding on fiddler crabs explained by component specific digestibilities. Ardea 78: 193–208.

Zwarts L. & Dirksen S. 1990. Digestive bottleneck limits the increase in food intake of Whimbrels preparing for spring migration from the Banc d'Arguin, Mauritania. Ardea 78: 257–278.

SAMENVATTING

Lachsterns *Gelochelidon nilotica* die in Guinee-Bissau overwinteren, eten vooral wenkkrabben *Uca tangeri* en af en toe vissen en sprinkhanen. Wenkkrabben hebben een lage energie-inhoud, waardoor relatief grote hoeveelheden gegeten moeten worden om aan de dagelijkse voedselbehoefte te voldoen. Bovendien bevatten wenkkrabben relatief veel niet-verteerbare delen, waardoor de capaciteit van het spijsverteringskanaal een beperkende factor zou kunnen zijn voor de voedselopname. Lachsterns die wenkkrabben eten, brengen een groot deel van de tijd rustend door. De rustperiodes nemen toe met de energieopname. Bovendien zijn de rustintervallen na het verorberen van een prooi positief gecorreleerd met de energie-inhoud van de gegeten krabben. Waarschijnlijk zijn deze rustperiodes, die de voedselopname begrenzen, nodig voor een goede vertering. Desalniettemin zijn wenkkrabben een goede prooikeuze voor de Lachsterns. Vanwege de hoge vangsnelheid kunnen de sterns met het eten van krabben gemakkelijk in hun dagelijkse voedselbehoefte voorzien. Wanneer Lachsterns 1,5 uur op wenkkrabben foerageren, rustpauzes inbegrepen, krijgen ze genoeg energie binnen voor de hele dag. Wanneer ze op vissen jagen, hebben ze hiervoor ongeveer 2,5 uur nodig. In vergelijking tot meer gespecialiseerde visetende sterns als Dwergstern *Sterna albifrons* en Grote Stern *S. sandvicensis* is het vangsucces van vis bij Lachsterns zeer laag. Energetisch gezien hebben overwinterende Lachsterns die in Guinee-Bissau wenkkrabben eten, dus een gemakkelijk leven.

Corresponding editor: Dik Heg
Received 11 February 2008; accepted 23 May 2008