

# SELECTIVITY OF WHIMBRELS FEEDING ON FIDDLER CRABS EXPLAINED BY COMPONENT SPECIFIC DIGESTIBILITIES

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**ABSTRACT** Whimbrels feeding on crabs took food with a low rate of return because half of the mass was inorganic, and 30% of the organic mass within the skeleton itself was not digestible. The digestibility of this prey (65%) was therefore below the average efficiency with which birds usually digest fish or flesh. The Whimbrel is able to metabolize 99% of the fat, 74% of the protein (correcting for urinary nitrogen production) and 1% of the carbohydrates (found mainly in the skeleton). The apparent and true metabolizable energy content of crabs was 7 and 8 kJ g<sup>-1</sup> dry mass, respectively. When more food was available, the bird became more selective by refusing a greater part of the skeleton. As a consequence, the relative amount of flesh in the food increased. Food digestibility decreased when more food was ingested per day. This was probably due to a third factor: intake rate increased with the amount of food taken and a higher intake rate reduced prey digestibility. However, since the decrease in digestibility was less than the increase in intake rate, ingesting food at the higher rate was a profitable strategy.

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## INTRODUCTION

Animals ingesting food with a low metabolizable energy content have to eat more, but there is of course a limit to the rate at which food can be taken (e.g. Barrett & Bailey 1972, Coleman & Boag 1987, Bédard & Gauthier 1989). The disadvantage of relatively low rates of return is obvious if feeding time is restricted and the storage of food is limited by the capacity of the digestive tract, due to a digestive bottleneck (Kenward & Sibly 1977, 1978). Recent papers stress the ecological significance of the rate at which food can be processed as a factor limiting energy intake (e.g. Hixon 1982, Diamond *et al.* 1986, Levey & Karasov 1989, Worthington 1989, Zwarts & Dirksen 1990, M. Kersten & W. Visser pers. comm.). On the basis of a simple optimal foraging strategy, birds could be expected to select a diet which guarantees a relatively high rate of return, i.e. a diet in which both the energy content as well as the proportion that can be utilized is as

high as possible, and moreover the extraction occurs at the fastest rate.

It is conceivable that waders eating gastropods, bivalves or crabs and ingesting the shell or exoskeleton may encounter the bottleneck problem, since 50-90% of such food consists of inorganic mass. The inorganic matter becomes even more detrimental if it reduces the efficiency with which flesh is digested. Thus Speakman (1987) suggested that either the mere presence of inorganic matter obstructing the access of digestive enzymes to the organic material and/or the presence of carbonates causing an unfavourably high pH in the gut could reduce digestive efficiency.

This paper describes an experiment on a captive Whimbrel *Numenius phaeopus* to investigate the metabolizable energy content of fiddler crabs *Uca tangeri*. Crabs are the staple diet for Whimbrels on intertidal areas all over the world. The Shore Crab *Carcinus maenas* is a main prey in late summer when Whimbrels pass through the Wadden Sea

(Zwarts pers. obs.), whereas fiddler crabs (*Uca* spec.) and other crab species are the main prey in tropical and subtropical wintering areas (e.g. Summers 1980, Colby & Fonseca 1984, Dann 1987, Zwarts 1985, Zwarts & Dirksen 1990).

## METHODS

### Experiment

A Whimbrel whose main prey was *Uca* was captured on the beach near Iouik, Mauritania, on 27 March 1986, (see Wolff & Smit 1990 for a description of the study area). The bird was kept in a cage with a board on the floor (1x1 m; for more details see Klaassen *et al.* 1990) and fed with freshly collected crabs. The cage could be approached and the bird observed without disturbance. Crabs were slid into the cage down a tube, usually one and, at most, five at a time. No new food was given until the crabs already offered had been taken. The time the Whimbrel needed to eat the crabs was determined by direct observation and was termed the 'crude feeding time'. It totalled many h a day and, although all crabs were eventually attempted (except day 2-4; see below), many were only incompletely consumed.

The bird was given food between 10.30 and 23.00 h and was weighed each day at 10.00 h, at which time the excreta and prey remnants were removed and the water replenished. The nocturnal starvation period was undoubtedly sufficiently long to allow the bird to empty its alimentary tract. A throughput period of 1 h is general in waders and ducks feeding on marine food (Grandy 1972, Swennen 1976: Table 29, Speakman 1987, Castro *et al.* 1989a). Furthermore the decrease in body mass after feeding stops, suggests that most of the ingested food goes in 2 to 4 h (Zwarts *et al.* 1990b).

The experiment began immediately after the bird's capture. At the start, the bird took all the crabs offered, but on the second day, it refused 11 out of 20. On day 3 the food consumption was even less (29 out of 32 prey refused) and on day 4 none were taken of the 40 given. The rejected prey were all dismembered in the way Whimbrels normally

do when feeding on large crabs. The bird lost 60 g, or 16% of its initial body mass of 369 g, and weakened noticeably. But immediately after fresh water instead of sea water was given, the bird recovered. During the rest of the experiment, its body mass was on average 333 g. The salt concentration of the sea water in the drinking dish increased through evaporation by 50% within one day (Klaassen & Ens 1990) and probably there was evaporation from the crabs. So the Whimbrel must have suffered from salt stress; see Klaassen & Ens (1990) for further discussion. During the rest of the experiment (12 days), fresh water was given. Days 2-5 were excluded from the analysis. Prey remnants were collected every day, but the excreta only on seven days (days 10-16).

Although we offered the bird a variable amount of food each day, its composition was always similar. Two male crabs were given for every one female and their masses averaged 800 to 1000 mg ash-free dry mass (AFDM).

### Laboratory

The fresh body mass of *Uca* was determined to the nearest 0.5 g in recently collected specimens. During the experimental period, crabs ( $n = 430$ ) were stored in 4% formalin solution. Another sample ( $n = 207$ ) taken in the same area in August 1988, was dried, after being killed in a deep-freezer. All crabs were taken to The Netherlands for further analysis. The crabs stored in formalin were rinsed. All the crabs were then dried at 70°C and weighed to determine dry mass (DM). Carapace width was measured to the nearest 0.1 mm with digital vernier calipers.

The CaCO<sub>3</sub> content of the DM of 123 crabs was determined according to Scheibler's gas-volumetric analysis (Hofstee 1980).

Ash weight was determined by burning at 550°C for 2 h. Separate burning of 100% CaCO<sub>3</sub> showed that 0.42% was lost during ignition. Hence the ash-free dry mass (AFDM) of crab samples were adjusted for these losses.

NaCl was derived from a titrimetric determination of the Cl<sup>-</sup> content in the ash (not in the DM, which gave unreliable results). The figures are

minimum estimates as some salt may have been lost during drying and, in the formalin-preserved crabs, during rinsing.

Fat was measured with a Soxhlet apparatus using petroleum-ether as solvent for a period of four h. The amount of nitrogen was determined with the Kjeldahl method. Protein was estimated as being 6.25 times the amount of nitrogen (Kleiber 1975). The remaining organic matter was regarded as carbohydrates.

Prey remnants and excreta from the captive Whimbrel were dried and the DM and AFDM and the amounts of NaCl, CaCO<sub>3</sub>, fat and nitrogen determined as in the *Uca*. To separate urinary and faecal nitrogen, the lead acetate method (Terpstra & de Hart 1974) was used to determine the precipitable or non-endogenous faecal nitrogen.

The energy content of crabs, prey remnants and excreta were measured with a recently calibrated Parr-1655 adiabatic calorimeter. In material with low energy content benzoic acid was used as an additive to guarantee complete combustion. A correction was made for the endothermic reaction during the combustion caused by decomposition of CaCO<sub>3</sub>. In *Uca*, this was 0.3 kJ g<sup>-1</sup>, given a heat equivalent of 0.0057 kJ for each per cent CaCO<sub>3</sub> (Paine 1966). No correction was made for acid formation because the heat loss is negligibly small (Schroeder 1977).

The AFDM does not represent only dried flesh, as organic matter also occurs in the skeleton. The enzyme collagenase allows the separation of flesh

from other organic matter, because it reacts with the collagen fibres that bind tissue together. Ten *Uca* were dried, weighed and broken into fragments and then held in a phosphate buffer (pH 7.4) with collagenase (Merck Art. 24015) at 37°C for several days. After the disintegrated flesh had been decanted, the residues consisted only of bony exoskeleton, soft endoskeleton, hairs and eyes. These remains were dried, and the DM and AFDM and the amounts of CaCO<sub>3</sub>, NaCl, fat and nitrogen were determined. The AFDM and the amounts of CaCO<sub>3</sub>, fat and nitrogen were also measured in a sample of cleaned exoskeletons.

All statistical analyses were performed with a standard statistical package (Norusis 1988).

## RESULTS

### *Uca* food offered to the Whimbrel

The water content of *Uca tangeri* was a constant 75%. The difference between wet and dry body mass was the same for all size classes. The mean dry mass ( $\pm$  SE) as a percentage of wet mass was 25.5  $\pm$  0.4 ( $n = 45$ ) for  $\sigma\sigma$  and 24.3  $\pm$  0.2 ( $n = 32$ ) for  $\varphi\varphi$ .

The relationships between the size (width of the carapace) and the dry, calcareous and ash-free dry mass (DM, CaCO<sub>3</sub>, AFDM, respectively) of the crabs are given in Table 1. About half of the DM was inorganic material. NaCl relative to DM was 7.5% ( $SE = 0.5$ ,  $n = 4$ ) in formalin-preserved

**Table 1.** Allometric relationships in *Uca tangeri*, collected in Iouik in April 1986, predicting DM, CaCO<sub>3</sub> and AFDM from carapace width ( $Y_{mg} = \exp(b \cdot \ln X_{mm} + a)$ ), given separately for  $\sigma\sigma$  ( $n = 206$ ) and  $\varphi\varphi$  ( $n = 153$ ), calculated over the mass averaged per mm; range 4-43 mm (DM and AFDM) or 14-40 mm (CaCO<sub>3</sub>). All regressions explain more than 99% of the variance. The predicted mass (mg) is given for 3 size classes.

Y	sex	b	a	10 mm	20 mm	30 mm
DM	$\sigma$	3.161	- 2.913	79	704	2534
DM	$\varphi$	3.104	- 2.852	73	631	2221
CaCO <sub>3</sub>	$\sigma$	3.422	- 4.992	(21)	226	910
CaCO <sub>3</sub>	$\varphi$	3.411	- 4.958	(18)	192	767
AFDM	$\sigma$	2.951	- 3.026	43	335	1007
AFDM	$\varphi$	2.989	- 3.174	41	324	1087

*Uca* and 7.0% ( $SE = 0.5$ ,  $n = 16$ ) in dried crabs.  $CaCO_3$  was least in small specimens ( $< 25\%$  of DM) and greatest in big  $\sigma\sigma$  ( $> 35\%$  of DM, due to the huge pincer).

The DM and AFDM of crabs of equal size collected in spring appeared to be 30% below the masses of crabs taken in late summer. Although formalin might have caused leaching of mass (Lasker 1966; Williams & Robins 1982), this cannot have occurred in the spring sample, at least not much. This is because the Whimbrel's calculated daily consumption of  $CaCO_3$  and nitrogen closely approximated the amounts of  $CaCO_3$  and nitrogen in the dried excreta. However, if the formulae derived from the dried specimens collected in late summer are used, the ingested and defecated masses of  $CaCO_3$  and nitrogen were very different from each other, even though the Whimbrel was in zero N balance (Zwarts & Dirksen 1990).

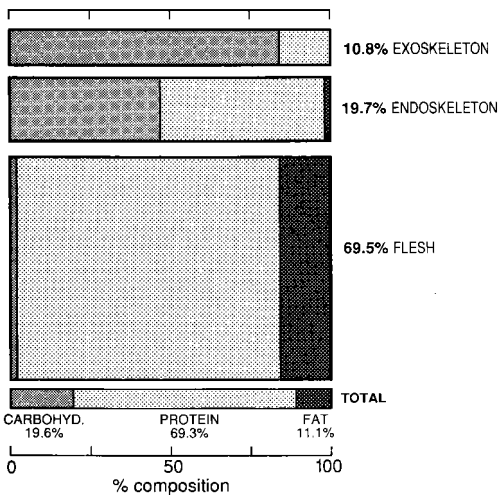
Since the exoskeleton consisted of  $CaCO_3$  (87%) and organic matter (13%), we calculated that 10.8% of the total organic matter of the food occurred in the exoskeleton ( $13 \times 0.72/87$ ; 0.72

being the average ratio  $CaCO_3 : AFDM$ ). The collagenase technique revealed that 30.5% ( $SE = 0.4$ ,  $n = 10$ ) of the organic mass was not flesh, so 19.7% (30.5-10.8%) was hairs, eyes and endoskeleton. Thus flesh was not more than ca. 70% of the total organic matter (Fig. 1). The cuticle, the main organic mass in the exoskeleton, consisted mainly of carbohydrates, viz. polysaccharides (Scheer & Meenakshi 1961, Hunt 1970, Abercrombie *et al.* 1977). Half of the endoskeleton also consisted of carbohydrates (Fig. 1). *Uca* flesh consisted of protein (83%), fat (15%) and carbohydrates (2%) (Fig. 1). Low concentrations of carbohydrates were also found by Pillay & Nair (1973) in the testes, ovaries and liver of another *Uca* species.

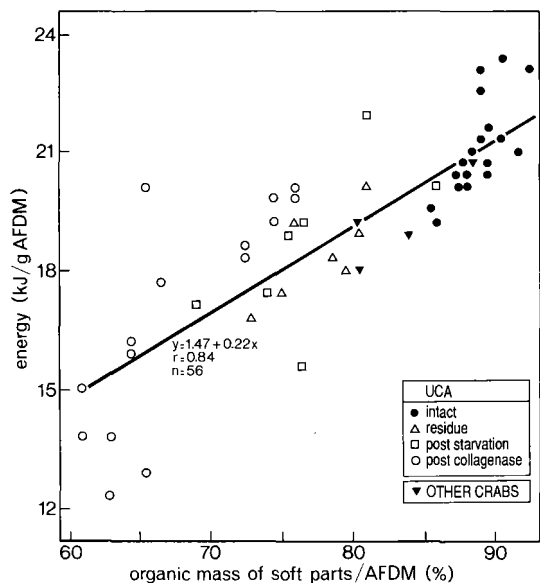
The composition of *Uca* shown in Fig. 1 is for specimens collected in late summer. The nutrient composition of the whole crab in spring did not differ much from that in late summer, but the fat content was lower: protein (66.1%), fat (1.6%) and carbohydrates (32.3%). Probably the low fat value was due to the relatively poor condition in spring, though the possibility that formalin dissolved some of the fat cannot be excluded.

The energy content of the organic mass of *Uca* varied between 12 and 24  $kJ g^{-1}$  (Fig. 2). Low values were found after collagenase had disintegrated the flesh and in crabs which had lost most of their flesh after being experimentally starved. The organic matter in pincers and carapaces left by the Whimbrel also had a low energy content (Table 2). This all suggests that the energy content depended on the percentage of flesh in the organic mass of the crab concerned. The energy content of *Uca* differed between the sexes, being lower in  $\sigma\sigma$  than in  $\varphi\varphi$ , partly because of the heavier male exoskeleton. The energy content of *Uca* (20-22  $kJ g^{-1}$  AFDM) is rather low, but within the range found in other estuarine animals: 20-25  $kJ g^{-1}$  AFDM (Thayer *et al.* 1973, Griffiths 1977, Wacasey & Atkinson 1987, Brey *et al.* 1988, Dauvin & Joncourt 1989).

Wacasey & Atkinson (1987) found that the energy content of DM depends on the relative amount of organic mass:



**Fig. 1.** Composition of *Uca* organic mass:  $\sigma$  and  $\varphi$  of 30 mm carapace width, collected in August 1988 in the Baie d' Aouatif. Nitrogen and fat were determined in the whole crab, in the cleaned exoskeleton and in the mass left after collagenase had removed the flesh (leaving the exo- and endoskeleton, hairs and eyes).



**Fig. 2.** Energy content of *Uca* depended on the percentage of soft parts in relation total organic mass. Soft organic mass was defined as AFDM minus AFDM in exoskeleton ( $13 \times 0.72/87$ ; see text). Low energy contents were found in *Uca* which had been starved, where the flesh was removed with an enzyme or in the remains left by the Whimbrel after it had eaten most of the flesh; see also Table 2. For comparison, the data are also given for two other main prey, also both crabs: *Callinectes marginatus* and *Panopeus africanus*, of the Whimbrels in the study area.

$$Y = -0.163 + 0.253 \cdot X$$

$$(r = 0.986, n = 213),$$

where  $Y = \text{kJ g}^{-1} \text{DM}$  and  $X = 100\% \cdot \text{AFDM DM}^{-1}$ . A comparison between this regression based on 213 benthic invertebrate species and that for *Uca* shows that the slopes are similar, but that the energy content of *Uca* was on average 2 kJ lower:

$$Y = -2.807 + 0.267 \cdot X (r = 0.982, n = 57),$$

where  $Y = \text{kJ g}^{-1} \text{DM}$ ,  $X = 100\% \cdot \text{AFDM DM}^{-1}$ . The suggestion (Wacasey & Atkinson 1987) that, when the ash content increases, the energy content of the organic material decreases, is supported by our data. The energy content of AFDM depended

**Table 2.** Energy content of *Uca* ( $\text{kJ g}^{-1} \text{AFDM} \pm \text{SE}$ ). Parts are pincers and carapaces.

treatment	$\text{kJ g}^{-1} \text{AFDM}$	$n$
with collagenase	$16.9 \pm 0.7$	16
parts left by Whimbrel	$18.3 \pm 0.4$	8
starved to death	$18.6 \pm 0.8$	7
$\sigma \sigma$ , formalin-preserved	$20.0 \pm 0.1$	7
$\sigma \sigma$ , dried	$20.2 \pm 0.2$	9
$\text{♀} \text{♀}$ , formalin-preserved	$21.4 \pm 0.2$	6
$\text{♀} \text{♀}$ , dried	$22.1 \pm 0.4$	7

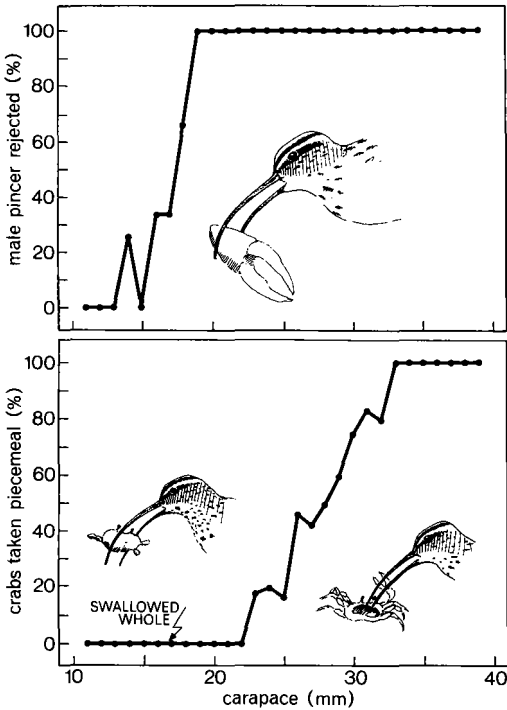
on the presence of exoskeletal AFDM (Fig. 2). The regression (Fig. 2) reveals that the energy content of *Uca* flesh was ca.  $23 \text{ kJ g}^{-1}$  while that of the skeletal AFDM was ca.  $16 \text{ kJ g}^{-1}$ .

#### *Uca* food taken by the Whimbrel

The Whimbrel dismembered the large *Uca* to eat the pincers and legs separately from the carapace. However, the pincers of  $\sigma \sigma > 14\text{--}18 \text{ mm}$  wide were refused (Fig. 3A). The carapaces of *Uca*  $> 22\text{--}32 \text{ mm}$  were not swallowed whole but were opened and the flesh taken piecemeal (Fig. 3B).

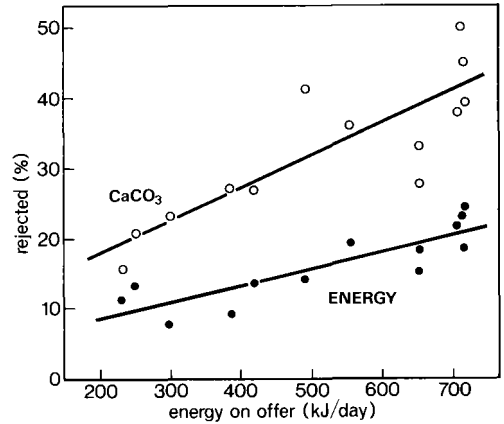
The sex and size of each *Uca* was determined and converted into mass according to formulae given in Table 1. The mass and composition of the prey remnants were measured directly. The Whimbrel took on average 76% of the DM offered (Table 3). By refusing pincers and eating flesh only out of the carapaces, the Whimbrel left 33% of the calcareous matter, 18% of the total organic matter and 16% of the total energy. The effect, however, was that the percentage of flesh in food increased. The flesh content was not measured in the prey remnants so the amount of flesh in the ingested part was unknown. However, assuming that the ratio of  $\text{CaCO}_3$  : skeletal organic mass were similar for the remnants and for the intact crabs, flesh as per cent of ingested AFDM was estimated as 74.9%, compared with 69.5% in intact *Uca*.

The bird was usually more thorough on days when the food supply was low. It left 20% of the energy when food was abundant, but only 10% on days with only few *Uca* (Fig. 4). The advantage of



**Fig. 3.** (A) The proportion of the pincers of ♂ *Uca* rejected by the captive Whimbrel as a function of crab size (width of the carapace) ( $n = 286$ ). (B) The proportion of the carapaces opened by the captive Whimbrel to remove the flesh, instead of swallowing the carapace as a whole, as a function of crab size ( $n = 421$ ).

being less selective when the food supply was high is that 40% of the exoskeleton was discarded, compared with 20% when food was scarce.



**Fig. 4.** Percentage of  $\text{CaCO}_3$  and total energy of *Uca* that was not ingested, as a function of the level of feeding offered to the Whimbrel. The more food was offered per day, the less was taken from the exoskeleton. As a result, the Whimbrel rejected a small but increasing part of the energy.

**Food consumption and crude feeding time**

The time required to eat is defined as ‘crude feeding time’ since digestive pauses were included. However, since not all the observations continued until all the crabs had been eaten, the total crude feeding time was imprecise for some days. There is a linear relationship between the estimated crude feeding time and the amount of food taken:

$$Y = 0.94 + 0.32 \cdot X$$

$$(r = 0.90, n = 13, p < 0.001),$$

**Table 3.** Average composition of the *Uca* food offered on 13 days (given as the percentage  $\pm$  SE of total DM) and really taken by the bird (also as percentage of total DM on offer). The last column gives for each component the amount taken ( $\pm$  SE) relative to the amount on offer. Soft organic mass (SOM) has been defined as AFDM minus organic mass in the exoskeleton.

	on offer (%)	taken (%)	taken/on offer (%)
DM (g)	100	76.48 $\pm$ 1.66	76.48 $\pm$ 1.66%
$\text{CaCO}_3$ (g)	34.61 $\pm$ 0.25	23.19 $\pm$ 0.89	67.13 $\pm$ 2.79
AFDM (g)	46.14 $\pm$ 0.39	37.67 $\pm$ 0.92	81.54 $\pm$ 1.54
SOM (g)	40.97 $\pm$ 0.42	34.21 $\pm$ 0.83	83.95 $\pm$ 1.38
energy (kJ)	83.61 $\pm$ 1.48		

where  $Y$  = feeding time ( $\text{h d}^{-1}$ ),  $X$  = g AFDM taken  $\text{d}^{-1}$  (range 9-27 g AFDM).

The intake rate amounted to 2.7 g AFDM  $\text{h}^{-1}$  or 5.5 g DM  $\text{h}^{-1}$  on average, but it increased with the amount of food ingested:

$$Y = 2.16 + 0.028 \cdot X$$

$$(r = 0.45, n = 13, p = 0.13),$$

where  $Y$  = g AFDM taken  $\text{h}^{-1}$ ,  $X$  = g AFDM taken  $\text{d}^{-1}$ , and

$$Y = 4.08 + 0.359 \cdot X$$

$$(r = 0.57, n = 13, p = 0.07),$$

where  $Y$  = g DM taken  $\text{h}^{-1}$ ,  $X$  = g DM taken  $\text{d}^{-1}$ ,

#### Organic mass in skeleton cannot be digested

These calculations allow the mass of *Uca* ingested and the amount defecated per day and the composition to be determined. The bird did not produce pellets. Comparison of the ingestion and defecation of DM, AFDM and energy allows the digestibility of *Uca* to be calculated in terms of both mass and energy (Table 4). The digestibility of DM was below 30% due to the presence of 50% inorganic mass (Table 3). Most of the salt (ca. 7% of the DM) would have been excreted via the nasal gland, but all the sand and  $\text{CaCO}_3$  ingested would have been expelled in the excreta. Table 4 gives the digestibility of organic mass and energy for the whole crab as well as for the flesh alone, assuming the skeletal organic mass was indigestible.

**Table 4.** Digestibility ( $\% \pm SE, n = 7$ ) of *Uca* food. The digestibility for only flesh is based upon the assumptions that 1) skeletal organic mass is completely indigestible and 2) flesh content of ingested organic mass is 74.9% and not 69.5 (Fig.1) due to selective feeding (Table 3; further explanation in text).

	digestibility (%)
DM (g)	29.5 $\pm$ 4.5
AFDM (g)	43.3 $\pm$ 4.5
energy (kJ)	65.1 $\pm$ 2.9
energy, flesh (kJ)	81.9 $\pm$ 3.6

The possibility that the organic mass in the skeleton was in fact digested was investigated by determining the flesh: AFDM ratio in the excreta, using the collagenase technique. This was difficult because the sample consisted of very fine particles. 53% ( $SE = 6, n = 4$ ) of the organic matter was not decanted and so was considered to be skeletal organic mass in the excreta. This is equivalent to 30% of the total ingested AFDM, because the excreted AFDM was 57% of the ingested AFDM (Table 4). This means that none of the organic mass in the exo- and endoskeleton was digested.

It is not surprising that the skeletal organic mass was indigestible. The chitin in the cuticle is known to be resistant to chemical action (Abercrombie *et al.* 1973, Castro *et al.* 1989a). When dried *Uca* were put in 20% HCl solution, the flesh and  $\text{CaCO}_3$  disappeared completely whereas the soft parts of the skeletons remained intact.

#### Fat is completely digestible while carbohydrates are not

The digestibility of particular nutrients cannot be easily determined because the excreta of birds consist of a mixture of urine, containing the end product of protein metabolism, and faeces. The digestibility of protein can only be calculated if the production of faecal protein is known.

Four methods are available to separate faeces and urine in birds. 1) Urine and faeces can be voided separately in colostomised birds (Terpstra & de Hart 1974). 2) Urinary energy can be estimated by giving a bird no food at all (Sibbald 1975) or 3)

**Table 5.** Breakdown of excreta into urine and faeces in two pooled samples (each representing two days  $\pm SE$ ). The formula for faeces has been taken from Terpstra & de Hart (1974). Excretory AFDM is 39.28%  $\pm$  0.02% relative to DM. Np is precipitable N.

	proportion N in DM of the excreta (%)
total	6.02 $\pm$ 0.24
precipitable	1.35 $\pm$ 0.08
faeces	1.29 $\cdot$ Np - 0.02 $\cdot$ total N = 1.62
urine	total - faeces = 4.40

food containing no nitrogen (Sibbald & Morse 1983). 4) Lead acetate can be used to precipitate the faecal nitrogen, i.e. the undigested protein from the food, and thus to separate faeces from urinary waste (Terpstra & de Hart 1974). In this way, 82% of the excreted nitrogen and 32% of the excreted organic matter in poultry were found in the urine (Terpstra & Janssen 1976).

The precipitation method of Terpstra & de Hart (1974) showed that 73% of the excretory nitrogen of the Whimbrel occurred in the urine (Table 5). The energy content of bird's urinary AFDM can be calculated from the energy content and chemical composition of its constituent compounds. 81% of urinary nitrogen is excreted as uric acid (Terpstra & de Hart 1974), and its energy content is 34.3 kJ g<sup>-1</sup> N or 11.5 kJ g<sup>-1</sup> AFDM (Brody 1945). The energy content of urea is 22.6 kJ g<sup>-1</sup> N, or 10.6 kJ g<sup>-1</sup> AFDM, of ammonia 28.0 kJ g<sup>-1</sup> N, or 23.0 kJ g<sup>-1</sup> AFDM, and of creatinine 56.1 kJ g<sup>-1</sup> N, or 21.9 kJ g<sup>-1</sup> AFDM (Brody 1945). This information allowed the energy content of urinary AFDM to be calculated as 34.4 kJ g<sup>-1</sup> N or 12.6 kJ g<sup>-1</sup> AFDM. Thus 27% of the excreted energy and 30% of the excreted organic mass was deduced to be in the urine.

The digestibility of fat, protein and carbohydrates can now be calculated (Table 6). Fat was virtually completely digested. Protein was quite well digested while carbohydrates were scarcely digested at all. The same results were obtained when the formalin-preserved specimens rather than dried *Uca* were used: 98.5% of the fat, 79.7% of the protein and 17% of the carbohydrates were digested, allowing for the different estimate of the nutrient composition (see above). These figures are based

**Table 6.** Digestibility (%  $\pm$  SE,  $n = 2$ ) of *Uca* food per nutrient. The last column gives for each nutrient the percentage found in flesh (cf. Fig. 1).

	digestibility (%)	in flesh (%)
fat	99.8 $\pm$ 0.1	95.1
protein	74.2 $\pm$ 0.1	83.1
carbohydrates	1.5 $\pm$ 1.1	6.9

upon total organic mass, including the skeleton (Fig. 1). The low digestibility of the carbohydrates is explained by the fact that only 7% occurred in the flesh.

### True and apparent metabolizable energy

We determined not only the apparent but also the true metabolizable energy content of *Uca* for Whimbrel because we were able to separate the amounts in the urine and the faeces. The apparent metabolizable energy is 'energy input minus energy output (faeces + urine)', whereas the true metabolizable energy is defined as 'energy input minus energy output excluding the urinary energy' (Miller & Reinecke 1984).

The energy content of the excreta amounted to 14.0 kJ g<sup>-1</sup> AFDM ( $SE = 0.6$ ,  $n = 7$  days; for each day, at least five measurements were made). The energy content of the faeces was 15.3 kJ g<sup>-1</sup>, assuming that the 30% of the excretory AFDM present in the urine had an energy content of 12.6 kJ g<sup>-1</sup>. However, the amount of urine was not a constant fraction of the excreta. When no food was ingested, the excreta consisted of urine only. As a consequence, the lower the consumption, the more the apparent metabolizable energy deviates from the true metabolizable energy (Kendeigh 1949, Sibbald 1975, Miller & Reinecke 1984). This cannot be checked with our data, since we determined precipitable nitrogen only in excreta taken for two pooled samples. However, an estimate can be made from the known excretory energy content over seven days. The energy content of the excreta appeared to depend on the amount of AFDM ingested, according to the equation:

$$Y = 12.45 + 0.081 \cdot X$$

$$(r = 0.77, n = 7, p < 0.01)$$

where  $Y =$  kJ g<sup>-1</sup> excreted AFDM,  $X =$  g AFDM ingested d<sup>-1</sup> (range 12-26 g AFDM d<sup>-1</sup>).

The proportion of the excreted AFDM present in the urine can be deduced from the estimated energy content of urinary and faecal AFDM (12.6 and 15.3 kJ, respectively). As the regression of percentage excreted AFDM in the urine against the

amount of energy ingested per day did not differ significantly from zero, it is assumed that, within the range of the daily consumption, the urine fraction in the excreta was constant.

The average apparent and true metabolizable energy content ( $\pm SE$ ;  $n = 7$ ) of *Uca* was  $6.95 \pm 0.31$  and  $7.96 \pm 0.23$  kJ g<sup>-1</sup> DM, respectively. The true metabolizable energy was thus 1.14 times higher than the apparent metabolizable energy. The difference depended not only on the amount of food taken, as discussed above, but also on the nutrient composition, it being higher as the proportion of protein increased. Storey & Allen (1982) compared true and apparent metabolizable energy for 18 types of food and found differences ranging from 1 to 29%.

### Digestibility, amount of food ingested and temperature

The digestibility of *Uca* varied from day to day between 55% and 76%. There was no relation

between the digestibility of the prey and their size or sex ratio. Digestibility improved when the Whimbrel rejected more of the skeleton and thereby diminished the proportion of indigestible organic mass, but this trend was not significant. The greater part of the variation in digestibility could be attributed to the total amount of food ingested (Fig. 5). The negative effect (Fig. 5) was even more pronounced when the decreasing proportion of skeletal organic mass ingested when the daily consumption was high was taken into account.

The air temperature was measured continuously (Wolff & Smit 1990) and varied between 16 and 30°C during the experiment. The average temperature during digestion could be determined, because the time at which each crab was offered was registered. Temperature did not affect digestibility ( $r = 0.14$ ,  $n = 7$ ,  $p > 0.05$ ) nor the residuals (using the regression shown in Fig. 5 to correct for the effect of total food consumption;  $r = 0.15$ ,  $n = 7$ ,  $p > 0.05$ ). However, the range of average daily temperature was very small (21 to 27°C).

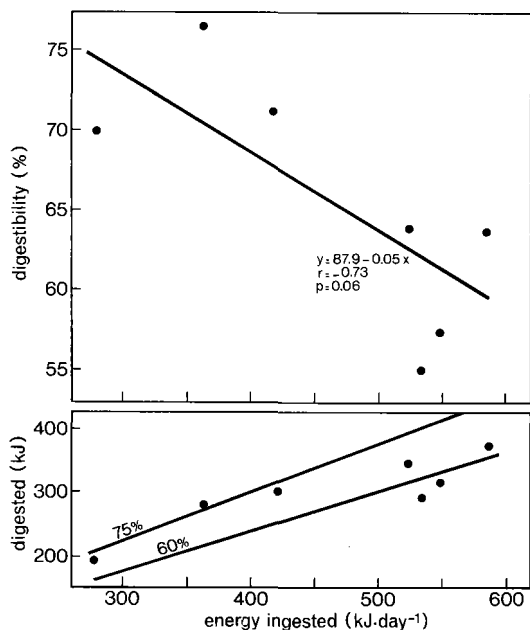


Fig. 5. Digestibility of *Uca* food as a function of energy ingested. The lower panel gives the absolute amount of digested energy along the Y-axis; the two lines are calculated for an average digestibility of 75 and 60%.

## DISCUSSION

### Indigestible organic mass depresses digestibility

Food processing can be described in terms of influx and efflux of energy, but animals are not bomb calorimeters (see McClintock 1986). Many studies on the digestion of carnivores implicitly assume that the food ingested consists only of an homogeneous type of nutrient (i.e. flesh). In fact, the prey swallowed by predators often include organic matter which cannot be digested (feathers in birds, fur in mammals and organic matter in the skeleton of prey in general).

Castro *et al.* (1989b) reviewed many studies of digestion in birds. The average digestibility of meat or fish was 78%, compared with an average of 74% for invertebrate prey. To investigate whether this difference was related to the amount of indigestible organic mass in the prey, a literature search was made of studies on the digestion of avian carnivores where enough relevant details were given (Table 7).

**Table 7.** Digestibility ( $Q$ ) and energy content of food, excreta ( $E$ ), rejecta ( $R$ ) and both combined ( $E+R$ ) in studies on avian carnivores. The studies are arranged according to the energy content of the excreta. The digit code in the first column is used in Fig. 6.

code	predator	prey	energy content (kJ g <sup>-1</sup> DM)				$Q$ (%)	source
			food	$E$	$R$	$E+R$		
1	Whimbrel	crab	10.68	5.50			65.1	this study
2	Australasian Harrier	fish	20.72	9.10			81.0	Tollan (1988)
3	Cape Gannet	fish	27.18	9.90			69.2	Batchelor & Ross (1984)
4	Cape Gannet	fish	25.34	10.10			79.4	Batchelor & Ross (1984)
5	Bald Eagle	rabbit	18.98	10.46			75.0	Stalmaster & Gessaman (1982)
6	Double-crested Cormorant	fish	23.85	10.59			84.9	Dunn (1975)
7	Australasian Harrier	mouse	22.60	10.90	18.70	13.07	75.5	Tollan (1988)
8	Oystercatcher	mussel	?	11.28			72.7	Hockey (1984)
9	Bald Eagle	bird	24.80	11.38			85.4	Stalmaster & Gessaman (1982)
10	Bald Eagle	fish	21.77	11.63			75.4	Stalmaster & Gessaman (1982)
11	Long-eared Owl	mouse	16.51	11.66	13.21	12.01	87.6	Graber (1962)
12	Broad-winged Eagle	meat	22.39	11.97			74.1	Mosher & Matray (1974)
13	Cattle Egret	meat	25.27	12.68			95.1	Siegfried (1969)
14	Jackass Penguin	fish	24.10	12.70			77.9	Cooper (1977)
15	Screech Owl	bird	24.55	12.77	18.82	15.33	72.5	Kirkwood (1979)
16	Cape Gannet	fish	22.35	12.80			72.3	Cooper (1978)
17	King Penguin	squid	22.10	13.20			81.3	Adams (1984)
18	Australasian Harrier	bird	21.70	13.40	20.10	15.08	70.2	Tollan (1988)
19	Blue/Coal Tit	mealworm	27.61	13.52			85.1	Gibb (1957)
20	Kestrel	bird	24.55	14.37	22.42	14.50	71.3	Kirkwood (1979)
21	European Bee-eater	bee	21.60	14.77	21.68	18.10	56.0	Krebs & Avery (1984)
22	European Bee-eater	dragonfly	20.36	15.02	20.55	17.97	62.0	Krebs & Avery (1984)
23	Coal Tit	insect	24.35	15.56			66.7	Gibb (1957)
24	American Robin	cricket	23.10	15.56			71.0	Levey & Karasov (1989)
25	Pacific Swallow	insect	24.36	15.78			67.6	Bryant & Bryant (1988)
26	Starling	cricket	23.37	16.20			73.0	Levey & Karasov (1989)
27	Red-backed Shrike	insect	24.06	16.36			70.0	Diehl (1971)
28	Blue-throated Bee-eater	insect	24.36	19.91	22.72	20.00	56.7	Bryant & Bryant (1988)

The energy content of excreta varied from 5 to 20 kJ g<sup>-1</sup> DM, this being 20-50% less than the energy content of the food. The low energy content of the excreta is due to the uric acid which, amongst organic substances, has one of the lowest energetic contents. The values for the energy content of the excreta in Table 7 were measured in terms of DM, since ash content was usually not given. Except for the crabs offered to the Whimbrel, the prey listed in the original papers did not contain much ash, and it is in fact possible that real variations would

be smaller than shown if the energy content of AFDM had been provided. The ash content is known for the two lowest values of excreta in Table 7: Whimbrel eating *Uca*: 5.5 kJ g<sup>-1</sup> DM (this study) and Australasian Harrier *Circus approximans*: eating fish: 9.1 kJ g<sup>-1</sup> DM (Tollan 1988). If a correction is made for the ash, an energy content of 14.0 and 12.2 kJ g<sup>-1</sup> AFDM, respectively, is found. The minimum energy content of excreta would, in any case, always be expected to be above 12-13 kJg<sup>-1</sup> AFDM, this being the energy content of uri-

nary AFDM as derived from its chemical composition and measurements in birds given no food or food without nitrogen (see Brody 1945, Sibbald 1975, Terpstra & Janssen 1976, Sibbald & Morse 1983, this paper).

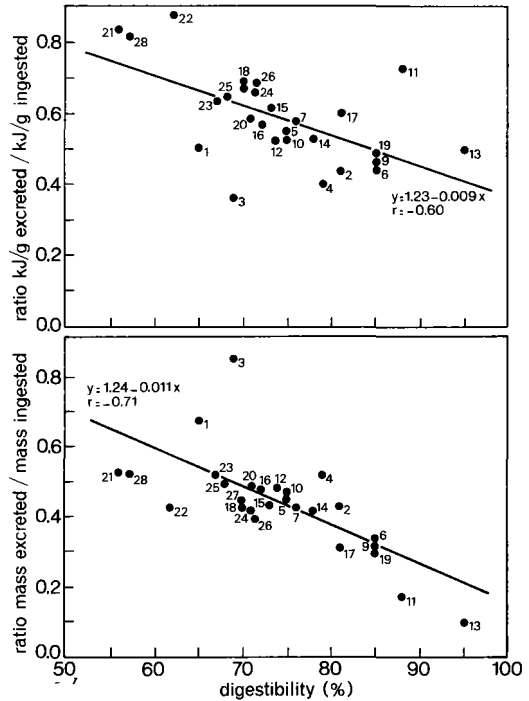
The variation in the energy content of the excreta (Table 7) cannot be attributed to the energy content of the food, but seems related to the presence of indigestible organic matter. The energy content of the excreta is low if the food consists almost entirely of flesh (fish or meat). The excreta + rejecta of insectivorous birds contain chitin skeletons which results both in a high energy content for the excreta + rejecta and a low digestibility. A similar, though less pronounced, effect is present in predators eating prey with hairs and feathers. Indeed, the seasonal fluctuation in the digestibility of mice for Kestrel *Falco tinnunculus* may be caused by variations in the mass of indigestible fur and carcass in the food (Masman *et al.* 1986).

The digestibility ( $Q$ ) depends on four factors: the amount of mass excreted ( $M_e$ ), the amount of mass ingested ( $M_i$ ), the energy content of excreta ( $E_e$ ) and the energy content of food ingested ( $E_i$ ), according to the equation:

$$Q = 1 - (E_e/E_i) \cdot (M_e/M_i)$$

The equation shows that the digestibility is determined by two ratios, which will be termed the energy ratio and the mass ratio. The energy ratio can be calculated directly from Table 7 and plotted against digestibility (Fig. 6A). The mass ratio is not given in most of the original papers but can be derived if the other terms in the equation are known. This ratio is plotted against digestibility in Fig. 6B. The digestibility is clearly determined by a combination of 'mass reduction' and 'energy reduction' during the digestion.

Redshank *Tringa totanus* feeding on mudsnails *Peringia ulvae* digest 65% of the AFDM (Speakman 1987). If it is assumed that, as in the Whimbrel, Redshank can not digest the organic matter in the shell, the efficiency for the flesh alone can be recalculated. According to Dekker (1979) 3% of the shell of *Peringia* consists of organic matter which



**Fig. 6.** The higher the digestibility of the food (A) the lower the energy content of the excreta relative to the energy content of the food and (B) the lower the amount of excreted mass relative to ingested mass. The original data are given in Table 7 (with corresponding digit codes); the correlations are shown in Table 8.

**Table 8.** Correlations between digestibility ( $Q$ ), energy content of food ( $\text{kJ g}^{-1} \text{DM}$ : kJ-in), energy content of excreta ( $\text{kJ g}^{-1} \text{DM}$ : kJ-out), ratio kJ-out/kJ-in (kJ-out/in) and ratio DM-out/DM-in (DM-out/in). The latter variable equals the quotient of  $Q$  and kJ-out/in. Original data are given in Table 7;  $n = 27$ ;  $p = 0.01^*$ ;  $p = 0.001^{**}$ .

	kJ-in	kJ-out	kJ-out/in	DM-out/in
$Q$	0.16	-0.50*	-0.60**	-0.71**
kJ-in		0.38	0.21	-0.06
kJ-out			0.82**	-0.12
kJ-out/in				-0.11

represents 15% of the total organic matter. Taking this into account, the re-estimated digestibility is 76%, which agrees well with Speakman's other

measurements of the digestibility of organic matter in wader food. We prefer the simple explanation that skeletal organic mass is indigestible over the hypothesis of Speakman (1987) that a high ash content directly depresses the capacity of the bird to digest the food.

The very low digestibility of 39% was found for the eggs of the Horseshoe crab *Limulus polyphemus* taken by Sanderling *Calidris alba* (Castro *et al.* 1989a). In this case, digestion was hampered by the resistance of the egg cuticle. The digestibility increased to 69% when the cuticle of the eggs was ruptured. This efficiency is still low (Table 7) because of the presence of indigestible organic mass (the cuticle).

We conclude that the presence of indigestible organic mass does indeed explain a significant part of the variation in digestibility.

### Digestibility of nutrients

The high digestibility of fat found in this study, corresponds with the results obtained by Martin (1968), Campbell & Koplín (1968), Collopy (1986) and Obst (1986); see also Fisher (1972: Table 11). A positive correlation between the fat content of food and its average digestibility has also been shown in several studies (Martin 1968, Smith & Follmer 1972, Blem 1976, Stalmaster & Gessaman 1982, Collopy 1986).

Estimates of the digestibility of animal protein are uncommon due to the presence of an unknown amount of urinary nitrogen in the excreta (but see Table 20 in Fisher 1972). Campbell & Koplín (1986), in experiments with Kestrels and Screech Owls *Otus kennicotti*, give quantities of nitrogen in the food, excreta and pellets. Assuming as in this study (Table 5), that 73% of the excreted nitrogen was found in the urine, protein digestibility would be 70% in both studies, thus approximating our estimate (Table 6).

### Digestibility and temperature

Although waders in W. Africa extracted more energy from artificial food at lower temperatures (Klaassen *et al.* 1990), the same did not occur in Whimbrel eating *Uca*. In fact, the effect of temper-

ature on the digestion of birds is in general not clear. Willson & Harmeson (1973) cited 9 studies showing a temperature effect and 6 studies showing none. In more recent papers, the effect was sometimes found (e.g. Blem 1976, Stalmaster & Gessaman 1982) but sometimes not (e.g. Wijnandts 1984).

### Digestibility and amount of food ingested

Of the factors examined (temperature, food composition and ingested mass), the only demonstrable effect on the digestibility of *Uca* for Whimbrel was the total ingested mass (Fig. 5). This was probably an indirect effect. The more food eaten during a day, the greater was the rate of ingestion per unit time. Hence it is likely that a higher intake rate resulted in a higher turnover rate and thus a lower digestibility. The intake rate of the Whimbrel increased by 30% (from 4.7 to 6.2 g DM h<sup>-1</sup>) as the ingested amount of food increased from 20 to 60 g DM d<sup>-1</sup>, while the digestibility decreased by under 10% (Fig. 5). It was therefore worthwhile for the bird to increase its intake rate.

The trade-off between 1) retaining food for longer periods in the gut, and so improving its digestibility, and 2) decreasing the throughput time, and thus facilitating a higher intake rate and accepting the lower digestibility, has been discussed in the context of optimality theory by Sibly (1981). Foragers eating food containing much indigestible matter must often choose the strategy of a high intake rate but low digestibility. The digestibility of gastropods or molluscs (inorganic mass 80-90% of DM) in ducks decreased as a function of the amount of food ingested, whereas this did not happen with a diet of invertebrates containing a much lower inorganic ballast (Jorde & Owen 1988). This suggests that foragers dealing with food containing large amounts of indigestible mass may approach the limits of their digestive capacities.

Free-living Whimbrels on the Banc d'Arguin feeding on crabs had a limited feeding time of 5-12 h per day and showed a maximum intake rate of 1 mg AFDM s<sup>-1</sup>, digestive pauses included (Zwarts & Dirksen 1990). The average intake rate of the experimental Whimbrel (0.75 mg s<sup>-1</sup>) ap-

proached the average rate in the field. The occurrence of pauses during feeding suggests that the intake rate was limited by the digestion rate. It is therefore likely that Whimbrels feeding at an even higher rate in the field fed at the maximum rate, resulting in a lowered digestibility of their food.

The importance of this negative effect was obvious during the pre-migratory period when the Whimbrels on the Banc d'Arguin increased their body mass by 1.1% per day (Zwarts *et al.* 1990b). This is possible only if the intake of metabolizable energy is raised by ca. 30% (Klaassen *et al.* 1990, Zwarts *et al.* 1990a). The experimental Whimbrel maintained a constant mass if it ingested 450 kJ d<sup>-1</sup> (Zwarts & Dirksen 1990), but had to increase its daily gross intake from 450 to 650 kJ, an increase of 45%, to realize a 30% increase in digested energy.

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## SAMENVATTING

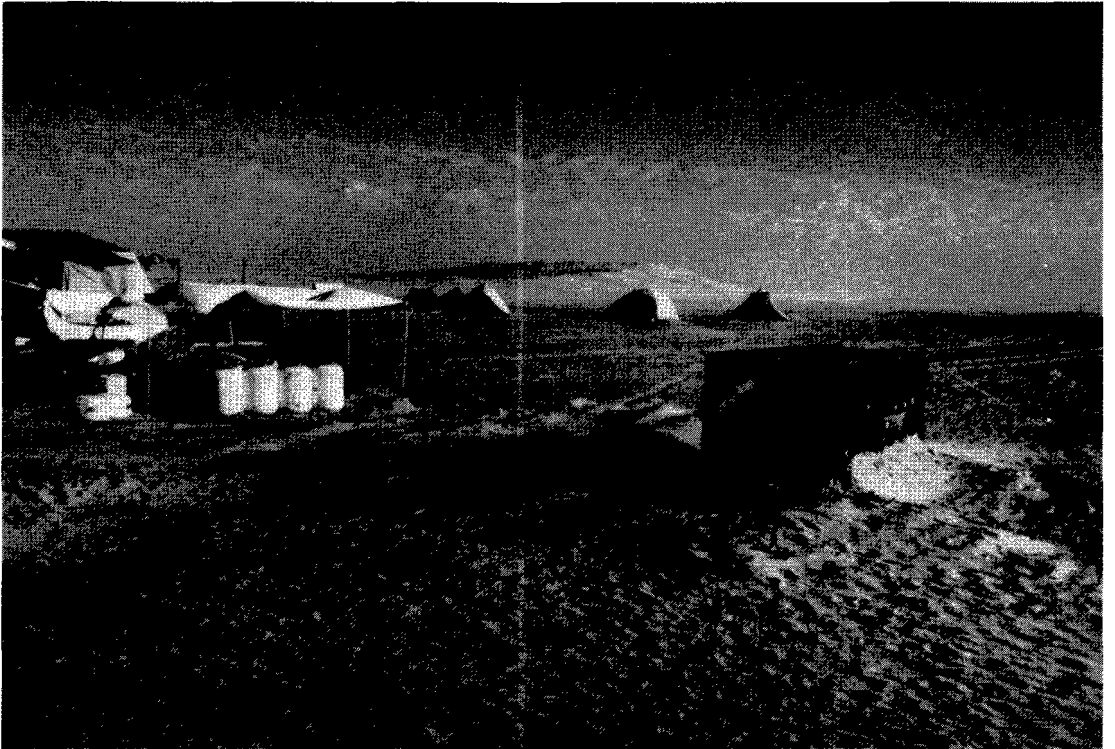
Regenwulpen die wenkkrabben eten, hebben te maken met prooien die een lage energie-waarde hebben. De helft van een wenkkrab bestaat uit anorganisch materiaal en bovendien blijkt dat het organische materiaal in het skelet onverteerbaar is. Van de energie die een Regenwulp in gevangenschap opnam, werd 35% weer uitgescheiden. Een verteringsefficiëntie van 65% is laag vergeleken met die van vlees- en visetende vogels. De Regenwulp verteerde vrijwel al het vet, 74% van de eiwitten (na correctie voor urinestikstof) en vrijwel niets van de koolhydraten, die zich grotendeels in het skelet bevinden. De schijnbaar en werkelijk omzetbare energie van wenkkrabben was respectievelijk 7 en 8 kJ g<sup>-1</sup> drooggewicht.

De vogel werd selectiever bij een groter voedselaanbod: skeletdelen werden minder gegeten, waardoor het vleesgehalte van het opgenomen voedsel toenam. Een grotere voedselopname ging gepaard met een lagere verteringsefficiëntie, waarschijnlijk doordat de opnamesnelheid en doorstroomsnelheid toenamen. We nemen aan dat hier sprake is van een optimale verteringsstrategie, omdat de afname van de verteringsefficiëntie kleiner is dan de toename van de opnamesnelheid.

## RÉSUMÉ

Le Courlis corlieu mangeur de crabes violonistes, *Uca tangeri*, a affaire à des proies ayant peu de valeur énergétique. La moitié du crabe se compose de matériel inorganique et, de surcroît, la matière organique du squelette s'avère être quasiment non digérable. 35% de l'énergie ingérée par un Courlis corlieu en captivité étaient excrétés. Une efficacité d'assimilation de 65% est basse comparée à celle des oiseaux carnivores et piscivores. Le Courlis corlieu assimilait pratiquement toute la graisse, 74% des protéines et le peu d'hydrates de carbone,

qui se trouvent en majeure partie dans le squelette. L'oiseau se montrait plus sélectif lors d'une plus grande disponibilité de nourriture: il mangeait une quantité moindre du squelette, augmentant ainsi la teneur en chair dans la nourriture avalée. A mesure que l'ingestion de la nourriture augmentait, l'efficacité de l'assimilation diminuait, probablement parce que la vitesse de l'ingestion était augmentée et que le temps de l'assimilation se trouvait abrégé. Nous supposons qu'il est question ici d'une stratégie d'assimilation optimale, étant donné que la diminution de l'efficacité de l'assimilation est moindre que l'augmentation de la vitesse de l'ingestion.



A view of the expedition camp in 1985 showing drums with drinking water, tents for working and sleeping and a birdcage housing waders (photo Bruno Ens).