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# Nonbreeding Eastern Curlews *Numenius madagascariensis* Do Not Increase the Rate of Intake or Digestive Efficiency before Long-Distance Migration because of an Apparent Digestive Constraint

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## ABSTRACT

The possibility of premigratory modulation in gastric digestive performance was investigated in a long-distance migrant, the eastern curlew (*Numenius madagascariensis*), in eastern Australia. The rate of intake in the curlews was limited by the rate of digestion but not by food availability. It was hypothesized that before migration, eastern curlews would meet the increased energy demand by increasing energy consumption. It was predicted that (1) an increase in the rate of intake and the corresponding rate of gastric throughput would occur or (2) the gastric digestive efficiency would increase between the mid-nonbreeding and premigratory periods. Neither crude intake rate (the rate of intake calculated including inactive pauses; 0.22 g DM [grams dry mass] or 3.09 kJ min<sup>-1</sup>) nor the rate of gastric throughput (0.15 g DM or 2.85 kJ min<sup>-1</sup>) changed over time. Gastric digestive efficiency did not improve between the periods (91%) nor did the estimated overall energy assimilation efficiency (63% and 58%, respectively). It was concluded that the crustacean-dominated diet of the birds is processed at its highest rate and efficiency throughout a season. It appears that without a qualitative shift in diet, no increase in intake rate is possible. Accepting these findings at their face value poses the question of how and over what time period the eastern curlews store the nutrients necessary for the ensuing long, northward nonstop flight.

## Introduction

Long-distance migratory birds deposit large amounts of excess tissue, both lipids and proteins, to allow for successful migration between the nonbreeding (wintering) and breeding grounds (Alerstam and Lindström 1990; Lindström and Piersma 1993). This requires a considerable increase in daily energy consumption before migration. Such an increase can be achieved by prolonging periods of foraging and/or increasing the rate of energy intake (Blem 1980; Zwarts et al. 1990a, 1990b). There are two ways for a bird to increase the rate of energy intake. One is to improve the efficiency of digestion of consumed food, thus increasing the rate of energy intake without increasing the rate of food consumption (Scott et al. 1994; Bairlein 2002). So far, there is little empirical evidence to suggest that this strategy is widespread in nature (Karasov 1996). However, this may be due to the lack of studies addressing the issue (e.g., Hume and Biebach 1996). The other way, which is very common among birds, is to increase the rate of food consumption per se (e.g., Blem 1980; Karasov 1996; Karasov and Pinshow 2000) and with it, its necessary correlate, the rate of gastrointestinal throughput of matter and energy (e.g., McWilliams et al. 1999). However, recent studies have demonstrated that while large spare capacity may exist in some species (reviewed in McWilliams and Karasov 2001), in species consuming high inorganic and/or high protein content foods (e.g., crustaceans or insects), the rate of intake can be limited by the rate of digestion (Zwarts and Dirksen 1990; Zwarts et al. 1996; Klaassen et al. 1997; Gannes 2002). This lack of spare capacity to intake rate may have important implications for the foraging strategies of these birds (e.g., time budget allocation, prey choice). Specifically, the presence of a digestive constraint (bottleneck) may preclude an animal from increasing its energy intake rate (e.g., before migration or in an anticipation of a food shortage) via the mechanism of increasing the rate of food consumption because the animal is forced to stop foraging while the food is being digested. How a digestively constrained wild animal foraging under strict time limitation (e.g., tidal cycle) will cope with an increase in energy demand thus represents an interesting life-history question that is addressed in this study.

The eastern curlew (*Numenius madagascariensis*) is a long-distance migratory shorebird spending the nonbreeding season on mudflats and estuaries of Australia (Lane 1987). Before

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northward migration to the coastline of East Asia and then to Siberia, the curlews have to build up nutrient stores sufficient for a nonstop flight in excess of 5,000 km (Driscoll 1999). A previous study (Y. Zharikov, unpublished data) demonstrated that before migration, these birds prolonged their foraging to the maximum permitted by the duration of a low-tide period. At the same time, the proportion of time the birds spent inactive was relatively high (34%–46%), and foraging was interrupted every 5 min even though potential curlew predators were seldom present and prey were readily available. Both observations are suggestive of a digestive bottleneck (e.g., Diamond et al. 1986; Zwarts and Dirksen 1990).

This study was designed to investigate the possibility of pre-migratory digestive modulation in a shorebird, the eastern curlew, foraging on abundant, high inorganic content prey (crabs and shrimp). First, we attempted to establish whether the rate of food consumption in eastern curlews is indeed limited by the rate of digestion, as suggested by the earlier observations. In the field, the existence of such a constraint can be inferred from an asymptotic relationship between the rate of intake achieved while actively foraging and the crude intake rate (the rate of intake calculated including periods of inactivity; e.g., Zwarts 1990; Zwarts et al. 1996). An asymptotic relationship between these two rates implies that inactive pauses are necessary for (a part of) the digestive system to be cleared before foraging can resume (Diamond et al. 1986; Weiner 1992). It is also expected to occur when the rate of gastric throughput is plotted against intake rate achieved while actively foraging for the same reason. A supplementary line of evidence suggesting the existence of a digestive constraint can be obtained by plotting the crude rate of intake against the length of time available for foraging (Swennen et al. 1989). An assumption here is that a certain daily energy intake has to be achieved (e.g., Zwarts et al. 1996). Therefore, if individual foragers are not bottlenecked, the (crude) rate of intake will increase as the time available for foraging decreases (e.g., Swennen et al. 1989).

Second, we hypothesized that before migration, eastern curlews would meet the increased energy demand by increasing energy consumption (as opposed, e.g., to lowering energy expenditure), as indeed is common in shorebirds. It was predicted that the rates of food consumption and gastric throughput would increase during pre-migratory preparations when daily energy requirements go up (Zwarts et al. 1990a) as compared with mid-nonbreeding period rates. Such an increase would signify that either (1) birds forage at under capacity during the mid-nonbreeding period when a neutral energy balance is expected or (2) their digestive system undergoes a modulation that allows a faster rate of food processing (Karasov 1996; McWilliams et al. 1999; McWilliams and Karasov 2001). A physiological alternative to an increase in the rate of food intake is an improvement in the efficiency of digestion of food (Scott et al. 1994; Karasov 1996). It was predicted that an increase in the efficiency of digestion (assimilation) would be observed

during the period of pre-migratory preparations as compared with the mid-nonbreeding period.

It is important to stress that the study specifically investigated only gastric digestive performance (throughput rate and efficiency). This is because the field nature of the study and methods employed allowed a precise measurement of only these parameters of digestive physiology in wild individuals. Nonetheless, data obtained in the process were sufficient to estimate in general terms seasonal trends in the overall digestive efficiency and the rate of apparent metabolizable energy intake in a wild population of curlews.

## Material and Methods

### *Study Area and Curlew Observations*

The study was conducted on the western shore of North Stradbroke Island, Moreton Bay, Queensland, Australia (27°25'S, 153°25'E) between November 18 and December 13, 2000, and February 5–22, 2001. Curlews depart from the study area by mid-March, so these periods were defined as mid-nonbreeding and pre-migratory, respectively. The specific study area represented a 450 × 2,340-m stretch of the intertidal zone occupied by ca. 100 eastern curlews.

All eastern curlews observed in this study defended a roughly rectangular segment of the unvegetated middle section of the mudflat between mangroves and sea grass beds. Although no birds were individually marked, the seasonally stable distribution of the individuals along the mudflat, their small home range (<1 ha), and individual differences in behavior helped in avoiding repeated sampling of the same individuals within a period. To standardize for the environmental conditions experienced by the birds, all observations were carried out during daylight hours, at clear to partially cloudy weather with no to moderate wind. The full low-tide exposure, defined as the period between emergence of the first and submersion of the last visible patches of sand, was measured to the nearest 5 min.

In the study area, the curlews primarily foraged on three species of large decapods: two crab species and a callinassid ghost shrimp. Because of the high inorganic content of these crustaceans, pellets consisting of indigestible matter are regurgitated by the birds at the end of a 1-hr foraging bout (Y. Zharikov, personal observation). A curlew pellet typically contains a full or near-full set of specifically identifiable internal body parts, the gastric mill ossicles, from the prey items consumed since the previous regurgitation. The size of the ossicles can be used to estimate the dry mass of each ingested prey item by using allometry. This approach to assessing food intake, when combined with visual observations of consumed prey, (1) provides a precise estimate of the amount of food consumed during a discrete foraging period (Dekinga and Piersma 1993) and (2) avoids numerous caveats arising when visual determination of prey types and sizes alone is used (Lee and Hockey 2001).

Curlews were observed using an  $\times 20$ – $60$  spotting scope from distances of 40–100 m. An observer always arrived onto the mudflats before the birds. Observations on a focal individual started when a curlew could be seen arriving onto the mudflat from a nearby roosting sandbank at the receding tide or immediately after regurgitating a (well-compacted) pellet. At this stage, its stomach (gizzard) was assumed empty. The bird was watched until a (new) pellet was produced, which was then collected. The period between commencement of foraging and regurgitation of a (new) pellet was defined as a foraging bout. During this period, the following data were recorded: (1) duration of the foraging bout from the moment foraging began until the moment a pellet was regurgitated, (2) the length of time spent on active foraging and nonforaging activities, (3) numbers and types of prey consumed, (4) number of defecations (for individuals that had fed for  $>1$  hr; Speakman 1987; Y. Zharikov, unpublished data), and (5) the air temperature ( $T^{\circ}\text{C}$ ) at the start and the end of the bout. The mean of the two temperature readings was used as a covariate in statistical analyses (Klaassen et al. 1990). The number of legs broken off prey by the birds during handling was noted whenever possible. Most curlews in the study area were females, as determined from their relatively long bills. In Moreton Bay, the bills of females are on average about 20% longer than those of males (189 cm vs. 153 cm, respectively; Driscoll, Queensland Wader Study Group, unpublished data).

In total, five prey types could be visually distinguished. They were the Indo-Pacific soldier crab (*Mictyris longicarpus*), orange-spined sentinel crab (*Macrophthalmus crassipes*), Australian ghost shrimp (*Trypaea australiensis*), unidentified small prey, and the proboscises from the echiurans *Listriolobus bulbocaudatus* and/or *Ochetostoma australiense*. Echiuran proboscises contain only soft tissue and leave no trace in excreta. Since the numerical and dry mass contribution of this prey type to the curlew diet was about 1% (Y. Zharikov, unpublished data), it was excluded from all calculations. The presence of unidentified small prey in the visually recorded diet was not perceived as a problem to calculations of energy intake because their numeric contribution was only  $6.4\% \pm 8.2\%$  (cf.  $>30\%$  in Turpie and Hockey 1996). Furthermore, most small prey items appeared to be juvenile *M. longicarpus* with carapace length  $<10$  mm, which were accounted for in pellet analysis.

#### Pellet Analysis

Pellets were collected only if they were found within 10 min of regurgitation to minimize curlew disturbance and avoid any matter loss (they were frequently dropped into shallow water pools and subsequently disintegrated). If a pellet was deposited onto sand, grains were removed by quickly submerging the pellet into a nearby water pool. All pellets were preserved for 1–10 d in 70% ethanol, subsequently dried (in ethanol) at  $75^{\circ}\text{C}$  for 72 hr in a drying oven to determine the dry mass (g DM),

and then again water saturated and sorted in Bogorov trays under a  $\times 6.7$ – $40$  binocular microscope. A representative subsample of each dried pellet, checked for the presence of identifiable crustacean parts, was ground and burned in a microbomb calorimeter using standard methods (Castro et al. 1989a) to determine its energy density. Samples were processed without the addition of benzoic acid, sometimes needed to ensure combustion of crustacean parts (e.g., Zwarts and Blomert 1990), after analysis of trial samples showed complete combustion without the acid. The same preservation, drying, and calorimetric procedures were applied to prey and fecal samples.

Gastric mills of decapod crustaceans are highly species specific (e.g., Kunze and Anderson 1979; Skilleter and Anderson 1986). As expected, only three different prey types were identified in curlew pellets: *M. longicarpus*, *M. crassipes*, and *T. australiensis*, whose gastric mill ossicles could be readily distinguished. These paired organs belong to the internal digestive apparatus of decapod crustaceans and are used to grind food matter (e.g., Heeren and Mitchell 1997). Because of their heavily chitinized structure and small size, unlike, for example, chelae (Zwarts and Dirksen 1990), they appeared to be resistant to crushing in curlew gizzards and were mostly intact.

All ossicles found in a pellet were counted, and their length was measured to the nearest 0.01 mm using an eyepiece micrometer. The total number of prey represented in the pellet was determined by matching individual right and left ossicles for each prey species by their length. A right and a left ossicle were considered a match and, thus, represented one prey item if the difference between their lengths was  $\pm 3\%$  of the mean. This margin was based on the mean difference in size for paired ossicles from a sample of 21 *Mictyris* crabs. Since ossicles of all three crustaceans were similar in size (0.5–2 mm), it was assumed that in *Macrophthalmus* and *Trypaea* within-pair ossicle-length variability would be similar to that in *Mictyris*. Some ossicles were missing edges, and their length was estimated by aligning them with intact exemplars of the same maximal width within the sample. A small number of ossicles that could not be paired was usually present in samples, and these were counted as representing separate prey items.

It was critical for the outcomes of the calculations of energy intake that the number of prey items seen to be ingested corresponded to the number found in a pellet. When comparing the number of prey recorded visually with that discovered in the corresponding pellet, a  $\pm 5\%$  error was allowed. If the numbers of prey detected in a pellet and recorded visually fit within this margin, the pellet was considered as having a full set of prey. Subsequent intake calculations were then based entirely on the number and size of ossicles found in the pellet. Because some small exo- and endoskeleton fragments did pass into the intestines and were found in feces, or perhaps were trapped in the folds of stomach lining, partial loss of ossicles was unavoidable. Therefore, if a pellet contained  $<95\%$  of the number of individual prey items seen ingested by the curlew,

the number of prey items recorded visually was used to correct intake calculations. Out of 50 pellets collected, two contained <50% of prey items noted visually. They were excluded from the data set. Thirty-four pellets (71%) contained full sets of prey as per the above definition, and in the remaining 14 (29%) pellets,  $20.3\% \pm 13.5\%$  of visually determined prey items were missing. For these 14 pellets, intake calculations were corrected using the visual data. The overall relationship between the number of prey counted visually and detected in the corresponding pellet was highly significant ( $R^2 = 0.92$ ,  $P < 0.001$ ,  $n = 48$ ).

#### Prey Energy Densities and Allometric Relationships

Small samples of the three prey types were collected in the study area in December 2000 and February 2001, and their full animal and leg energy density was determined as above. Separate calculations of leg energy density were done because infrequently legs of crabs captured by the curlews were lost during handling (Tables 1, 2).

The observed prey energy density (ED) values were within the range reported for crabs and callinassid shrimp elsewhere in the Southern Hemisphere (Turpie and Hockey 1996). To develop allometric relationships between the ossicle length and dry mass, samples of various sizes of the three prey species were collected in the study area at different times from October to March 1999–2001. Allometric relationships were constructed first between the ossicle length and carapace length/width and then between carapace length/width and dry mass (App. 1).

#### Meal Mass and Energy Content, Intake Rate, and Gastric Throughput Rate

The mass of an ingested meal (g DM) was estimated as the sum of dry-mass estimates of separate prey items allometrically derived from the mean lengths of paired or individual lengths of unpaired ossicles found in the corresponding pellet. The meal mass determined from pellets missing some prey was calculated as the sum of dry-mass estimates derived from the ossicle found in the pellet plus the product of the difference between the number of prey in the visual record and in the pellet and the mean prey dry-mass value. The total mass was then corrected for any crab legs lost during handling. The ED of a meal was calculated by multiplying the prey-specific DM part of the meal by the mean prey type ED for the period, adding them together to determine the total energy content, and dividing by the total meal dry mass. When necessary, the energy content of a meal was corrected for leg loss as well. Because *Mictyris* ED did not differ significantly between the periods (Table 2), the overall mean of  $13.75 \text{ kJ g DM}^{-1}$  was applied across the data set; otherwise, period-specific values were used.

The rate of food consumption was expressed as crude intake rate (CIR), that is, meal mass (energy content) divided by time

Table 1: Mean ( $\pm$ SD,  $n$ ), dry mass (g DM), and energy density ( $\text{kJ g DM}^{-1}$ ) values of a full set of legs (10) of crabs *Macrophthalmus crassipes* and *Mictyris longicarpus* collected in the study area in December 2000 and February 2001 used to correct calculations of DM and energy intake

	Month	
	December	February
<i>Macrophthalmus crassipes</i> :		
DM	.391 (.154, 2)	.354 (.132, 4)
Energy density	9.4 (1.6, 2)	7.5 (3.0, 4)
<i>Mictyris longicarpus</i> :		
DM	.262 (.086, 3)	.243 (.093, 2)
Energy density	12.3 (.9, 3)	12.3 (2.2, 2)

of a full bout and intake rate (IR), that is, meal mass (energy content) divided by time spent actively foraging within a bout. The rate of gastric throughput (GTR) was calculated as the difference between the estimated mass (energy content) of the meal and that of the pellet divided by the bout time. Gastric digestive efficiency was defined as the proportion of the original meal that passed into the intestines.

#### Fecal Sample (Dropping) Analysis

Because wild animals were observed in the study, it was impossible to obtain fecal samples from the same individuals from which pellets were collected. To allow for an overall estimate and the intake of apparent metabolizable energy (AME) to be calculated, 14 fresh curlew droppings (feces + urine) were collected in each period. AME has been recommended for use in field studies of energy intake because it equals the gross energy consumed less that lost in excreta (pellets, feces, urine) and thus represents energy truly available for the animal (Miller and Reinecke 1984). Therefore, for each fecal sample (= individual dropping), care was taken to collect both uric acid and the fecal matter itself, which involved scooping up a small amount of sand from the substratum surface with a razor blade. In the laboratory, each sample was diluted with distilled water to about 50 mL, vigorously shaken, and placed into an ultrasonic water bath for periods of 15–20 min. After a period of shaking, supernatant containing homogenized fecal matter and urine was pipetted off, the water was replaced, and the process was repeated until only sand grains remained in the sample container. DM and ED values of the fecal samples were determined as above.

#### Statistical Analyses

Because of recent criticism of the application of ratio-based nutritional indices in digestive-efficiency studies (e.g., Raubenheimer and Simpson 1992; Beaupre and Dunham 1995), sea-

Table 2: Mean ( $\pm$ SD,  $n$ ) energy density ( $\text{kJ g DM}^{-1}$ ) values of the three major prey consumed by the eastern curlews in the study area collected in December 2000 and February 2001

	Month		Statistics
	December	February	
<i>Macrophthalmus crassipes</i>	14.83 (5.30, 10)	8.44 (3.14, 10)	$t = 2.53, P < .020$
<i>Mictyrus longicarpus</i>	14.66 (1.69, 12)	12.84 (2.67, 12)	$t = 1.99, P = .058$
<i>Trypaea australiensis</i>	13.49 (2.75, 13)	17.16 (4.56, 15)	$t = 3.46, P < .003$

Note. Statistics are given for a  $t$ -test for independent samples. The sample of *Trypaea australiensis* given under the December column was actually collected in May 2001. In both months, however, most of the population of the shrimp consists of postspawning individuals (Hailstone and Stephenson 1961); therefore, we assumed that their energy densities would be similar.

sonal changes in gastric digestion of dry matter and energy were investigated using ANCOVA as suggested by these authors. Predictive equations were estimated for (1) pellet DM and (2) pellet energy content using the air temperature ( $^{\circ}\text{C}$ ) and the respective ingested meal mass and meal energy-content values as covariates. The ambient air temperature was included into the model because it may negatively affect digestive efficiency (Klaassen et al. 1990).

Apparent energy assimilation coefficient ( $Q$ ) was calculated following Zwarts and Blomert (1990):

$$Q = 1 - (E_e/E_c) \times (M_e/M_c),$$

where  $E_e$  and  $E_c$  were energy densities in  $\text{kJ g DM}^{-1}$  of excreta (pellets + feces) and ingested meal, respectively, and  $M_e$  and  $M_c$  were rates of DM loss in  $\text{g DM min}^{-1}$  in excreta (pellets + feces) and CIR, respectively. Overall seasonal differences in assimilation coefficients and rates of intake of apparent metabolizable energy (AME) were calculated on the basis of the relevant parameters for energy consumption and digestion given in the "Results."

The rate of AME intake was calculated as

$$\text{AME} = Q \times \text{CIR},$$

with CIR expressed in  $\text{kJ min}^{-1}$ . All values in the text are given as mean ( $\pm$ SD). Rates of matter and energy intake and throughput are expressed in  $\text{g DM}$  and  $\text{kJ min}^{-1}$ , respectively. The Statistica software package (Statsoft 1997) was used for all analyses.

## Results

### *Evidence for Digestive Limitation of Food Intake*

CIR formed an asymptotic relationship with IR (Fig. 1A), and on the basis of the relationship, it appeared that in general the birds were not able to achieve a CIR much greater than  $0.30 \text{ g DM min}^{-1}$  regardless of an IR value, which could be up to five times greater. The same relationship is obtained if the rate

of gastric throughput is plotted against IR, showing that the ceiling throughput rate was about  $0.22 \text{ g DM min}^{-1}$  regardless of the instantaneous speed of food consumption (Fig. 1B). In both cases, however, the asymptotic function provided a considerably better fit for the data in February than in December. Since in themselves CIR and GTR did not change significantly between the periods, the better fit in February suggests that a larger proportion of birds fed at the maximal rate immediately before departure rather than earlier in the season. CIR was not greater during shorter low-tide periods as would be expected if the birds were compensating for the lack of time available for foraging by increasing the rate of intake (Fig. 2).

The rate of food intake achieved during active foraging reached  $1.40\text{--}1.75 \text{ g DM min}^{-1}$ , while the apparent instantaneous stomach-holding capacity (pellet mass) leveled off at  $4\text{--}5 \text{ g DM}$  and was largely independent of the length of a foraging bout (Fig. 3A). (The 7-g pellet came from an individual that ingested several unusually large *Macrophthalmus*. Removing it did not improve the relationship.) This implies that a curlew foraging at maximum IR would have to stop after  $2.7\text{--}4.2 \text{ min}$  (e.g.,  $4/[1.75-0.22] = 2.7$ ) to allow for some digestion to take place. The maximum amount of food processed during one foraging bout appeared to be linearly related to the length of the bout, but most values did not exceed  $14\text{--}16 \text{ g DM}$  (Fig. 3A).

Although overall CIR appeared to be slightly ( $\approx 10\%$ ) lower in December than in February ( $0.21 \pm 0.07$  and  $0.24 \pm 0.08 \text{ g DM}$  or  $2.94 \pm 1.09$  and  $3.32 \pm 1.00 \text{ kJ min}^{-1}$ , respectively), the difference was not significant (ANOVA,  $F_{1,46} < 1.65, P > 0.15$ ). The same was true for the estimated meal mass ( $10.85 \pm 4.53$  and  $11.57 \pm 4.17 \text{ g DM}$ ; ANOVA,  $F_{1,46} = 0.32, P = 0.57$ ) and pellet mass ( $3.18 \pm 1.08$  and  $3.69 \pm 1.21 \text{ g DM}$ ; ANOVA,  $F_{1,48} = 2.45, P = 0.12$ ) for December and February, respectively.

### *Gastric Throughput Rate and Digestion*

The raw variables had homogenous variances between the treatments (Cochran's  $C$ -test, all  $P$  values  $> 0.05$ ) and thus did not

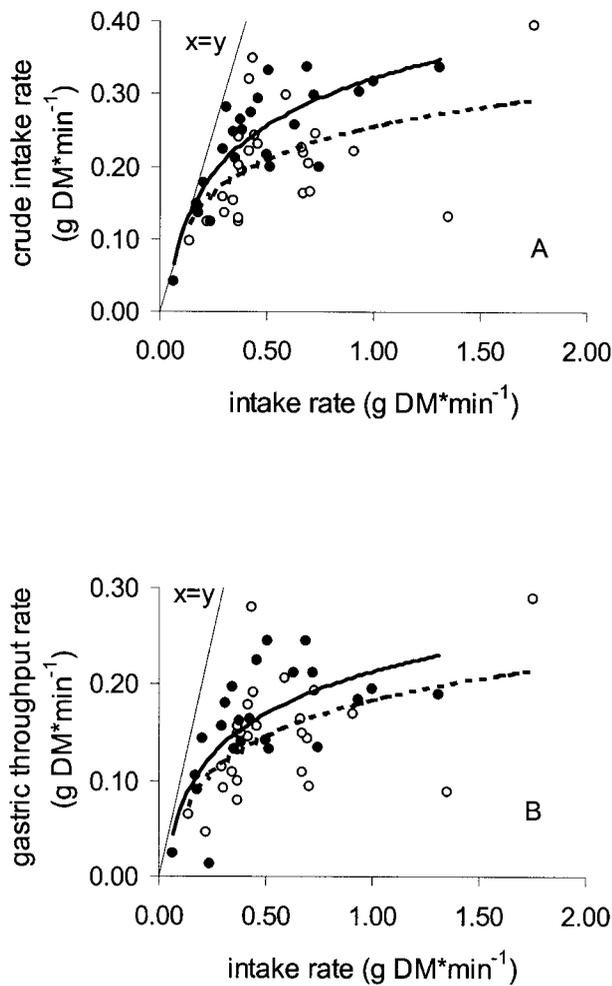


Figure 1. Crude intake rate as a function of intake rate (A; fitted log function, December: *dashed line*,  $y = 0.07 \times \ln(x) + 0.26$ ,  $R^2 = 0.23$ ,  $P < 0.01$ ; February: *solid line*,  $y = 0.10 \times \ln(x) + 0.32$ ,  $R^2 = 0.69$ ,  $P < 0.01$ ) and gastric throughput rate as a function of intake rate (B; fitted log function, December: *dashed line*,  $y = 0.05 \times \ln(x) + 0.18$ ,  $R^2 = 0.24$ ,  $P < 0.01$ ; February: *solid line*,  $y = 0.06 \times \ln(x) + 0.21$ ,  $R^2 = 0.48$ ,  $P < 0.01$ ) achieved by eastern curlews. December ( $n = 25$ ) and February ( $n = 23$ ) data are represented by open and closed circles, respectively.

need to be transformed. The slopes of lines relating covariates to the pellet DM and energy content were also homogenous between the treatments. The overall model was significant in each case (pellet DM,  $F_{2,44} = 13.38$ ,  $R^2 = 0.38$ ,  $P < 0.001$ ; pellet energy content,  $F_{2,44} = 11.09$ ,  $R^2 = 0.34$ ,  $P < 0.001$ ), but the main effect (period) was not significant nor was the effect of air temperature ( $P$  values  $> 0.15$ ). Indeed, the proportion of ingested DM and energy that passed through the stomach and became available for intestinal absorption (assimilation) was nearly identical between November/December and February (Table 3). Although GTR seemed to be greater in February than

in November/December (Fig. 1B), no significant differences between the two periods were detected (DM, energy  $P$  values  $> 0.20$ ; Table 3).

In summary, while a small ( $\approx 10\%$ ) seasonal increase in the rate of food processing may occur in the eastern curlews, no clear major seasonal change in either gastric digestive efficiency or the rate of throughput of matter and energy through the stomach were detected. The only gastric digestive parameters that differed between the two periods were the rate of loss of dry mass in pellet and pellet ED (Table 3). This difference, however, (1) did not affect the digestive parameters specifically tested (see above) and (2) if anything, suggested that the curlews were digesting their food less efficiently before migration.

#### Defecation Rate

The rate of defecation was 0.047 dropping per minute in December and 0.076 dropping per minute in February, differing significantly between the periods (ANOVA,  $F_{1,36} = 11.17$ ,  $P = 0.002$ ). In contrast, neither the mean DM nor ED value of a dropping differed significantly between December and February (ANOVA,  $F_{1,26} < 2.24$ ,  $P > 0.15$ ; Table 4).

#### Overall Assimilation Coefficients and Apparent Metabolizable Energy Intake

Fecal data showed a highly significant seasonal increase (30%) in the rate of defecation. However, if it is accepted that the rate at which food matter was entering the intestines (GTR) remained the same between the periods, the average DM value of a dropping should have decreased by a similar percentage. The month-specific mean DM values of droppings suggest this, but the difference was not significant. Therefore, in calculations of Q and AME, month-specific defecation data and CIR means

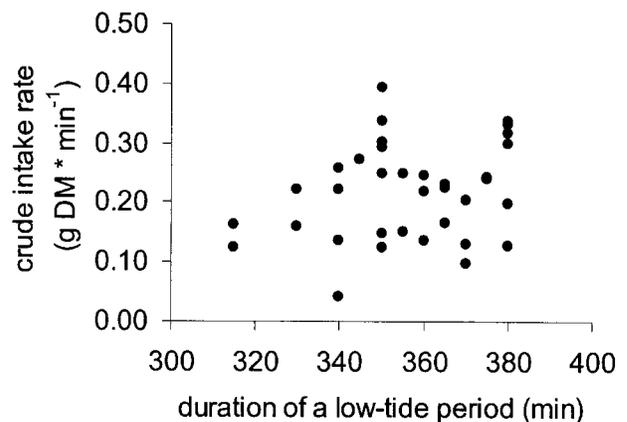


Figure 2. Relationship between the crude intake rate and the duration of the respective low-tide period (November/December and February data combined;  $R^2 = 0.08$ ,  $P > 0.25$ ,  $n = 37$ ).

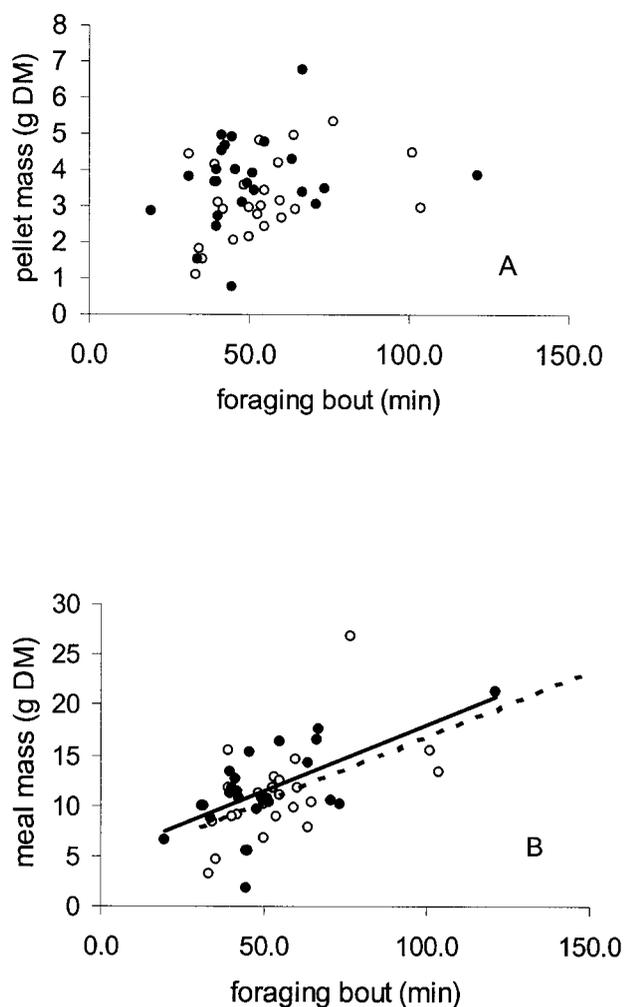


Figure 3. Eastern curlew pellet mass (g DM; A; fitted linear function, December:  $R^2 = 0.02$ ,  $P > 0.05$ ; February:  $R^2 = 0.04$ ,  $P > 0.05$ ) and estimated processed meal mass (B; December, *dashed line*,  $y = 0.13x + 3.86$ ,  $R^2 = 0.28$ ,  $P < 0.01$ ; February, *solid line*,  $y = 0.13x + 4.85$ ,  $R^2 = 0.40$ ,  $P < 0.01$ ) as a function of duration of a foraging bout (min). December ( $n = 25$ ) and February ( $n = 23$ ) data are represented by open and closed circles, respectively.

were used. The obtained Q values were 62.8% and 57.9% for November/December and February, which resulted in the respective AME intake rates of 1.85 and 1.88  $\text{kJ min}^{-1}$ .

Although the sample size for fecal analysis was relatively small and accuracy of these data may be lower than for energy consumption and gastric digestion data, this does not change the main result of the study. The gastric digestive parameters, overall assimilation coefficients, and energy acquisition rates of the eastern curlews remain remarkably constant over the time period when the animals are required to have a strong positive energy balance to build up nutrient reserves for the flight back to the breeding grounds.

## Discussion

Eastern curlews spending the nonbreeding season in an austral subtropical estuary exhibited remarkably constant seasonal rates of food consumption of 0.22 g DM or 3.09  $\text{kJ min}^{-1}$  (estimated AME intake rates of 1.85–1.88  $\text{kJ min}^{-1}$ ) between the time periods when their daily energy requirements were expected to differ greatly. The animals could not be challenged to increase their rate of consumption as would happen in a controlled experimental setting (e.g., Klaassen et al. 1997). However, the asymptotic relationship between CIR/GTR and IR (e.g., Zwarts and Dirksen 1990), the lack of an increase in CIR in response to a shorter foraging period (cf. Swennen et al. 1989), and frequent interruption of foraging (e.g., Diamond et al. 1986; Y. Zharikov, unpublished data) all suggest that food is collected faster than it can be digested. Therefore, a digestive bottleneck is experienced by the birds throughout a nonbreeding season.

It was predicted that in order to increase energy intake rate before northward migration, when the daily metabolizable energy demand is expected to go up by 25%–30% (Zwarts et al. 1990a), either (1) intake (gastric throughput) rate or (2) digestive (assimilation) efficiency would increase. Neither of these predictions was upheld. Both CIR/GTR and gastric energy digestion efficiency (91%) and overall apparent assimilation coefficient (62.8% and 57.9%) were similar between the mid-nonbreeding (November/December) and premigratory (February) periods. While a small ( $\approx 10\%$ ) increase in the rate of food consumption may be real, it appears that neither of the digestive parameters tested can be improved considerably (e.g., Bairlein 2002) to satisfy adequately the energy intake requirements before migration.

Regurgitated pellets mostly consisted of crushed exo- and endoskeleton fragments of the crustacean prey of the curlews and contained 35% of DM and 10% of energy value of the respective meal. Because organic matter accounts for approximately 50% of crab dry mass (Zwarts and Blomert 1990), this implies that most of the organic matter present in the original meal, as well as some inorganic bulk, passed into the intestines. Furthermore, if energy densities are compared, mean pellet ED (4.04  $\text{kJ g DM}^{-1}$ ) represents 28.6% of the mean meal ED (14.15  $\text{kJ g DM}^{-1}$ ). This is close to the proportion of energy (30%) contained in the structural proteins of crab skeleton that is not available for digestion (Zwarts and Blomert 1990). Therefore, one may assume that most of the 10% of meal energy discarded in a pellet is contained in structural (skeleton) organic matter and would not be available for intestinal assimilation anyway. Thus, it seems likely that the efficiency with which organic matter is extracted in the stomach could not be improved any further, although differential digestibility of arthropod cuticular proteins and carbohydrates may, in itself, represent an interesting research question.

The lump assimilation coefficients of 62.8% and 57.9%

Table 3: Mean ( $\pm$ SD) December 2000 ( $n = 25$ ), February 2001 ( $n = 23$ ), and overall ( $n = 48$ ) values of variables relevant to the eastern curlew gastric digestive performance

	Month		Overall
	December	February	
% DM digested	.69 (.09)	.65 (.14)	.67 (.12)
% energy digested	.91 (.02)	.91 (.04)	.91 (.03)
Gastric throughput rate, DM	.144 (.059)	.157 (.059)	.151 (.059)
Gastric throughput rate, energy	2.66 (1.02)	3.04 (.93)	2.85 (.98)
Rate of loss in pellet, DM	.063 (.025)	.080 (.032)	$F_{1,46} = 4.1, P = .05$
Rate of loss in pellet, energy	.27 (.09)	.29 (.15)	.28 (.12)
Pellet energy density, $\text{g}^{-1}$ DM	4.35 (.52)	3.72 (1.03)	$F_{1,46} = 10.8, P < .002$
Meal energy density, $\text{g}^{-1}$ DM	14.12 (.55)	14.17 (.80)	14.15 (.90)

Note. Proportion digested =  $1 - (\text{pellet dry mass [DM] or energy content/meal DM or energy content})$ ; rate of gastric throughput ( $\text{g DM or kJ min}^{-1}$ ) =  $(\text{meal DM or energy content} - \text{pellet DM or energy content}) / \text{foraging bout time}$ ; rate of loss in pellet ( $\text{g DM or kJ min}^{-1}$ ) =  $\text{pellet DM or energy content} / \text{foraging bout time}$ . DM, energy, and time were measured in grams, kilojoules, and minutes, respectively. Overall data means are given for those variables where no significant seasonal differences in mean values were detected; otherwise, one-way ANOVA statistics are presented.

found in the eastern curlew are close to the 65% found in its smaller relative, the whimbrel (*Numenius phaeopus*), foraging on a similar diet of *Uca* crabs (Zwarts and Blomert 1990). The similarity of the results of these two studies, one of a population of free-ranging individuals (this study) and another of a single, caged bird (Zwarts and Blomert 1990), is noteworthy because of an earlier warning that digestive efficiency may vary between captive and wild animals consuming similar diets (Sibly 1981). The similarity in results suggests that in this case, assumptions made in laboratory studies are also valid in the field. The observed assimilation coefficient values were also similar to other captive birds (60%–65%) offered high inorganic content prey (reviewed in Castro et al. 1989b). Therefore, these values may represent the maximal proportion of energy that can be extracted from such a diet.

Is improved digestion of food matter a viable option to increase energy intake for birds? There is an emerging view among avian digestive physiologists that while the metabolizable energy intake is limited by the nutrient digestion rate (Karasov 1996), the food passing through the intestines is always digested to the same extent (Kersten and Visser 1996; McWilliams and Karasov 2001). Results of the experimental studies where no improvement in digestion efficiency took place in response to increased energy demand support this argument (e.g., thrush nightingale [*Luscinia luscinia*], Klaassen et al. 1997; blackcap [*Sylvia atricapilla*], Karasov and Pinshow 2000). In studies where digestive improvement was noted, the increase was either small relative to the increase in the rate of food consumption (garden warbler [*Sylvia borin*], Bairlein 1985; Hume and Biebach 1996) or occurred quickly after a switch to a new diet (sanderling [*Calidris alba*], Castro et al. 1989a) but not in response to higher energy demands per se. Therefore, any increase

in metabolizable energy intake is more likely to come from increased food consumption and gastrointestinal throughput, as allowed by the holding capacity of the digestive system (Klaassen et al. 1997; McWilliams et al. 1999), than from improved digestion. It appears that manakins (Worthington 1989) and cedar waxwings (*Bombycilla cedrorum*; McWilliams et al. 1999) foraging on a fruit diet and sanderlings consuming horseshoe crabs (*Limulus polyphemus*) eggs (Castro et al. 1989a) are able to use this strategy. In the first two examples, however, the diet was easily digestible (carbohydrate rich), whereas in the second example, it consisted of small (<1 mm) items and thus probably did not require extensive gastric processing. Therefore, an increase in passage rate had little effect on digestibility, while the energy turnover increased considerably, producing a net increase in metabolizable energy intake (Sibly 1981). Even intraspecifically, birds consuming carbohydrate-rich foods (fruit) are capable of processing much greater volumes than birds consuming protein-rich (insect) diets (Gannes 2002 referring to W. H. Karasov, unpublished data). Shorebirds foraging either on bulky (Zwarts and Dirksen 1990; this study) and/or protein-rich (Zwarts et al. 1996) foods appear to be on the other side of the digestive adaptation spectrum because they have to allow for much longer gastric digestion periods (Piersma et al. 1993). If the passage rate were to increase under this dietary scenario, for example, because of an increased pyloric aperture (Piersma et al. 1993), this could result in a flux into the intestines of indigestible bulk, in general, and the chitinous content of crustacean exoskeletons, in particular. These elements would either interfere with energy assimilation in the intestines (Speakman 1987), constrain intestinal passage rate (Sorensen 1984), or possibly even suppress the rate of body weight gain (e.g., Jackson et al. 1992). Therefore, it is doubtful

Table 4: Mean ( $\pm$ SD) dry mass (g) and energy density (kJ g DM<sup>-1</sup>) of eastern curlew droppings (feces + urine) collected in December 2000 ( $n = 14$ ) and February 2001 ( $n = 14$ )

	Month		Overall
	December	February	
Dropping DM	.997 (.363)	.769 (.525)	.883 (.458)
Dropping energy density	6.15 (1.46)	5.83 (.91)	5.99 (1.20)

Note. No values differed significantly between the months. The obtained dropping energy density values were similar to those of whimbrel (*Numenius phaeopus*) foraging on *Uca* crabs (5.5 kJ g DM<sup>-1</sup>; Zwarts and Blomert 1990).

that such an adjustment would be adaptive, and the option of increased passage rate may be open only to species consuming easily digestible food with low inorganic content (Worthington 1989). Another possibility could be to increase the overall holding capacity of a digestive system by increasing the length/volume of the intestines (e.g., McWilliams et al. 1999). However, shorebirds are known to decrease rather than increase the size of their gastrointestinal system immediately before long-distance migration, presumably to decrease the wing load during a sustained flight (e.g., Piersma 1998; Piersma and Gill 1998; Piersma et al. 1999).

Overall, curlew digestive performance was well tuned to the decapod-dominated diet consumed in the Australian wintering grounds (Lane 1987) and elsewhere along the East Asia–Australasian flyway (Piersma 1986). Interestingly, in the Siberian breeding grounds, at least a part of the eastern curlew diet consists of carabid, dytiscid, and hydrophilid beetles (A. Antonov, unpublished data), which are also likely to have high inorganic and protein content. Such optimization of digestive performance is to be expected if an animal experiences constant dietary conditions over an extended period of time (Karasov 1996), and one may ask whether the hypothesis of improved assimilation efficiency should be raised at all (e.g., Scott et al. 1994) unless a dramatic shift in diet quality occurs (e.g., Bairlein 2002). If the instantaneous rate of intake cannot be improved, the options remaining for a digestively and time-constrained bird before migration are few indeed. It could either increase the proportion of time spent foraging at maximal CIRs (e.g., Zwarts and Dirksen 1990) or store food in the stomach/oesophagus to extend the period of energy acquisition beyond the foraging period (low-tide) limits (Kersten and Visser 1996). The first option is available only if prey availability improves, that is, CIR approaches the absolute digestive constraint throughout a foraging period (Zwarts 1990). The second strategy would make a difference only if a considerable amount of energy-rich matter could be stored (Kersten and Visser 1996). Neither of these conditions is applicable for our study system. First, prey conditions remained relatively unchanged between December and February (Zharikov 2002), and prey availability was not a limiting factor anyway. Second, even if a curlew

departed for the roost with a full stomach, this would extend energy acquisition time by only 40–50 min (cf. estimated 11 hr in Eurasian oystercatchers [*Haematopus ostralegus*]; Kersten and Visser 1996) beyond low-tide time available for foraging.

All curlews in this study were adult territorial individuals who, judging by their abdominal profiles (Wiersma and Piersma 1995), accumulated considerable nutrient stores by early mid-March and then migrated out of the study area. Assuming the findings of nearly identical crude and/or AME intake rates between the mid-nonbreeding and premigratory periods are a true representation of the situation, the question of how the curlews achieved an increase in daily intake to allow for reserve deposition becomes an issue.

Several possibilities may be considered. (1) Curlews achieve a greater intake per nocturnal low tide, when no observations were obtained, than by day. Such a suggestion does not seem likely because by day the birds already use all the time available for foraging (Y. Zharikov, unpublished data). Under these conditions, a greater intake by night could be achieved only by increasing the rate of intake. However, all of the data presented in this article suggest that rate of intake cannot be increased any further. (2) Final premigratory fattening may occur not at the study sites but elsewhere in the Bay or along the Australian east coast. If the former was true and greater rates of intake could be achieved elsewhere in the Bay by, for example, hunting energy-rich prey, it would be logical to expect higher curlew densities at such sites. However, Finn et al. (2001) have demonstrated that sites with sandy substrates, as in the study area, typically occupied by *Trypaea australiensis* (Hailstone and Stephenson 1961) and *Mictyrus longicarpus* (Cameron 1966), support the highest local densities of curlews. Also, in the study area, curlews maintained their territories until mid-March, when northward departure of these birds begins (Driscoll 1999; Y. Zharikov, personal observation). Finally, satellite-tracking data (Driscoll 1999) show that eastern curlews departing from Moreton Bay in March do not make another stop along the eastern Australian seaboard but, if migration is not aborted, fly nonstop as far as the coastline of China. Therefore, these birds ought to fatten at the sites they appear to occupy throughout a season and depart with enough fuel to fly in excess of

5,000 km. (3) The observation periods have not captured the final 2–3 wk before migration when most of reserve deposition may take place (e.g., Zwarts et al. 1990a, 1990b). However, assuming that a major increase in the rate of intake was not possible, all the behavioral mechanisms available for an increase in daily intake, namely increase in foraging time and a switch in diet, were already employed by the birds at the time of observations in February (Y. Zharikov, unpublished data). This leaves two more possibilities. (4) If reduction in the size of the gastrointestinal system does take place 1–2 wk before migration as shown by Piersma (1998), Piersma and Gill (1998), and Piersma et al. (1999), then energy needed for the maintenance of (larger) digestive organs can be reallocated to nutrient deposition. Suggestions that such reallocation may indeed take place have already been voiced (e.g., Piersma and Lindström 1997; Karasov and Pinshow 1998), but how important such a reallocation is in maintaining a positive energy budget during premigratory preparations remains to be determined (Piersma et al. 1999). (5) A simpler, but complimentary rather than alternative, explanation can also be offered. It is apparent that a small (13.6%) but significant increase in the overall time spent on the mudflat was achieved by the eastern curlews in February by arriving before the mudflat surface exposure and by leaving after flooding (Y. Zharikov, unpublished data). Even if we assume that the rate of intake similar to that at mid–low tide could be achieved during this period, the corresponding increase in the daily energy intake will be far less than the 25%–30% achieved by premigratory shorebirds elsewhere (e.g., Zwarts 1990; Zwarts et al. 1990b). However, it is likely that the increase in energy intake due to foraging on inundated flats is disproportionately lower. This is because crabs become surface active and easy to capture only after a mudflat is fully exposed (e.g., Cameron 1966), and water flushes used by the birds as visual cues to hunt *Trypaea* (Y. Zharikov, personal observation) will likely be invisible in water more than a few centimeters

deep. Still, since the curlews invest time and energy in this behavior, it must produce some, albeit a small, net energy gain.

Accepting findings of this study at their face value poses a truly intriguing question of how and over what time period the eastern curlews store the nutrients necessary for the ensuing long, northward nonstop flight. We propose that eastern curlews spending the nonbreeding season in eastern Australia do not rely on a single major strategy to increase the daily energy intake before migration but rather several subtle adjustments (e.g., increase in the rate of intake, greater foraging time, diet shift, internal energy reallocation) take place and allow the birds to successfully prepare for migration. Because no considerable increase in the daily energy intake seems possible, we predict that the period of premigratory preparations in the eastern curlews in Australia will be much longer than the 4 wk recorded in shorebirds elsewhere (Zwarts 1990; Zwarts et al. 1990a, 1990b). However, at present, there is no solid data to test this prediction. If eastern curlews or other waders consuming high inorganic content prey do require a long migratory preparation period, a temporally and spatially stable and predictable nature of food supply in their nonbreeding grounds would be necessary to facilitate successful migratory preparations.

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#### Appendix

Table A1: Published and derived allometric equations used to convert the length (mm) of gastric mill ossicles found in the eastern curlew pellets first into carapace length (*Mictyris longicarpus* and *Trypaea australiensis*) or width (*Macrophthalmus crassipes*; mm) and subsequently into individual dry mass (g) of consumed prey items

Species	Equation	Source
<i>Macrophthalmus crassipes</i>	$\text{Log}_e(\text{DM}) = 3.57 \times \text{Log}_e(\text{carapace}) - 11.41$ ( $R^2 = .91$ , $P < .001$ , $n = 23$ )	This study
	$\text{Log}_e(\text{carapace}) = .81 \times \text{Log}_e(\text{ossicle}) + 2.53$ ( $R^2 = .98$ , $P < .001$ , $n = 16$ )	This study
<i>Mictyris longicarpus</i>	$\text{Log}_e(\text{DM}) = 3.01 \times \text{Log}_e(\text{carapace}) - 2.25 \times 10^{-3}$	Quinn 1983
	$\text{Log}_e(\text{carapace}) = .89 \times \text{Log}_e(\text{ossicle}) + 2.42$ ( $R^2 = .96$ , $P < .001$ , $n = 131$ )	This study
<i>Trypaea australiensis</i>	$\text{Log}_e(\text{DM}) = 3.72 \times \text{Log}_e(\text{carapace}) - 10.04$ ( $R^2 = .92$ , $P < .001$ , $n = 103$ )	This study
	$\text{Log}_e(\text{carapace}) = .97 \times \text{Log}_e(\text{ossicle}) + 2.13$ ( $R^2 = .96$ , $P < .001$ , $n = 35$ )	This study

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