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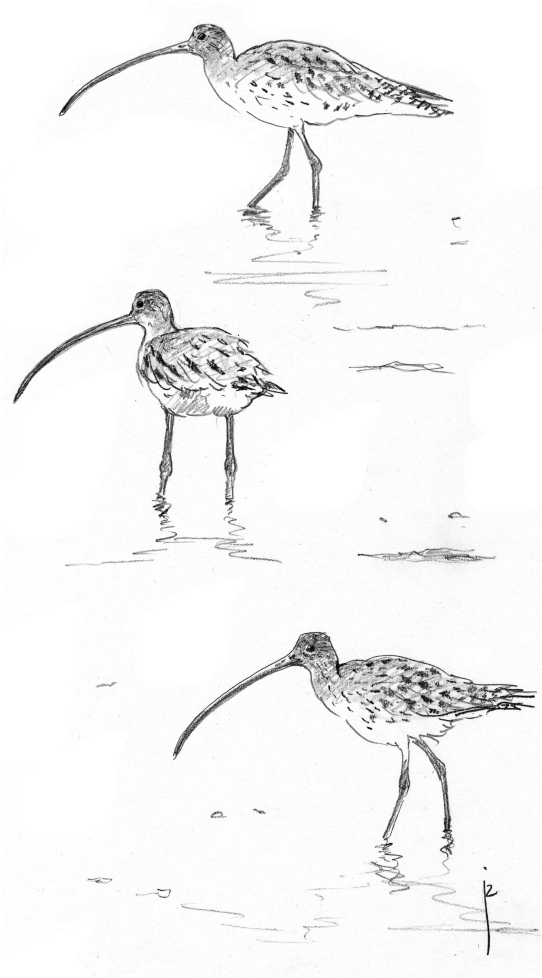
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Prey availability, and not energy content, explains diet and prey choice of Eastern Curlews *Numenius madagascariensis* in southern Australia

Peter Dann



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Eastern Curlews breed in Siberia in the boreal spring and summer and migrate to Australia in the austral spring and summer. The Eastern Curlew is notable for its very long, decurved bill; this sexually dimorphic characteristic represents approximately 25–30% of total body length. Female curlews have the longest bill of any wader. Diet and prey choice in relation to availability and profitability were examined over two non-breeding periods in Western Port in southern Australia. Diet was determined from direct feeding observations, examination of pellets collected at high-tide roosts (during daytime and night-time) and by following tracks of foraging curlews. Male and female curlews used the intertidal feeding areas differently: females used more sandy areas and males more muddy areas. This difference may be related to sexual dimorphism in bill length and could reflect substantial dietary differences. Tasselled Crab *Pilumnus fissifrons* was the most common prey, followed by Australian Ghost Shrimp *Trypaea australiensis*, Two-spined Crab *Litocheira bispinosa* and Sentinel Crab *Tasmanoplax latifrons*. The availability of prey was examined in aquaria through examination of burrowing behaviour and other activity patterns in relation to tidal movements and levels of daylight. Prey behaviour explained the greater consumption of male Ghost Shrimps and the differences in diet between day and night. More Ghost Shrimps and Sentinel Crabs and fewer Two-spined Crabs were taken during the day than during night. Prey choice was examined by measuring the calorific values of prey and potential prey species. Generally, curlews took the more energy valuable prey, but prey behaviour and prey availability mostly determined prey choice, not the energetic value of prey.

Key words: Eastern Curlew, *Numenius madagascariensis*, diet, prey choice, prey availability, sexual dimorphism, prey behaviour, prey energy value, Australia

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The Eastern Curlew *Numenius madagascariensis*, the largest wader in the family Scolopacidae, breeds in Siberia in the boreal summer and migrates to southern Australia in the austral spring and summer (Lane 1987, Marchant & Higgins 1996). The East Asian-Australasian flyway population was estimated to be approximately 38,000 birds (Barter 2002), with most birds spending their non-breeding period in southern and eastern Australia (Lane 1987). Population declines have been reported throughout much of south-eastern Australia (Close & Newman 1984, Dann *et al.* 1994, Reid & Park 2003, Gosbell & Clemens 2006, Minton *et al.* 2012) and currently the population may not exceed 20,000 individuals (Conklin *et al.* 2014). The Eastern Curlew is classed as 'vulnerable' by the IUCN (2012).

Eastern Curlews have very pronounced bill lengths, with a bill to body length ratio of 25–30%, and females are distinctly larger than males. The strong sexual dimorphism in bill length suggests sex-related differences in diet and habitat selection. Previous studies have described the feeding ecology and behaviour of Eastern Curlews (Piersma 1986, Congdon & Catterall

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1994, Tulp & de Goeij 1994, Hodder 2000, Finn *et al.* 2001, 2002, 2007, 2008, Zharikov & Skilleter 2003, 2004a & b), yet little is known about the functionality of their long bills. In general, relationships between morphology and foraging ecology have been widely studied in birds (e.g. Newton 1967, Grant 1986). In waders, a relationship has been shown between bill morphology and diet (Strauch & Abele 1979, Lifjeld 1984, Dann 2005), prey handling techniques (Swennen *et al.* 1983) and microhabitat selection (Baker 1979, Gerritsen & van Heezik 1985, Dann 1999, Zharikov & Skilleter 2004a, Nebel *et al.* 2005), often leading to sex differences in distribution. Dann (2005) reported that in the genus *Numenius*, longer bills are associated with greater dependence on feeding in soft sediments in intertidal areas during non-breeding periods, suggesting that the costs of specialisation (and contraction of alternate feeding habitats) are compensated with greater access to prey in intertidal areas, and that long bills act as a buffer against variability in prey availability.

The aim of this study was to describe the diet of the Eastern Curlew when feeding in intertidal habitats in southern Australia during the non-breeding period and to examine prey choice in relation to bill morphology and the calorific value and behaviour of main species of prey.

METHODS

Study areas

The study area was in Western Port, a marine bay located 60 km southeast of Melbourne, Victoria, Australia. Western Port is on the northern side of Phillip Island (38°28'S, 145°18'E). The two main study sites were at Rhyll Inlet and the mudflats offshore known as Churchill Tidal Flats (Marsden *et al.* 1979, Figure 1). Tidal mudflats, mostly covered by seagrass beds, comprise about 40% of the bay's total area of 680 km^2 (Shapiro 1975); Western Port contains one of the most extensive seagrass areas in southern Australia (Clough & Attiwill 1980). The seagrass meadows are dominated by Tasman Grass-wrack *Zostera tasmanica*, occurring in dense stands on lower areas of the mudflats that retain water at low tide (Bulthuis 1981). The mudflats in Rhyll Inlet are basin-shaped with central areas at a slightly lower elevation than the bank margins, so that they retain a shallow covering of water at low tide. The exposed intertidal areas of both study sites are largely bare or sparsely covered by Dwarf Grass-wrack *Zostera muelleri*. There are some sandy beaches around the fringes of the bay, which are formed from longshore sediment movements and *in situ* erosion of cliffs. Since European settlement, a large volume of sediment has entered the bay from the north as a result of swamp drainage associated with intensive agricultural activities.

Four types of curlew feeding area were distinguished on the basis of vegetation cover and particle size of sediment: sandbanks (no vegetation, sand substratum); muddy sands (no vegetation, substratum a mixture of sand and silt); mudflats (covered to varying degrees with *Zostera muelleri* with predominantly silt substratum); and mudflat/pools complex (a mosaic of pools retaining water at low tide covered with *Zostera tasmanica* underlain by fine sediment; and areas of fine mud exposed at low tide and generally bare of vegetation except in spring when they are covered with sea lettuce *Ulva* sp.).

The tides are semi-diurnal and tidal ranges are mesomareal, increasing from 2.0 m in the south to 2.6 m in the north (Victorian Channel Authority 1999). Tidal flows are a major influence on coastal processes in Western Port and the pattern of water movement in the Bay is complex, due to the presence of the two large islands (Figure 1).

Availability of curlew feeding areas

The availability of each type of feeding area in the tidal cycle was calculated from the estimated total area of that type of feeding area multiplied by the relative exposure time on a mean diurnal tide and expressed as a percent of the total. Activity scans of all curlews visible in Rhyll Inlet were made at 15-min intervals throughout an entire tidal cycle and individuals were classed as either feeding or not feeding (Altmann 1974). The sex of individuals was estimated from the relative lengths of their bills with females having longer bills (Dann 2005).

Diet

The diet of curlews was established using three methods: direct observations of feeding birds, examination of regurgitated pellets collected at the high-tide roost at Observation Point in Rhyll Inlet and sampling remains of prey along tracks left by feeding curlews.

Direct observation of prey capture

Observations of feeding behaviour of birds were made with the aid of 8 × 40 binoculars or a ×20 telescope at ranges of 10–400 m. During observations of feeding curlews, prey was separated into three categories: crabs, Australian Ghost Shrimps *Trypaea australiensis* and small unidentified taxa. A total of 736 prey captures was observed.

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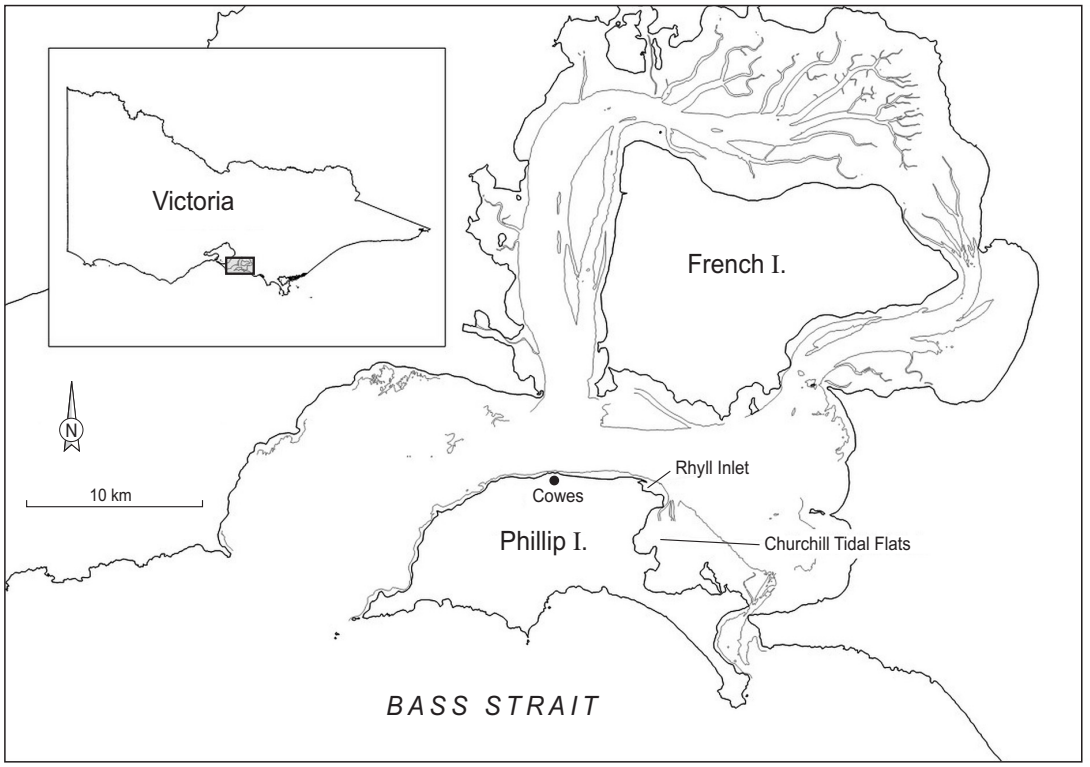


Figure 1. Map of Western Port, Victoria, Australia. The study areas were on the northern side of Phillip Island at Rhyll Inlet and the mudflats offshore known as Churchill Tidal Flats. Shading indicates intertidal areas.

Regurgitated pellets

Pellets regurgitated by curlews were collected from areas where birds roosted at high tide between November 1978 and February 1979. While two other species also produced pellets at the roost (Whimbrel *Numenius phaeopus* and Pacific Gull *Larus pacificus*), curlew pellets could be recognised by size, shape, cohesion, accompanying footprints and faeces and position on the roost. Curlew pellets were oblong, tightly packed with a sand matrix and variable in size, particularly in length. A sample of curlew pellets ($n = 73$) had a mean ($\pm$ SD) length of 31.9 $\pm$ 6.7 mm, width of 19.9 $\pm$ 2.2 mm and depth of 15.0 $\pm$ 1.6 mm. Curlews and the other pellet-producing birds were observed producing pellets at the high-tide roosts. Whimbrel pellets were almost circular, half the size of curlew pellets and loosely bound, while those of Pacific Gulls were circular, twice the volume of curlew pellets and lacked cohesion (pers. obs.). Prior to each collection, all pellets were removed from the roost so that those gathered subsequently were known to be from the feeding period immediately preceding collection. A total of 131 pellets was collected following six tidal cycles in November (one diurnal cycle), January (one diurnal cycle) and February (four tidal cycles, including two nocturnal feeding periods (36 pellets) and the two diurnal periods (35 pellets)). Only pellets collected after daylight feeding periods were used for comparisons of the pellet composition between November and February. Curlews also regurgitated pellets while feeding, but this was very rarely observed and none were included in the analysis. At the roost, each pellet was placed in an individual plastic bag. Before analysis in the laboratory, pellets were soaked in water and sieved through a 0.5-mm mesh. The number of each prey species was determined by dividing the number of recognisable hard parts (portions of claw or leg) by the number characteristic of a whole animal. The recognisable and measurable hard parts in pellets varied between prey species (Table 1, Brachyuran nomenclature following Wescott (1976)). Measurements of hard parts of some species (Table 1) were taken to the nearest 0.1 mm using vernier callipers. Hard remains of polychaetes (jaws and setae) were also particularly sought in the pellets and ten pellets were searched prior to sieving in case small parts were lost in the process, but none were found.

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Table 1. The hard parts of each prey species found in pellets of Eastern Curlews feeding in Rhyll Inlet in Western Port in southern Australia. Parts were just counted, or counted and measured (marked with an asterisk).

Prey species	Hard parts counted, and counted and measured (*)
Tasselled Crab *Pilumnus fissifrons*	propodus*, dactylus* or tip of claw
Australian Ghost Shrimp *Trypaea australiensis*	whole major claw*, dactylus* or tip of claw
Two-spined Crab *Litocheira bispinosa*	tip of claw*
Sentinel Crab *Tasmanoplax latifrons*	legs or tip of claw*
Mottled Shore-crab *Paragrapsus gaimardii*	propodus*, dactylus* or tip of claw
Rough Rock-crab *Nectocarcinus tuberculosus*	tip of claw
MacCulloch's Shrimp *Synalpheus t. tumidomanus*	tip of claw
Smooth Pebble-crab *Bellidilia laevis*	propodus, legs or tip of claw
seaweed crab *Naxia* sp.	tip of claw
Snapping Shrimp *Alpheus euphrosyne*	dactylus
Three-pronged Sea-spider *Halicarcinus ovatus*	whole carapace

PREY REMAINS ON FORAGING TRACKS

After curlews had been feeding for several hours, their tracks were followed over the sandbanks and the size and sex of predated Australian Ghost Shrimps were identified from the remains found at the place of capture. In many of the Ghost Shrimp captures the larger claw was broken off and there was clear evidence of the probe marks in the sand. It was found too difficult to follow the birds over substrata other than sand. To be able to convert the number of prey remains to actual captures, I determined the proportion of Ghost Shrimp captures that left remains on the tracks. For this, in five curlews, feeding rates from observations and from the tracks were estimated simultaneously. The obtained ratio of deposited remains/prey captures was used to calculate how many prey captures were represented by the remains on sandbanks. The number of steps feeding curlews made per second and their stride length were measured to convert the number of prey remains per linear metre along the tracks to number of prey taken per hour.

From prey remains, approximations of carapace size of predated Ghost Shrimps and crabs were estimated by measuring propodus lengths using allometric regression equations to determine size and sex of the predated individuals. A reference collection of 79 Ghost Shrimps (36 males, 43 females) was collected from Rhyll Inlet, to determine the allometric relationship between claw length and carapace size. In Ghost Shrimps, the shape of the major claws is consistently different between the sexes (Hailstone & Stephenson 1961), therefore the sex of predated individuals could be determined from claw dimensions. The carapace length of the shrimps was measured from the tip of the rostrum to the most posterior portion of the cephalothorax. The claw length was measured from the junction of the propodus and dactylus to the posterior end of the propodus. The derived regression was: claw length = 0.4 × carapace length + 4.8 ($r^2 = 0.77$, $df = 78$, $P < 0.001$).

Similarly, crabs were sexed by examination of genitalia (males have a longer and wider claw with a strongly decurved propodus and a more prominent spur than females) and sizes of predated crabs were established from the allometric relationship between claw size and carapace width of intact crabs collected from Rhyll Inlet. The derived regression for Tasselled *Pilumnus fissifrons*, Two-spined *Litocheira bispinosa* and Sentinel Crabs *Tasmanoplax latifrons* (pooled data) was: claw length = 1.2 × carapace width – 7.5 ($r^2 = 0.95$, $df = 31$, $P < 0.05$).

Behaviour and ecology of prey species

To establish the distribution of prey species in Rhyll Inlet, between 10–25 core samples were collected in February 1979 at random sites in each of the four types of feeding area identified: on the sandbanks ($n = 25$), in sandy muds ($n = 12$), mudflats ($n = 10$) and in the mudflat/pools complex ($n = 24$). A high-sided (45 cm) coring device sampled 0.1 m^2 of substratum to a depth of 20 cm. Samples were sieved through a 1-mm mesh, preserved in 5% seawater formalin and later hand-sorted in the laboratory.

With a purpose-designed sampling device, I measured the stratification in the sediment of three benthic invertebrates that are important prey species for curlews (Ghost Shrimp, Snapping Shrimp *Alpheus euphrosyne* and Sentinel Crab). The device was an open-ended rectangular metal prism (15 cm across × 15 cm deep × 24 cm wide) with slots at 4-cm intervals into which plates could be inserted latitudinally, thus dividing the sediment sample into strata. During sampling, the sampler was first inserted into the sediment, then the base plate slotted in before the sampler was removed from the sediment. In very soft sediments it was possible to install all the dividing plates *in situ*

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but in most cases the sampler had to be withdrawn from the sediment (after the installation of the base plate) before the remaining dividing plates could be put in place. Between three and five samples were taken to depths of 24 cm in each of the four feeding area types (sandbanks, muddy sands, mudflats and mudflat/pools complex) in February 1979.

The burrowing behaviour and activities of male and female Ghost Shrimps and four crab species were examined in a narrow aquarium (100 × 150 × 7 cm) and two rectangular aquaria (50 × 50 × 25 cm). Shrimps were captured at low tide using a bait pump (Hailstone & Stephenson 1961). Crabs were captured by sieving. Animals were transported in a bucket with sand and seawater and placed in the aquaria within an hour of capture. The aquaria, filled with sand (15 cm depth) and seawater (30 cm depth) from the capture site, had walls covered with black plastic and were kept aerated throughout the experiments. The tidal regime in the tanks was the same as the tidal cycle at the capture site and the animals were left undisturbed for two tidal cycles before observations started. Fresh seawater was siphoned into the aquaria at the time of each flood tide, using 1-mm plastic tubing, and siphoned out on the ebb tide.

In the aquaria, the locations of each individual Ghost Shrimp and the four main crab prey species for curlews (Tasselled Crabs, Two-spined Crabs, Sentinel Crabs and Mottled Shore-crabs *Paragrapsus gaimardii*) were recorded approximately once per hour by removing the black plastic that covered the aquarium walls and observing the animals in their burrows. Sexes were kept separated and sample sizes were limited by the number of animals that burrowed beside the aquaria walls; usually between six and eight individuals. The distance moved per hour for each crab species was recorded for at least two entire tidal cycles spanning two daylight periods and a night.

Calorific values of prey species

Thirty individuals (15 male, 15 female) of eight invertebrate species (including the major prey of curlews) were collected in Rhyll Inlet in December 1979 and frozen within half an hour of collection. Later they were thawed, oven-dried to a constant mass at 50°C and weighed. Twenty randomly-selected individuals of each species were then placed in a muffle furnace for 12 hours at 500°C to determine dry mass and ash-free mass. The remaining ten specimens of each species were finely ground, divided into three parts and each part was burnt separately in a Gallenkamp ballistic bomb calorimeter to provide calorific values. Statistical analyses were performed using χ^2-tests and ANOVA and linear and polynomial regression (Sokal & Rohlf 1969).

RESULTS

Feeding areas of curlews

Curlews used different parts of the Rhyll Inlet and Churchill Tidal Flats depending on the state of the tide. Sandbanks and muddy sands were first to be exposed as the tide fell and these were usually occupied by territorial birds, but accommodated only five to seven curlews. Other birds remained at the roost on Observation Point, until later in the tidal cycle the mudflat and mudflat/pools complex became exposed; very few birds held territories in these areas. Female curlews fed in all types of feeding area in Rhyll Inlet but spent more feeding time on sandbanks (32.7%, n = 4243 min observation of feeding curlews) and muddy-sand areas (26.7%). The feeding areas of males were significantly different to the females (χ^2 = 10,460, df = 3, $P < 0.001$) particularly because few males fed on the sandbanks and most used the mudflat/pools complex (59%, n = 3262 min) and mudflats with less than 50%

Table 2. The habitat use by female and male Eastern Curlews feeding in Rhyll Inlet in spring and summer. % available = area of habitat type times time exposed by tide/total area times time exposed by tide × 100.

	Females		Males		
Microhabitat	Time spent feeding (min)	%	Time spent feeding (min)	%	Available (%)
Sandbank	1387	32.7	0	0	25.6
Muddy sands	1131	26.7	281	8.6	21.4
Mudflat	835	19.7	1056	32.4	35.4
Mudflat/pools complex	890	21.0	1925	59.0	17.7
Total	4243	100.1	3262	100	100.1

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Table 3. Prey identified from 736 observations of prey captures by Eastern Curlews feeding in four types of feeding areas in Rhyll Inlet during daylight (percentages in parentheses).

Type of feeding area	Crabs	Australian Ghost Shrimp	Unidentified taxa	Total
Sandbank	1 (0.2%)	375 (89.7%)	42 (10.1%)	418
Muddy sands	4 (6.3%)	50 (78.1%)	10 (15.6%)	64
Mudflat	144 (91.7%)	2 (1.3%)	11 (7.0%)	157
Mudflat/pools complex	80 (82.5%)	1 (1.0%)	16 (16.5%)	97
Total	229 (31.1%)	428 (58.2%)	79 (10.7%)	736

Table 4. Number of identified prey remains and frequency of occurrence of prey items in 131 pellets of Eastern Curlews collected at the high-tide roost in Rhyll Inlet between the start of November and the end of February. The data have been pooled for all samples.

Prey species	Number	Frequency (%)
Tasselled Crab	571 (31.6%)	60.3
Australian Ghost Shrimp	440 (24.3%)	50.4
Two-spined Crab	423 (23.4%)	43.5
Sentinel Crab	199 (11.0%)	89.3
Mottled Shore-crab	118 (6.5%)	48.9
Rough Rock-crab	22 (1.2%)	10.7
MacCulloch's Shrimp	13 (0.7%)	3.8
Smooth Pebble-crab	12 (0.7%)	3.8
seaweed crab	5 (0.3%)	1.5
Snapping Shrimp	3 (0.2%)	2.3
Three-pronged Sea-spider	1 (0.1%)	0.8
Total	1807	

covering of eelgrass (32.4%; Table 2). Neither sex was distributed randomly with respect to the available feeding areas ($\chi^2 = 132$, $df = 3$, $P < 0.001$; Table 2).

Diet

During observation of feeding birds, prey was classified into three categories: crabs, Ghost Shrimps and small unidentified taxa. In all feeding areas the diet mainly consisted of crabs or shrimps (Table 3). Crabs were significantly more frequent in the diet on the mudflats and in mudflat/pools complex areas, whereas Ghost Shrimps predominated on the sandbanks and in the muddy sands ($\chi^2 = 694$, $df = 3$, $P < 0.05$).

A total of 1807 prey items, all decapods, was identified from 131 pellets (Table 4). The Tasselled Crab was the most common prey species (32%), followed by Ghost Shrimp (24%), Two-spined Crab (23%) and Sentinel Crab (11%). These four species comprised 90.3% of the prey items in the pellets. The Sentinel Crab had the highest frequency of occurrence in the pellets (89%), followed by Tasselled Crab (60%), Mottled Shore-crab (49%), Ghost Shrimp (50%) and Two-spined Crab (44%). Both the Sentinel Crab and the Mottled Shore-crab occurred frequently in the pellets but were relatively less numerous than the other three species (Table 4). Forty-six (35%) pellets contained only Ghost Shrimps (18) or Sentinel Crabs (3) or both (25), 57 (44%) combinations of Tasselled Crab, Two-spined Crab and Mottled Shore-crab. The remaining combinations accounted for 21%.

Dietary differences between night and day

At Rhyll Inlet in February, the nocturnal and diurnal diets were significantly different (Table 5). More Ghost Shrimps and Sentinel Crabs and fewer Two-spined Crabs were taken during the day than during night time ($\chi^2 = 126$, $df = 3$, $P < 0.05$). Mottled Shore-crabs and Tasselled Crabs were eaten in similar proportions during day and night.

Dietary shifts between November and February

The proportions of the diet of most prey species remained unchanged from November to February 1979, except for Tasselled Crabs and Sentinel Crabs (Table 6). Tasselled Crabs were taken less frequently in February and Sentinel Crabs were taken in much greater numbers in February ($\chi^2 = 137.3$, $df = 3$, $P < 0.05$).

Direct observations of feeding versus analysis of pellets

Direct observations and pellet analysis identified similar proportions of the main prey: 67% and 74.8% crabs, and 23.5% and 25.2% shrimps, respectively (plus 9.5% small unidentified taxa during direct observations). Observations suggested that a claw was discarded after >90% of Ghost Shrimp captures. From tracking curlews, it was estimated that 54 claws were left behind per hour. This estimate followed from multiplying the number of claws left per metre (14 claws/189 m) by

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Table 5. The numbers and frequencies of occurrence of identified remains of prey in 36 pellets of Eastern Curlews from nocturnal feeding periods and 35 pellets from diurnal periods collected at Rhyll Inlet in February.

	Diurnal feeding		Nocturnal feeding	
Prey species	Number	Frequency	Number	Frequency
Tasselled Crab	93 (20%)	13 (37%)	117 (24%)	26 (72%)
Australian Ghost Shrimp	148 (31%)	10 (29%)	83 (17%)	22 (61%)
Two-spined Crab	91 (19%)	21 (60%)	164 (34%)	14 (39%)
Sentinel Crab	98 (21%)	14 (40%)	69 (14%)	17 (47%)
Mottled Shore-crab	41 (9%)	13 (37%)	46 (10%)	26 (72%)
Total	473		486	

Table 6. The numbers (percentages in parentheses) of the main prey of Eastern Curlews in pellets collected in Rhyll Inlet in November, January and February.

Prey species	November	January	February
Tasselled Crab	244 (52%)	117 (33%)	93 (20%)
Australian Ghost Shrimp	91 (20%)	118 (33%)	148 (31%)
Two-spined crab	86 (18%)	82 (23%)	91 (19%)
Sentinel Crab	17 (4%)	15 (4%)	98 (21%)
Mottled Shore-crab	11 (2%)	20 (6%)	41 (9%)

the mean number of metres per curlew step (0.1976) by the mean number of steps per second (1.025), equalling 0.015 claws left per second or 54 claws left per hour. The observed success rate on the sandbank territories prior to the claws being collected, was 52.2 Ghost Shrimps per hour (58 Ghost Shrimps captured in 4008 s), indicating that at least one claw was left at each Ghost Shrimp capture site. The discarded claw remaining was almost always the larger one (which can be either left or right in this species). Hence the claws collected at capture sites accurately reflected the prey composition in sandbank areas and the size and sex of Ghost Shrimps taken.

Predation on Ghost Shrimps

More male (69%) than female (31%) Ghost Shrimp claws (n = 458) were found along the tracks of feeding curlew (χ^2 = 64.6, df = 1, $P < 0.001$). Similarly, 206 of the 355 claw remains recovered from the pellets were from males and 149 from females. The sex ratios of the November and January samples were not significantly biased but in the February sample there were significantly more males than females in the pellets (χ^2 = 12.4, df = 1, $P < 0.001$). The size-frequency histogram of carapaces of Ghost Shrimps taken by curlews (Figure 2) was derived from the sizes of the claws left at capture sites using a claw length to carapace length regression, where carapace length = 4.8 + 0.4 × claw length (r^2 = 0.77, df = 57, $P < 0.001$). The mean carapace length (±SE) of Ghost Shrimp eaten by curlews on the sandbanks was 12.19 ± 0.07 mm (range 10–14 mm, n = 173).

Behaviour and ecology of prey species

Prey occurrence in each type of feeding area

In February, when the prey distribution was sampled, the Ghost Shrimp was the only species that occurred in three of the four types of feeding area. Ghost Shrimp was the only prey species found in the sandbanks, it was present but less abundant in sandy muds and mudflats (where the sediment particle size was reduced), but absent in the mudflat/pools complex. Sentinel Crabs appeared to favour areas with relatively little macrophyte cover: sandy muds and mudflats. Tasselled Crabs occurred on mudflats and in the mudflat areas with vegetation, the mudflat/pools complex. Two-spined Crabs were found only in areas with more than 50% seagrass cover (mudflat/pools complex).

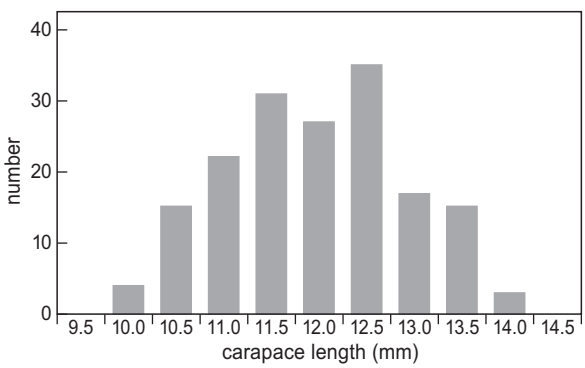


Figure 2. Size-frequency distribution of Australian Ghost Shrimps taken by Eastern Curlews as estimated from shrimp claws left at capture sites.

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ACTIVITY PATTERNS OF CRABS

Crabs were active either at high tide (Tasselled Crab, Two-spined Crab and Mottled Shore-crab) or at low tide (Sentinel Crab). The Two-spined Crab was also active at low tide at night but the Mottled Shore-crab and Tasselled Crab were active only at high tide during the day and at night. The Sentinel Crab was the only species to dig a relatively large burrow in the aquarium studies, although some Tasselled Crabs excavated shallow burrows under rocks. Both Tasselled Crabs and Mottled Shore-crabs sheltered under rocks and seagrass or partially buried the majority of the carapace in the sediment with the anterior exposed. The Two-spined Crabs usually spent inactive periods at the base of seagrass plants or under detritus.

GHOST SHRIMP – GENERAL BEHAVIOUR IN AQUARIA

Most burrows were approximately J-shaped and extended down to 40 cm. They usually had a number of side tunnels off the main shaft whose function was unclear but some contained obviously larger-sized sand grains which appeared to have been deposited there. Burrows had an enlarged area on the main shaft, near the entrance, where shrimps turned to face the entrance as they surfaced. The burrows usually had only one entrance at the surface. Ghost Shrimp were relatively inactive when the tide was low but became active immediately the water level started to rise. In the wild, the entrances of some burrows were covered as a result of Soldier Crab *Mictyris platycheles* activity at low tide and these were reopened as soon as the tide started to flood. In two aquarium experiments, 30% (10) of the Ghost Shrimps came to the surface and had their claws partially protruding within minutes of the tide turning. Simulated curlew probing in the main shaft caused the Ghost Shrimp to retreat to the base of the burrow very quickly.

The approximate burrowing depths of Ghost Shrimps at low tide in the study area were determined concurrently with the aquarium experiments to provide some form of 'ground-truthing'. Nearly 50% of Ghost Shrimps in the stratified samples taken in Rhyll Inlet at low tide (February 1979) were found 16–20 cm below the surface and the rest were spread fairly evenly throughout the other levels (Figure 3). The mean depth of Ghost Shrimps (both sexes pooled) in the aquaria at an equivalent stage of the tide was 21.0 ± 2.7 (SE) cm. The Ghost Shrimps in the aquaria were a few centimetres deeper than those sampled in the Inlet at the same stage of the tide and time of day.

The mean burying depths of Ghost Shrimps in the aquaria for males were 15.8 ± 3.0 cm (experiment 1) and 24.8 ± 2.9 cm (experiment 2); and for females, 21.5 ± 2.6 cm (experiment 1) and 27.5 ± 2.4 cm (experiment 2). Females buried significantly deeper in the sediment than males in both experiments (F = 60.1, df = 19, $P < 0.001$; Figure 4). Mean depths at low tide of both sexes of Ghost Shrimps were similar during day and night observations.

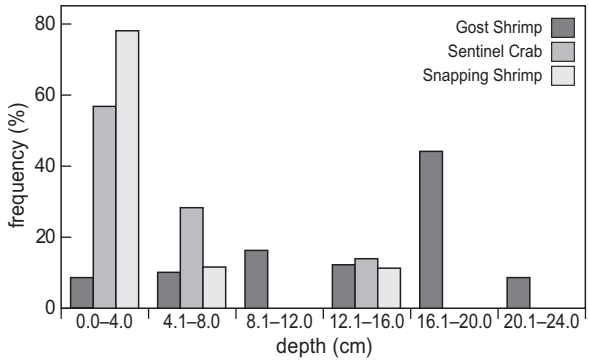


Figure 3. Vertical distribution of Australian Ghost Shrimp, Sentinel Crab and Snapping Shrimp in stratified samples taken in Rhyll Inlet at low tide in February 1979.

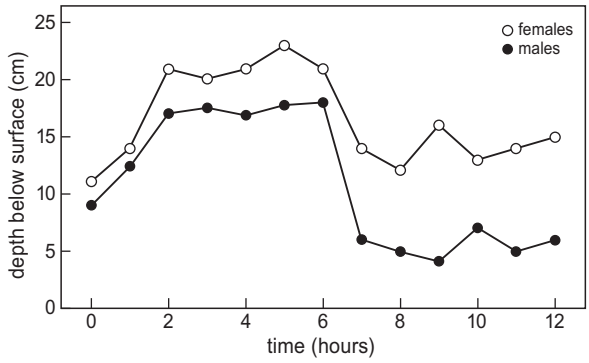


Figure 4. Mean burrowing depths of male and female Australian Ghost Shrimps in aquaria throughout a tidal cycle. The tide was full (high) for the first six hours and was low for the second six hour period.

Energetics of prey choice

ENERGY VALUES OF POTENTIAL AND ACTUAL PREY SPECIES

Snapping Shrimps had the highest energy values of the benthic invertebrates examined and, overall, shrimps and polychaetes had higher values per gram ash-free dry mass (AFDM) than crabs (Table 7). There was a 2.5-fold variation in mean energy value among prey ranging from 3.54 J/g AFDM (Tasselled Crab) to 10.33 J/g AFDM (Snapping Shrimp; Table 7). For the mean sizes of prey taken, the energy values were calculated from regressions of dry mass against carapace width for

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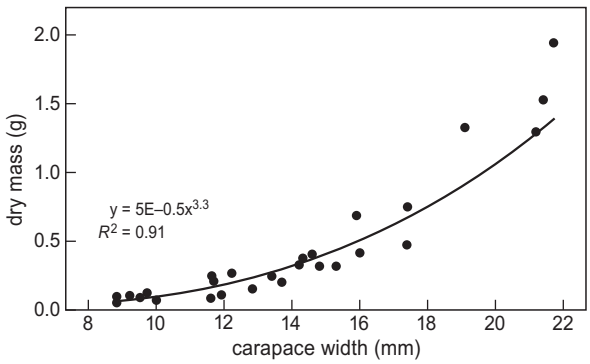


Figure 5. The relationship between carapace width (mm) and dry mass (g) of crabs (pooled data, $r^2 = 0.91$).

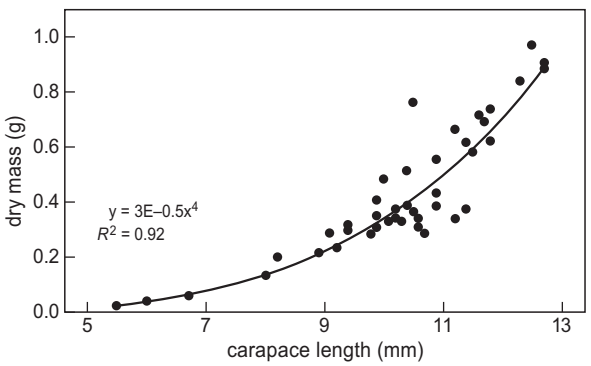


Figure 6. The relationship between carapace length (mm) and dry mass (g) of Australian Ghost Shrimps (pooled data, $r^2 = 0.92$).

crabs (pooled data, Figure 5) and dry mass against carapace length for Ghost Shrimps (y = 0.0012 + 2.4478 × carapace length, $r^2 = 0.44$). The mean prey dry masses for crabs and shrimps were calculated from regressions of dry mass against carapace width for crabs (Figure 5) or carapace length for shrimps (Figure 6). The energy values of prey of the mean size taken by curlews were also used to calculate prey profitability (energy intake/handling time; *sensu* Piersma 1986). Profitability was 0.134 J/s handling time for Ghost Shrimp and 0.019–0.043 J/s handling time for crabs, depending on species.

DISCUSSION

Diet

In Rhyll Inlet, during the non-breeding period, Eastern Curlews fed largely on Australian Ghost Shrimps and crabs. Crustaceans, particularly crabs, have been previously recorded as the main prey type of curlews (Piersma 1986, Barker & Vestjens 1989, Tulp & de Goeij 1994, Hodder 2000, Zharikov & Skilleter 2004). Taylor & Mackay (1999) noted that crabs made up about 89% of all prey items taken in the Tamar Estuary in northern Tasmania and that a further 4.7% of prey items were polychaetes. Crabs were the only prey recorded in South Korea (Piersma 1986) and made up 81% of identified prey identified by Hodder (2000) in northwestern Australia. In the same area, Tulp & de Goeij (1994) recorded 53 crabs and one worm in their observations of feeding curlews. Non-crustacean prey such as polychaete worms, which may not have been detected in pellets, may have been taken in small quantities in Rhyll Inlet and recorded as unidentified taxa in field observations (9.5% of prey items observed). Polychaetes were commonly observed to be taken by Bar-tailed Godwits *Limosa lapponica* and Curlew Sandpipers *Calidris ferruginea* in Rhyll Inlet, but not by Eastern Curlews.

Table 7. The energy values (J/g), in descending order, of common benthic invertebrates in Rhyll Inlet. The four more important prey for Eastern Curlew are in bold.

Species	Mean energy value (J/g dry mass) ± SE	Ash-free dry mass (%)	Mean energy value (J/g AFDM) ± SE
Snapping Shrimp	14.77 ± 0.21	69.95	10.33 ± 0.15
Polychaete *Lumbrineris* sp.	13.39 ± 0.08	65.24	8.74 ± 0.05
Australian Ghost Shrimp	12.72 ± 0.25	58.72	7.47 ± 0.15
Little Shore-crab *Brachynotus spinosus*	12.97 ± 0.13	51.65	6.70 ± 0.07
Two-spined Crab	9.92 ± 0.08	54.35	5.39 ± 0.04
Soldier Crab *Mictyris platycheles*	9.46 ± 0.34	52.34	4.95 ± 0.18
bivalve *Tellina deltoidalis*	7.58	63.46	4.81
Sentinel Crab	9.17 ± 0.17	49.34	4.53 ± 0.08
Tasselled Crab	7.62 ± 0.34	46.51	3.54 ± 0.16

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The diet of the curlews was strongly influenced by where they fed, by prey activity and by availability and possibly profitability (J/s handling). The species representation in pellets corresponded strongly with the species found in different feeding areas in the Inlet. For example, some pellets contained only Ghost Shrimp and some curlews were observed to feed exclusively on sandbanks where Ghost Shrimp were the only prey species found in the sediment. This is consistent with the finding of Goss-Custard & Jones (1976) that the diet of Eurasian Curlews *Numenius arquata* at the Wash in England varied between different areas. The choice of feeding area determined the suite of potential prey available and the actual prey within these feeding areas could be correlated with the behaviour or the energy value of prey species. For example, Ghost Shrimps had higher energy values per g AFDM than crabs and higher profitability in terms of energy gained per foraging effort (i.e. handling time). The mean profitability of Ghost Shrimps was 3–6 times greater than that of crabs, and Ghost Shrimps would be the expected preferred prey when available. Ghost Shrimps were the most common prey during daylight in the two sandier types of feeding area (sandbanks and muddy sands).

The proportion of Ghost Shrimp eaten was less at night, presumably because burrow entrances were more difficult to see then. Burrowing depth of Ghost Shrimps was not a factor as, in aquaria, they were at similar depths by day or by night at the same stage of the tidal cycle. The availability of crabs was greater at night because most were more active then (at least in aquarium studies) and the numerical importance of crabs in the diet at night increased accordingly. Crabs varied little in energy content, strongly suggesting that the selection of species was determined by habitat or patterns of crab activity.

Prey-switching (from fewer Ghost Shrimps to more crabs) might be favoured if availability of crabs at night was high enough to compensate for the loss in profitability. However, the advantage would be limited at some stage by a 'digestive bottleneck' (Zwarts & Dirksen 1990) due to the higher ratio of carapace volume to digestible material of crabs. Burrowing depth did seem to be an important factor in determining the sex of Ghost Shrimps available to curlews, although it appeared to have no influence on Ghost Shrimp availability during the day or at night. Male Ghost Shrimps were more likely to be eaten than were females and aquarium studies indicated that females burrowed deeper than males and hence were less available. If the aquarium studies are representative of Ghost Shrimp burrowing depths in the study area, both sexes of Ghost Shrimps were rarely available to shorter-billed curlews (males) at low tide because they were buried deeper in the substratum.

Surprisingly, some potential prey (Snapping Shrimps, the smaller Sand Ghost Shrimp *T. arenosa*, polychaetes and soldier crabs Mictyridae), that occur in high densities in the intertidal areas of Western Port (Robertson 1978) and had high or moderate energy value, were not significant components of the curlews' diet. Snapping Shrimps had the highest energy values of the invertebrate species sampled here, lived in moderate-sized burrows (thus facilitating detection by curlews) and had hard parts that were found in pellets (so would have been detected). It may be that their conspicuous and frequent snapping behaviour is a successful anti-predator device. The species of ghost shrimp not taken by curlews occurred in some areas where they foraged but had burrows of smaller diameter which may have made them harder to capture. Polychaetes had a higher energy value per g AFDM than crabs and, accordingly, the birds might be expected to show some dietary preference for them. However, their unimportance in curlew diets in this study suggests that difficulty of detection and capture in long, narrow burrows by curlews was not compensated for by the energy value per prey item. Soldier crabs were often very abundant and active during daytime low tides on the surface of the sandbanks but curlews were very rarely observed to eat them. Their bright coloration (red and purple) may be aposematic, indicative of unpalatability. However, young soldier crabs are eaten by Sooty Oystercatchers *Haematopus fuliginosus* (Considine 1979) and were seen being taken by curlews on rare occasions, perhaps because young crabs have not acquired the defence mechanism of the adults. However Zharikov & Skilleter (2004a) listed the related crab species *Mictyris longicarpus* as an important prey species for curlews in southeastern Queensland.

Sexual dimorphism in curlew bill length, diet and feeding areas

The evolutionary significance of sexual dimorphism in feeding morphology of birds has been the subject of considerable debate (Selander 1972, Payne 1984, Jehl & Murray 1989, Mueller 1989, Shine 1989, Jonsson & Alerstam 1990). Dimorphism in bill length has been recorded for Eastern Curlews by Barter (1990) who used bivariate analysis to separate two groups from measurements of live birds. The limited number of individuals in Australian museum collections sexed by dissection that were examined by Dann (2005) support Barter's assumption that the longer-billed cohort are

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females. The mean bill length (±SD) of female Eastern Curlews is 183.6 ± 8.8 mm and of males is 150.9 ± 7.2 mm (Barter 1990).

Sexual dimorphism in the Eastern Curlew bill morphology appears to determine habitat and prey selection in the birds. Sexual difference in bill length in the curlews is associated with considerable differences in diet and feeding dispersion in the non-breeding grounds. Females feed more in the sandier substrata, on more deeply burrowing prey such as Ghost Shrimps and Sentinel Crabs, and males feed primarily in the structurally more complex mudflat and pool areas or barer mudflats on cryptic, primarily less burrow-dependent species such as Tasselled Crabs, Mottled Shore-crabs and Two-spined Crabs. It appears likely that sexual differences in prey available determine the different dispersions of male and female curlews across the intertidal zone. Presumably limited food resources and intersexual competition were precursors to the development of sexual differences in feeding ecology.

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SAMENVATTING

De Siberische Wulp *Numenius madagascariensis* broedt in Siberië en brengt de noordelijke winter in Australië door. De vogels hebben een opmerkelijk lange en gebogen snavel. De lengte is bij benadering 25–30% van de totale lichaamslengte en verschilt sterk tussen de geslachten. Vrouwelijke Siberische wulpen hebben de langste snavel van alle steltlopersoorten. Gedurende twee winterseizoenen werd in Western Port in het zuiden van Australië de voedselsamenstelling en prooikeuze van overwinterende Siberische Wulpen bestudeerd in relatie tot de voedselbeschikbaarheid en de profijtelijkheid van de prooisoorten. Uit het onderzoek bleek dat beide geslachten de getijdengebieden verschillend gebruikten. Dit verschil wordt toegeschreven aan het grote verschil in snavellengte tussen mannetjes en vrouwtjes, mogelijk samenhangend met een verschil in voedselkeuze. De voedselsamenstelling werd bepaald via directe waarnemingen, door het ontleden van braakballen die waren verzameld op de hoogwaterrustplaats en door het (achteraf) volgen van sporen van foeragerende wulpen. De krab *Pilumnus fissifrons* werd het meest gegeten, gevolgd door de garnaal *Trypaea australiensis* en de krabben *Litocheira bispinosa* en *Tasmanoplax latifrons*. De beschikbaarheid van prooien werd onderzocht in aquaria door het ingraafgedrag en algemene activiteitspatronen van de dieren in relatie tot getijde en daglicht te meten. Het gedrag van de prooisoorten verklaarde grotendeels de algemene voorkeur voor mannelijke *T. australiensis* en de verschillen in voedselsamenstelling tussen overdag en 's nachts. Overdag aten vogels meer *T. australiensis* en *T. latifrons* en minder *L. bispinosa* dan 's nachts. Vergelijking van de calorische waarde van de gegeten prooien met die van de potentiële prooisoorten leerde dat de vogels in het algemeen prooien aten die veel energie bevatten, maar dat prooigedrag en voedselbeschikbaarheid de prooikeuze sterker bepaalden dan de energetische waarde.

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