Habitat selection, foraging ecology and conservation of Eastern Curlews on their non-breeding grounds

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Abstract

Migratory shorebirds generally utilise very different habitats, great distances apart, during breeding and non-breeding seasons. The coastal intertidal flats in their non-breeding range provide a wide variety of benthic prey and shorebirds are primarily utilising these habitats for there foraging potential. Feeding strategies among shorebirds are largely determined by morphology and broadly range from visual pecking at the substrate surface to tactile probing deep within the sediment. Some shorebirds are capable of very deep (>15 cm) and complex probing of the sediment and this feeding guild is represented globally by three very large curlew species: Eastern Curlews (*Numenius madagascariensis*), Eurasian Curlews (*N. arquata*) and Long-billed Curlews (*N. americanus*). These deep-probing shorebirds are threatened globally due to recent declines in population sizes, largely resulting from habitat loss and hunting pressure. To prevent further loss and possible extinction of shorebirds at risk, better knowledge of their feeding ecology outside the breeding grounds is required. Moreton Bay on Australia’s subtropical east coast supports over 15% of the global population of Eastern Curlews during the austral summer months and is therefore of worldwide importance for this species during its non-breeding season. The present study investigates the feeding ecology of the Eastern Curlew in Moreton Bay and what drives their habitat choice on these non-breeding grounds.

Initially the broadscale distribution of Eastern Curlews among tidal flats within Moreton Bay was assessed. Low-tide surveys were conducted with the help of 60 skilled volunteers who made repeated counts at defined sections of tidal flat (sites) totalling approximately 41.3% (9,500 ha) of the intertidal habitat within Moreton Bay. Sites varied in size (0.68–474 ha), substrate, topography, and other features. There
was a very high consistency between counts on different days within a month and different months within a season, across all sites. Winter numbers of Eastern Curlews totalled about 25% of those in summer, and the proportional distribution of birds among sites was generally similar across both seasons. The within-season constancy of curlew numbers across sites suggests that short surveys can give reliable results. Curlew densities (birds/ha) also showed a strong correlation between summer and winter counts. Curlew density varied greatly among tidal flats and important intertidal feeding habitat was identified.

Numbers of Eastern Curlews on low-tide feeding grounds were then compared with those at high-tide roosts in order to understand their habitat use more fully. Counting shorebirds on feeding grounds provided an accurate population census tool but a relatively large area had to be covered compared with counting birds at roost sites. The correspondence between numbers of curlews at high-tide roosts was compared with those on low-tide feeding grounds at several spatial scales, leading to the conclusion that the typical distance birds travelled between roosts and feeding grounds would be in the order of 5–10 km, with high mobility between alternative roosts and/or feeding grounds occurring at or below this distance.

The habitat preferences of curlews were next investigated at large (between-flat) and small (within-flat) spatial scales in order to determine factors underlying habitat selection. Using data from the low-tide surveys of feeding grounds, 32 defined sections of intertidal flat (sites; 200–400 ha in area) which varied greatly in their curlew density and other environmental characteristics were analysed. Of ten environmental characteristics measured for each site, substrate resistance was the best predictor of curlew density at the broad scale. Sites with the least resistant substrates had curlew densities three times those with the most resistant substrates.
Characteristics that were poor predictors included distance to the nearest roost, level of human disturbance and intertidal area and width. For a finer-scale assessment, microhabitat use and feeding behaviour were recorded during low tide within 12 intertidal flats, which varied in size (23–97 ha), curlew density, substrate and other features. Across all flats, curlews strongly preferred to feed relatively close (0–50 m) to the moving low water line. They fed on a variety of substrates (including sand, sandy-mud, mud and seagrass) in broadly similar proportions to their occurrence in the habitat. There was a statistically significant preference for sand, although its magnitude was not strong. These results indicated that curlews selected habitat more strongly at the between-flat rather than the within-flat scale.

The curlews' diet was next quantified across the same 12 intertidal flats described above, though 970 focal observations (each of 3 minutes duration). Food resources were also estimated from substrate core samples. Curlew density, estimated at each site using low-tide surveys from every site visit, showed a strong positive association with both the density and biomass of prey across the 12 flats. However, the density and biomass of prey also showed a strong negative correlation with substrate resistance, which was the best predictor of curlew density. Curlews were most abundant at sites with the least resistant substrate, and these sites also generally had the highest prey density and biomass. When the effect of substrate resistance was statistically removed, curlew density was no longer significantly correlated with prey density and biomass. This suggests that broadscale habitat choice by Eastern Curlews on their non-breeding grounds is more strongly influenced by prey availability (which is higher when substrate resistance is lower) than by prey density or biomass, although in Moreton Bay a positive correlation across sites meant that these factors were synergistic.
Finally, the present study tested whether foraging success could explain choice of feeding sites by curlews. Foraging success was assessed at 11 of the 12 intertidal flats described above. Biomass intake rate explained 57% of the variation in curlew density across sites, and was a far better predictor of curlew density than either the feeding or success rate. Both the biomass intake rate and curlew density were highest on substrates with higher penetrability. There were some differences in feeding behaviour between sexes, which were generally consistent with expectations given the females’ greater body size and bill length, although neither sex had a clear energetic advantage. The positive relationship between curlew density and biomass intake rate was stronger than the previously-established positive relationship between curlew density and substrate penetrability, suggesting that the curlews in Moreton Bay choose feeding habitat directly on the basis of the food supply. Low aggression rates suggest relatively little constraint from intraspecific competition during most of the overwintering period. These results also suggest that the population of Eastern Curlews in Moreton Bay is not limited by the availability of food resources but perhaps by factors either on the breeding grounds or at stop-over sites during migration.

These findings indicate that, for assessing and monitoring the quality of feeding grounds for deep-probing shorebirds, a time-efficient measure of the physical properties of the substrate (such as penetrability) would be useful. Any structural modification of the curlews’ soft-sediment feeding flats that reduces substrate penetrability may inhibit successful foraging and be detrimental to them. Direct effects on the structure of soft sediments could come from activities including intertidal oyster farming, the compaction of sediments by vehicles and the dumping of rubbish.
In the present study, curlews foraged in a broad variety of habitats and consumed a variety of different types and sizes of prey. Even impenetrable flats, delivering a low foraging success, were used for feeding by some birds. The use of their long bills to obtain many different types of prey in widely-varying habitats may aid them in coping with future habitat changes. However, it is possible that curlews are reliant on the high quality prey buried within soft sediment during crucial periods such as prior to migration and during migratory stop-overs, especially during pre-breeding migration. Therefore it would be prudent to confer the highest protection possible on the curlews’ remaining soft-sediment intertidal habitat at non-breeding grounds and along migration routes.
Statement of originality

This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

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Preface

Slightly modified versions of Chapters 2, 3, 4 and 5 of this thesis have been previously published as scientific papers in peer-reviewed journals, and Chapter 6 is a manuscript in preparation. I was responsible for conducting all research reported in those papers: the other authors were my doctoral program supervisors, and were listed in recognition of their contributions in that regard. Another publication, a book chapter (Finn 2007) arose from work carried out during my PhD and corresponds broadly with certain sections of Chapter 1. Publications resulting from work reported in this thesis are listed below:

Chapter 1 (Sections 1.1.1–1.1.3 and 1.1.5).

Chapter 2.

Chapter 3.

Chapter 4.

Chapter 5.

Chapter 6.
Chapter 1

General introduction

1.1 Shorebird feeding ecology and habitat selection

1.1.1 Lifestyle of migratory shorebirds

Most shorebirds (Suborder Charadrii) occurring throughout Australasia migrate long distances between breeding and non-breeding grounds, sometimes travelling up to 14,000 km between high latitude areas in both hemispheres (Battley and Rogers 2007). Their between hemisphere movements keep them in a perpetual summer. However, some migratory shorebirds, mostly young birds, remain on non-breeding grounds during winter (Thompson 1990a, Driscoll 1997, Wilson 2000).

In their coastal non-breeding habitats, the daily routine of shorebirds is driven by the tide. At high tide, shorebirds generally spend time roosting in flocks above the high water mark. As the tide recedes, they move onto adjacent intertidal flats to feed. Shorebirds, especially in the lead-up to migration, have the largest daily food requirement relative to body weight of any marine predator (Schneider 1983). While on their non-breeding grounds, shorebirds are primarily concerned with feeding, and as such these areas are an ideal place to study their foraging habitat selection. Shorebirds are a diverse avian group with an equally diverse range of foraging techniques.

Feeding behaviour and habitat selection in shorebirds is heavily influenced by their morphology, particularly leg length and bill length and shape (Baker 1979,
Harrington 1982, Ferns and Siman 1994, Barbosa and Moreno 1999, Zeffer et al. 2003, Nebel et al. 2005). In a study comparing the feeding behaviour of 17 shorebird species, Barbosa and Moreno (1999) demonstrated that longer bills were associated with probing into the substrate and plunging or sweeping bill movements in water, whereas shorter bills were associated with routing and pecking at the substrate surface. Baker (1979) showed that leg length was positively correlated with the depth of water in which shorebirds foraged and Harrington (1982) reported differences in habitat use in sandpipers due to variation in bill length, longer-billed individuals foraged in muddier habitats than shorter-billed individuals.

1.1.2 Features of different shorebird foraging guilds

There are two main foraging techniques employed by shorebirds on intertidal feeding grounds: the ‘sandpiper strategy’, characterised by a slow methodical walk with periodical probing into the substrate and the ‘plover strategy’, characterised by a run-stop-search sequence where each foraging move ends in a peck if prey is sighted, followed by a search pause. The sandpiper strategy is a tactile method of hunting (Zwarts and Blomert 1992), conversely, the plover strategy is a visual method of locating prey (Pienkowski 1983). Shorebirds that employ the sandpiper strategy of feeding (including: curlews and Whimbrels, Numenius; godwits, Limosa; and, knots and sandpipers, Calidris) are more versatile foragers, as they have the extra option of using visual foraging techniques when it is profitable to do so. For example, Whimbrels (Numenius phaeopus) feeding on fiddler crabs may use the plover strategy for most of the time, switching briefly to tactile probing of the substrate during the ebbing and flooding phases of the tide when there are no crabs at the surface (Zwarts 1985).
Probing shorebirds range in size from the very small Red-necked Stints (*Calidris ruficollis*, length: 13–16 cm), capable of probing to a depth of about 2 cm with their short, straight bills, to the very large Eastern Curlews (*Numenius madagascariensis*, length: 60–66 cm), capable of probing to a depth of about 20 cm with their long, curved bills (Higgins and Davies 1996). Shorebirds with long bills have a higher propensity to probe than those with shorter bills (Puttick 1981, Barbosa and Moreno 1999, Zharikov and Skilleter 2002, Nebel et al. 2005). Deep-probing shorebirds are capable of very deep (>15 cm) and complex probing of the sediment. The deep-probing shorebird feeding guild is represented globally by three almost identical species from the genus *Numenius* (Family Scolopacidae): Eastern Curlew (*N. madagascariensis*), Eurasian Curlew (*N. arquata*) and Long-billed Curlew (*N. americanus*). Eastern Curlews overwinter throughout coastal Australasia, Eurasian Curlews throughout Europe, Africa and Asia, and Long-billed Curlews throughout North America. These three species are the largest shorebirds in the world, ranging in weight from 600 to 1300 g depending on the time of year and sex of the bird (Driscoll and Ueta 2002), and have extremely long (up to about 200 mm; Barter 1990, Rogers 1995a, b), decurved bills.

1.1.3 Factors affecting the distribution of deep-probing shorebirds

The determinants of choice of feeding area on non-breeding grounds by deep-probing shorebirds have not been thoroughly investigated and are therefore poorly understood. Congdon and Catterall (1994) analysed factors influencing choice of feeding areas by Eastern Curlews among tidal flats in Moreton Bay and reported that although curlews preferred broader tidal flats, they showed little or no preference for different broadscale substrate types. However, they only counted birds within 100 m either side of the waters’ edge which is not ideal for surveys of low-tide feeding
grounds (Burton et al. 2004, Dias et al. 2006; see Section 7.2.1). Congdon and Catterall (1994) themselves concluded that considerably more research was needed to understand choice of feeding area by curlews. Summers et al. (2002) analysed the broadscale substrate preferences of 12 shorebird species among the Orkney Islands north of Scotland, and found that Eurasian Curlews exhibited only weak preferences (Summers et al. 2002). Other studies on the foraging ecology and habitat use of both Eastern and Eurasian Curlews have suggested that they prefer feeding on wet substrates (Piersma 1986, Rohweder and Baverstock 1996, Riak et al. 2003). However, none of the studies described above measured prey abundance. Studies of Eurasian Curlews on six estuaries in south east England (Goss-Custard et al. 1977a) and on the Forth Estuary, south east Scotland (Bryant 1979) showed that bird density was significantly associated with their main prey (marine worms), but properties of the substrate were not assessed. Consequently, much remains unknown about how deep-probing shorebirds select feeding habitat.

Two important conceptual frameworks have been developed to explore issues related to spatial variation in the density of resources and associated animal distributions among different habitats: optimal foraging theory (Pulliam 1974, Evans 1976, Pyke et al. 1977) and ideal-free distribution theory (Fretwell and Lucas 1970, Parker and Sutherland 1986). Optimal foraging theory states that animals should forage in a manner that maximises their net energy gain (Pulliam 1974, Pyke et al. 1977). Ideal-free distribution theory states that if all individuals are completely informed about the quality of different habitats and are able to move freely between habitats then they will be able to select the habitat in which they gain the greatest quantity or quality of resources (Fretwell and Lucas 1970). In an ideal-free distribution, the density of individuals among different habitats is in direct proportion
to the relative amount of available resources in each habitat. Therefore in relation to
shorebird distributions on non-breeding grounds, one would expect more birds at
intertidal flats which provide greater densities of available prey. It has been widely
suggested that shorebirds choose to feed in habitats where they experience the greatest
foraging success (Goss-Custard 1970, Hale 1980, Quammen 1982, Dann 1987,
2005b, 2006).

Many factors can influence the foraging success of shorebirds and affect their
spatial distribution on an intertidal flat (see Figure 1.1), including: morphology; prey
density; the properties of the substrate and intertidal flat; environmental inputs such as
nutrients and pollutants; proximity to high-tide roost sites; and human disturbance.
Deep probers are able to access more of the sediment than other shorebirds and
therefore the properties of the substrate may be particularly important in terms of
foraging success. However, this has not been previously investigated.

All three large curlews are sexually dimorphic. Females are larger than and
socially dominant to males. The female bill is approximately 3 cm longer on average
than that of the male (Barter 1990, Rogers 1995a, Colwell and Mathis 2001). Morphology not only dictates which feeding techniques can be employed but in which
habitats the greatest foraging success may be gained (Ferns and Siman 1994, Zeffer et
al. 2003). In curlews, the female’s longer bill allows the bird to penetrate further into
the sediment and to be more adept at extracting prey from deep burrows, whereas the
male has a more manoeuvrable bill and is technically more adept at catching prey
from in and around rocks and small cavities (Ferns and Siman 1994, Colwell and
Mathis 2001). This degree of sexual dimorphism has the potential to cause
differences in the habitat preferences of males versus females.
Figure 1.1. Factors that commonly influence foraging habitat selection by shorebirds. ‘H’ denotes factors which may be affected by human impacts. Shaded boxes indicate base inputs (i.e. those that do not have any other factor leading into them).

A number of studies have reported that the abundance of shorebirds in general is directly related to the density of their main prey species (e.g. Goss-Custard 1970, 1977a, Biljsma and de Roder 1991, Botton et al. 1994, Mercier and McNeil 1994, Meire 1996, Placyk and Harrington 2004, Ribeiro et al. 2004) and these prey species are often distributed according to their preferences for certain substrates (Yates et al. 1993). However, the availability of prey may be more important than prey density, particularly for deep-probing shorebirds that locate and capture prey from well below.
the substrate surface (Quammen 1982, Grant 1984, Gerritsen and van Heezik 1985, Kelsey and Hassall 1989, Mouritsen and Jensen 1992, Danufsky and Colwell 2003). Substrate type can affect the availability of prey by affecting their behaviour, making them more or less susceptible to predation (Esselink and Zwarts 1989). For example, marine worms may bury deeper in sand than in mud (Esselink and Zwarts 1989). Substrate type also affects how easily the bird can penetrate the substrate with its bill to gain access to prey (Myers *et al.* 1980, Grant 1984, Gerritsen and van Heezik 1985, Kelsey and Hassall 1989, Mouritsen and Jensen 1992). For example, sandy substrates are more penetrable than rocky substrates.

The state of the tidal cycle alters the area of habitat available for foraging and also affects prey behaviour and substrate penetrability, which in turn affect the availability of prey to shorebirds in general (Esselink and Zwarts 1989, de Vlas *et al.* 1996). The amount of time that bottom-dwelling marine worms spend at the substrate surface depends on the feeding technique they employ, which is governed by the state of the tide (Esselink and Zwarts 1989). Wet substrates are more penetrable than dry substrates (Myers *et al.* 1980, Mouritsen and Jensen 1992, Milsom *et al.* 2002), and probing shorebirds tend to probe more often on wet substrates and peck more often on dry substrates (Zwarts and Esselink 1989).

Environmental inputs, such as nutrients and pollutants, can lead to the presence of different types of prey as well as different feeding conditions which often affect prey biomass and availability (Thompson 1993b, Raffaelli 1999, *et al.* 1999, Kennish 2002). For example, primary treated effluent discharged from sewage treatment plants has been associated with an increase in the local density of certain types of invertebrates and their shorebird predators (Thompson 1993b). However, nutrient enrichment often leads to the proliferation of thick algal mats, which may
decrease the availability of prey buried within the sediment by reducing the penetrability of the substrate surface (Raffaelli et al. 1999).

Close proximity to a good quality high-tide roost site can be an overriding factor determining the distribution of feeding shorebirds on intertidal flats (Hale 1980). Energy reserves can be conserved by minimising the flight distance between roosting and feeding areas (Zwarts 1981, Orians and Wittenberger 1991, Rogers 2003). Birds can also better conserve their energy at sites where there is little disturbance and which provide protection from extreme hot or cold conditions (Rogers 2003). Disturbance can adversely affect shorebirds in many ways, ultimately reducing food intake and increasing energy expenditure (Fitzpatrick and Bouchez 1998). Human disturbance can lead to reduced frequency of use and even abandonment of preferred feeding and roosting areas (Pfister et al. 1992). However, it is possible for shorebirds to adapt to human disturbance, by either extending their feeding period or by becoming habituated to the disturbance (Urfi et al. 1996). It has been suggested that larger shorebirds may be less tolerant of human disturbance than smaller shorebirds (Rohweder and Baverstock 1996, Blumstein et al. 2005). Global climate change is an emerging threat to many species and could affect the distribution of shorebirds (Hughes 2000, Parmesan and Yohe 2003, Root et al. 2003). Its affects on shorebird feeding habitat could be positive, negative or neutral because with the rise in global sea level some suitable habitats may disappear while others may become available (Austin and Rehfisch 2003, 2006). Considerable further research is required before precise predictions of the likely affects of climate change on shorebird populations can be made (Piersma and Lindstrom 2004). The issue of climate change and its affects on shorebirds is not going to be considered further in this thesis.
1.1.4 Foraging and feeding by deep-probing shorebirds

Much research has been conducted on the diet and foraging techniques of deep-probing shorebirds, even though little is known about how this affects their choice of feeding habitat. Their long bills make them versatile and opportunistic foragers (Baker 1979, Zwarts and Esselink 1989), consuming whatever foods are available. Consequently, their diets are quite variable depending on their specific location and the time of year (Allen 1980, Leeman et al. 2001).

The three large curlews have a similar bill shape to the smaller *Numenius* species such as Whimbrels (*N. phaeopus*) and Bristle-thighed Curlews (*N. tahitiensis*), though their bills are twice as long. Their much longer bills and greater body size mean that large *Numenius* species are able to probe the sediment to more than double the depth capable by small *Numenius* species, and therefore they have different foraging techniques and abilities (Higgins and Davies 1996).

The decurved bills of curlews gives them a search-arc or sediment inspection volume up to eight times greater than that of birds such as godwits (*Limosa* sp.) which have bills of a similar length but are straight or slightly upturned (Zweers and Gerritsen 1997). There are several other advantages associated with bill decurvature. A decurved bill is more able to search along complex capture paths within the sediment (e.g. prey burrow systems or crevices) than a straight bill (Davidson et al. 1986, Ferns and Siman 1994). Bill decurvature also aids the gripping of prey (Burton 1974) and extraction of whole worms without breaking them (Davidson et al. 1986).

A disadvantage of the decurved bill design is that it is not as strong structurally as an equivalent straight bill (Burton 1974, Owens 1984). As a consequence of the bony and muscular reinforcement required to strengthen decurved
bills, there is a reduction in the relative length of the tongue which prevents transport of prey along the bill while it is still inserted in the sediment (Burton 1986). Therefore, curlews must remove their prey from the sediment in order to swallow it.

All three large curlews migrate long distances between their breeding and non-breeding grounds and the habitats in these two places are very different. Their breeding grounds are located at high latitudes in the northern hemisphere. On their breeding grounds they feed in a range of habitats, including: short, mixed-grass prairies; tilled, sown or fallow farmland; sphagnum bogs; or moss tussock (Berg 1992a, b, 1994, Gerasimov et al. 1997, Currie and Valkama 2000, Ueta and Antonov 2000, Jones et al. 2008). Within these habitats they feed on a range of insects and their larvae (e.g. beetles), earthworms and berries (Allen 1980, Berg 1993, Gerasimov et al. 1997).

Most descriptions of curlew feeding behaviour come from the non-breeding grounds (see below). I found only two studies which described the feeding behaviour of curlews on their breeding grounds: Allen’s (1980) work on Long-billed Curlews and Berg’s (1993) work on Eurasian Curlews. These two studies from curlew breeding grounds describe very similar feeding strategies to those observed on non-breeding grounds (e.g. Stenzel et al. 1976, Davidson et al. 1986, Piersma 1986, Zwarts and Esselink 1989, Zwarts and Wanink 1993, Zharikov and Skilleter 2004b; see below), even though these habitats are very different.

Curlews hunt both visually and by touch via pecks and probes. Probes are used to capture prey in a variety of different ways, including rapid thrusts down the burrows of visually detected prey or solely by tactile means into homogeneous sediment, when bills may be kept slightly ajar to increase the effective touching area (Stenzel et al. 1976, Allen 1980, Piersma 1986, Zwarts and Esselink 1989, Berg 1993, Zwarts and Wanink 1993, Zharikov and Skilleter 2004b). Often the whole head is inserted into the sediment and twisted upside-down (Piersma 1986, Zharikov and Skilleter 2004b). In order to extract buried soldier crabs (*Mictyris longicarpus*) that do not use burrows, Eastern Curlews repeatedly remove small amounts of sediment to gain access to them (Zharikov and Skilleter 2004b). Pecks are mainly used to capture prey seen on the surface of the substrate (Stenzel et al. 1976, Allen 1980, Zwarts and Esselink 1989, Zharikov and Skilleter 2004b) but may also be used to detect prey within the substrate (Allen 1980, Davidson et al. 1986; personal observation) or possibly to elicit a detectable response from such prey. When curlews forage visually, deep probes are not preceded by a shallow peck (Davidson et al. 1986). Turpie and Hockey (1997) noted similar behaviour in Whimbrels, when foraging by tactile means.
their step rates were low and peck rates were high, suggesting that shallow pecks were being used to help detect prey.

### 1.1.5 Concepts of prey supply

Only a small proportion of all prey on an intertidal flat can be consumed by a shorebird at any particular time (Reading and McGrorty 1978, Zwarts and Wanink 1991, 1993). It has been suggested that this “harvestable” prey fraction must be both available and profitable (Zwarts and Blomert 1992, Zwarts et al. 1992). Available prey are those that are detectable, accessible and ingestible. First, prey must be detected either visually or by touch. Accessible prey must be within reach of the birds’ bill which is limited by the maximum probe depth of the bird. Larger prey may be less accessible than smaller prey, even to deep-probing shorebirds, because they can bury more deeply (Reading and McGrorty 1978). Ingestible prey must be able to be swallowed, and this is limited by the bird’s gape width. Profitable prey are those that are energetically worth consuming. Profitability is measured as energy intake divided by handling time, and prey that provide a lower intake rate than the average over an extended feeding period tend to be avoided (Piersma 1986, Zwarts and Blomert 1992, Zwarts and Wanink 1993). Prey may be unprofitable if they are too small or require too much searching and handling (Piersma 1986, Zwarts and Wanink 1993). Piersma (1986) found that Eastern Curlews overwintering on the Nakdong Estuary in South Korea ignored crabs with a carapace width of less than 0.5 cm, and attributed this to low profitability. The weight and energy content of prey items increase exponentially with linear dimensions but the associated increase in handling time is much less (Piersma 1986, Zwarts and Wanink 1993).

The digestibility of prey may also be important as the rate at which food is processed is restricted by the capacity of the gut (Zwarts and Blomert 1992, Zharikov
and Skilleter 2003, 2004b, Van Gils et al. 2005a, b). Digestive pauses are necessary throughout the feeding period to allow the gut to empty. Different prey types can be equally profitable (i.e. offer equal amounts of energy relative to their required handling time) but differ in their digestive quality (i.e. their amount of soft flesh relative to indigestible material; Van Gils et al. 2005a).

Large shorebirds spend less time feeding during each low-tide period compared with small shorebirds (Dann 1987, Fasola and Biddau 1997, Ntiamoabaidu et al. 1998). It has been suggested that this difference occurs because larger birds are able to eat larger, more profitable prey, are more efficient at feeding and storing fat and have a relatively lower metabolic rate per unit of body weight (Dann 1987, Zwarts and Wanink 1993).

1.2 Assessing and monitoring habitat quality for deep-probing shorebirds

Deep-probing shorebirds are threatened worldwide (Allen 1980, Garnett 1992, Berg 1992a, b, Watkins 1993, Berg 1994, Stanley and Skagen 2007, Jones et al. 2008). Most of the global population of Eastern Curlews overwinter on intertidal flats around Australia (Watkins 1993). Recent declines in their numbers (Close and Newman 1984, Reid and Park 2003) have been attributed to loss of habitat, pollution, disturbance and hunting while on migration through Asia (Lane 1987, Garnett 1992, Watkins 1993). Eurasian Curlews overwinter throughout Europe, Africa and Asia and their numbers have also declined in recent decades. These declines may have been caused by the alteration of their breeding habitat due to the modernisation of farming and also from hunting during migration (Berg 1992a, b, 1994). Modern farming
practices have lead to a decrease in grassland area (their preferred nest sites) and an increase in habitat fragmentation (Berg 1992a, b). Long-billed Curlews have the smallest geographical range of the three large curlews, being confined to North America. Their numbers had declined markedly by the early 1900s due to hunting and loss of breeding habitat to cultivation (Allen 1980, Stanley and Skagen 2007, Jones et al. 2008). Although hunting Long-billed Curlews is now prohibited, habitat loss and fragmentation on their breeding and non-breeding grounds continue (Stanley and Skagen 2007, Jones et al. 2008).

Although events within their breeding range have been implicated in declines of deep-probing shorebirds, it is also important to know more about the role of the non-breeding grounds (Watkins 1993, Straw 2006). In the midst of severe declines in shorebird numbers on non-breeding grounds (Baker et al. 2004, Crowe et al. 2008, Koivula et al. 2008, Ma et al. 2009, Paton et al. 2009), it is becoming increasingly important to monitor their feeding habitats in order to ensure that deterioration of these habitats is not jeopardising local populations (Barter 1993). However, there is not yet sufficient understanding of the habitat requirements of deep-probing shorebirds to provide a basis for monitoring or assessing the status of their feeding grounds. It is therefore important to develop an understanding of what factors affect the quality and use of feeding grounds by deep-probing shorebirds. Furthermore, the habitat requirements of a species may be useful in predicting how that species will respond to changes in its environment (Okes et al. 2008).

Surveys of shorebird numbers and distribution patterns are useful for providing an increased understanding of the environmental factors that underlie density differences and habitat preferences (Kirby 1989, Thompson 1989, Congdon and Catterall 1994, Leitao 1999). However, monitoring bird numbers may not be a
reliable way to assess the quality of a site (Winker et al. 1995, Gill et al. 1997, West et al. 2005, 2007, Johnson 2007). Inferences about habitat quality based on bird distribution can be erroneous because there are situations which could cause birds to select poor quality habitats or avoid good quality habitats (for a review see Johnson 2007). For example, if good quality habitat is in short supply and overcrowded or defended by territorial or despotic individuals, then some birds (possibly the less fit or young) will be forced to settle in poorer quality areas (Goss-Custard and Durell 1990, Johnson 2007). Theoretical models suggest that after habitat deterioration or loss it may take some time before bird numbers decline and in some cases numbers may initially increase within remaining suitable habitat (Goss-Custard and Durell 1990, West et al. 2005, 2007). Therefore, management agencies may require an alternative method to assess the quality of local habitats. For example, West et al. (2005) suggested measuring the prey biomass available per bird as a way of monitoring habitat quality for shorebirds. However, this variable is difficult and time-consuming to measure (Durell et al. 2005, Stillman et al. 2005), and a simpler alternative may be necessary to achieve widespread adoption.

1.3 The Eastern Curlew in Moreton Bay

The Eastern Curlew is the largest migratory shorebird in the world and numbers have declined in Australia over recent decades (Close and Newman 1984, Reid and Park 2003). The species has been listed as “near-threatened” globally (Collar et al. 1994) and of “special concern” in Australia (Garnett 1992, Watkins 1993). In Queensland, curlews are described as “rare wildlife” under the Nature Conservation (Wildlife) Regulation 1994 (Nature Conservation Act). Despite several
international agreements (The Japan- and China-Australia Migratory Birds Agreements and Ramsar Convention on Wetlands) designed to conserve shorebirds and their habitats, there is growing concern that local and global environmental changes will lead to continued species declines at ever increasing rates in the Australasian region (Close and Newman 1984, Pfister et al. 1992, Thompson 1993a, Straw 1997, 2006, Nebel et al. 2008).

Intertidal flats along Australia’s coastline provide major feeding grounds for a diverse community of shorebirds (Lane 1987). Moreton Bay is situated on the subtropical east coast of Australia and is one of the country’s largest estuarine bays at 132 km in length. It has international conservation significance for shorebirds, which is acknowledged through its status as a Ramsar site. Estimates of the numbers of Eastern Curlews overwintering in Moreton Bay during the austral summer months have been evolving with progressive surveys covering greater areas of habitat. Lane (1987) reported a minimum population estimate for Moreton Bay of 1,080 curlews based on maximum roost counts. Thompson (1990b) surveyed 20% of the total intertidal area of Moreton Bay counting 921 curlews. It was suggested that multiplying this figure by five, giving a total of about 5,000 curlews for Moreton Bay as a whole, was likely to be an overestimate (Thompson, 1990b). However, neither Lane (1987) or Thompson (1990b) sampled the eastern side of the Bay where many birds occur. The most recent estimate which comes from roost counts covering both sides of Moreton Bay suggested it does indeed support around 5,000 curlews during the austral summer months (Driscoll 1997). This figure represents over 15% of the estimated global population of 31,000 Eastern Curlews. Therefore the Bay is of major, worldwide importance for this species (Watkins 1993, Thompson 1993a, Driscoll 1997).
Eastern Curlews overwinter in Moreton Bay from about August through to about April after migrating from breeding grounds ranging from north east China to north east Russia (Lane 1987, Driscoll and Ueta 2002). Approximately 25% of curlews remain in Moreton Bay during the breeding season (the austral winter), many of which are young birds that require up to 4 years to mature (Barter 1990, Wilson 2000, Driscoll and Ueta 2002). Moreton Bay provides curlews with a complex system of intertidal flats totalling 23,000 ha at low tide, including extensive mangrove stands and seagrass meadows in certain areas (Hyland and Butler 1989, Hyland et al. 1989, Blackman and Craven 1999). Substrate types within Moreton Bay are diverse and have been broadly categorised into sand, coral, sandy-mud and mud (Young 1978). Curlews are distributed widely among all the broad intertidal habitats the Bay provides, however densities are highly variable and broad flats tend to support the greatest numbers (Congdon and Catterall 1994). See Plates 1–5 for illustrations of the Eastern Curlew and its habitat in Moreton Bay.

Curlews forage as individuals or loose aggregations and may even defend territories (Congdon and Catterall 1994, Zharikov and Skilleter 2004a). Crustaceans are a frequent prey item on the sandflats of the eastern side of the Bay but curlews have also been recorded consuming marine worms (Zharikov and Skilleter 2003, 2004b, c). Eastern Curlews tend to have a greater flush distance on approach than smaller shorebirds and are therefore particularly sensitive to human disturbance (Close and Newman 1984, Lane 1987, Garnett 1992, Rohweder and Baverstock 1996).
1.4 Aims and structure of this thesis

The present study investigates the feeding ecology of the Eastern Curlew in Moreton Bay and what drives their habitat choice on these non-breeding grounds. Low-tide feeding surveys of curlews, habitat assessments, and high-tide roost counts are combined to investigate habitat preference. This study also identifies the feeding habitats and food organisms of the curlews in Moreton Bay, and considers the ecological and behavioural processes that underlie patterns of habitat selection by curlews on their non-breeding grounds.

In particular, Chapter 2 assesses the curlews’ broadscale distribution among tidal flats within Moreton Bay, and evaluates the difference in curlew numbers obtained from low-tide counts across different days, months and seasons. Low-tide counts covering approximately 41% of the intertidal habitat in Moreton Bay are analysed in order to identify preferred foraging areas at the scale of the entire Bay.

Chapter 3 investigates the correspondence between roosting and feeding counts across Moreton Bay. This question is important because proximity to a good quality high-tide roost site can be an important factor in determining the low-tide distribution of feeding shorebirds, or vice versa. The degree of correspondence between numbers of curlews counted on low-tide feeding grounds and those counted on high-tide roosts is also compared between several spatial scales, and their daily operational distance is inferred from the results.

Chapter 4 aims to elucidate which factors are most important in driving the curlews’ choice of feeding area, and predicting their local densities on feeding flats. Analyses are conducted at both large (between-flat) and small (within-flat) spatial scales. The environmental factors that are considered include: properties of the
substrate, the state of the tidal cycle, the height of the tide, width and area of the flat, position within the flat, proximity to roost sites, the level of human disturbance and the occurrence of seagrass and mangroves.

Chapter 5 investigates the curlews’ diet, and food resources, across different tidal flats in which curlew densities varied greatly. Diet was measured from 970 focal observations of feeding curlews. Food resources were measured from benthic coring at 19 intertidal flats. This chapter also investigates whether measures of intertidal prey abundance are better or worse than properties of the substrate in their ability to predict curlew density.

Chapter 6 compares the foraging success of curlews among different tidal flats and substrate types. Foraging success was measured from 831 focal observations of feeding curlews and incorporated three main components (feeding rate, success rate and biomass intake rate). This chapter tests whether foraging success can explain choice of feeding site by curlews in Moreton Bay, and analyses the differences between males and females.

Finally, Chapter 7 integrates the findings and approaches presented in previous chapters. This chapter develops a picture of the foraging strategy and ecological logic of deep-probing shorebirds, using the Eastern Curlew and Moreton Bay as a case study. The results are used to infer the species’ likely responses to changes in its environment.

There are eight types of data used in the present study, and each chapter of this thesis reports on one to five of these data sets (Figure 1.2). For example, Chapter 2 draws upon only one data set whereas Chapters 4 and 5 draw upon five data sets each.
Chapter 1. General introduction

(Figure 1.2). Chapters 2, 3, 4, 5 and 6 have been written as individual manuscripts, and consequently there is some repetition in the text of different chapters.

The present study investigates many of the factors which potentially affect the spatial distribution of shorebirds on an intertidal flat (Figure 1.1) with particular reference to the Eastern Curlew in Moreton Bay. These factors include: the properties of the substrate (Chapters 2 and 4); the topography and width of the intertidal flat (Chapters 2 and 4); the prevailing physical conditions (Chapters 2 and 4); proximity to high-tide roost sites (Chapters 3 and 4); nutrients and pollutants (Chapter 4); disturbance (Chapter 4); prey density (Chapters 5 and 6); and sex of the bird (Chapter 6). As Moreton Bay provides some of the most important overwintering grounds available to curlews, the outcomes of this study will have significance for the worldwide conservation of this species.

**Types of data:**

<table>
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<tr>
<th>Broadscale counts</th>
<th>Chapter:</th>
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</thead>
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<tr>
<td>High-tide roost counts</td>
<td>2. Low-tide distribution of curlews</td>
</tr>
<tr>
<td>Environmental characteristics</td>
<td>3. Curlew numbers at roosts and feeding grounds</td>
</tr>
<tr>
<td>Fine-scale assessment of substrate</td>
<td>4. Intertidal feeding habitat of curlews</td>
</tr>
<tr>
<td>Curlew feeding observations</td>
<td>5. Determinants of habitat choice in curlews</td>
</tr>
<tr>
<td>Curlew feeding scan counts</td>
<td>6. Curlew distribution and foraging success</td>
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<td>Benthic fauna sampling</td>
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<td>Benthic fauna curlew counts</td>
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</table>

**Figure 1.2.** The different types of data used in the present study and the corresponding thesis chapters that draw upon them.
Chapter 2

The low-tide distribution of Eastern Curlews on feeding grounds in Moreton Bay.

2.1 Introduction

The conservation of declining shorebirds depends on developing an adequate understanding of what types of intertidal environment are utilised by the birds on their feeding grounds (Watkins 1993). To date most shorebird surveys in Australia have focussed on counts of roost sites (e.g. Close and Jaensch 1981, Thompson 1989, Houston and Mitchell 1997, Wilson 2000). A few studies have counted shorebirds in their intertidal feeding grounds (e.g. Garnett 1986, Thompson 1990a, b, Driscoll 1993, Congdon and Catterall 1994, Gill and Crawford 1999).

The Eastern Curlew, *Numenius madagascariensis*, has declined in numbers in Australia over recent decades (Close and Newman 1984) and is a species of particular concern (Garnett 1992, Watkins 1993). Many curlews spend their non-breeding season on feeding grounds in eastern Australia (Driscoll 1997). Moreton Bay is a Ramsar site in eastern Australia that supports over 15% of the world’s population (estimated at 31,000) during the summer months and is therefore of international importance for the species (Watkins 1993, Thompson 1993a, Driscoll 1997). Juvenile curlews require 3 years to mature and some individuals may use feeding grounds in Moreton Bay year round during this period (Driscoll and RAOU 1993, Wilson 2000). Moreton Bay is also the focus of Australia’s fastest growing region in human
population terms and there is some evidence that foreshore conditions are impacting on the local distribution of shorebirds in the Bay (e.g. Thompson 1993b). It is therefore particularly important to develop an understanding of which areas are the curlews’ main feeding grounds, and what factors affect their quality and use by the birds.

The aim of this chapter is to assess the curlews’ broadscale distribution among tidal flats within Moreton Bay, and to evaluate the difference in low-tide count numbers across different days, months and seasons.

2.2 Methods

Moreton Bay extends north east and south east of the City of Brisbane, in south east Queensland (27° 20’ 01” S, 153° 17’ 35” E). At 300,177 ha, it is one of the largest estuarine bays in Australia, enclosed on its western side by the mainland and on its eastern side by two of the largest sand islands in the world (Moreton and North Stradbroke Islands; Blackman and Craven 1999). Moreton Bay extends approximately 132 km along the coast in a north–south direction and reaches a maximum width and depth of 40 km and 40 m respectively (Blackman and Craven 1999). Salinity is highest on the eastern side of the Bay because the western side receives an input of freshwater from coastal drainage (Young 1978). The majority of this drainage comes from the Coomera, Logan, Brisbane, Pine and Caboolture rivers (Blackman and Craven 1999). Moreton Bay contains a complex system of intertidal flats totaling 23,000 ha at low tide (Blackman and Craven 1999). Substrate types within the Bay are diverse and have been broadly categorised into sand, coral, sandy-mud, and mud (Young 1978). Moreton Bay supports eight mangrove species and
extensive seagrass meadows in certain areas (Hyland et al. 1989, Blackman and Craven 1999).

The Eastern Curlews’ use of feeding grounds in Moreton Bay was assessed during a series of low-tide surveys covering 160 intertidal flats (sites). Sites spanned a north–south distance of approximately 115 km, from the northern end of Pumicestone Passage to the southern Moreton Bay islands, and varied in area from 0.68 to 474 ha. Individual sites typically comprised a section of intertidal flat from high water to low water, or a sandbank or collection of banks at low tide. Sites were defined on the basis of convenience of access and survey logistics. Site locations were predetermined to achieve maximum coverage of the Bay’s intertidal flats and their varying characteristics (e.g. size, substrate, topography). An effort was made to delineate sites based on natural disjunctions. On the western side of the Bay observers using cars and gaining access from the shore covered the majority of sites, many of which were small in area. On the eastern and southern islands, along inlets, creeks, and rivers, and in Pumicestone Passage, the majority of sites were surveyed by boat and some sites were very large in area.

A total of approximately 9,500 ha or 41.3% of the intertidal habitat within Moreton Bay was surveyed. Within major sections of the Bay: the north west (i.e. western Bay sites from Pumicestone Passage to the Brisbane River), the south west (i.e. western Bay sites from The Brisbane River to Redland Bay), the east islands, and the south islands, the intertidal area surveyed was 37%, 35%, 25% and 3% of the total area respectively. In the western section of the Bay, where intertidal habitat coverage was the greatest, sites formed an almost continuous length of coastline. The main gaps in coverage were confined to the eastern and southern Bay islands and the northern half of Pumicestone Passage.
Chapter 2. Low-tide distribution of curlews

Curlew counts were conducted on 8 days, four in each of summer and winter. Summer counts took place during one weekend in November 1998 (28th and 29th) and one in January 1999 (30th and 31st). Winter counts were also on two weekends: 26th and 27th of June and 24th and 25th of July 1999. For various reasons some sites could not be surveyed on the allocated count days. These sites were surveyed as close as possible to the allocated days and were usually restricted to four areas: Pumicestone Passage, Peel Island, Moreton Island, and North Stradbroke Island. During summer and winter respectively, 125 and 108 of the 160 sites were surveyed on the allocated count days. Data were collected by 60 experienced volunteers. Counts were made using spotting scopes, at least 20× magnification.

Curlew densities (number of birds per ha of feeding ground) were calculated for most sites (128 of 160). A digital map, in the form of a raster image on compact disk, was obtained from the Australian Hydrographic Office of the Royal Australian Navy. This map was set up as a base layer within the GIS program MapInfo. Hard copy maps showing the boundaries of the sites surveyed in this study were then used to digitise the site areas on screen. The intertidal area was defined at its potential maximum, from highest water to zero datum.

2.3 Results

During summer, over 2,000 curlews were counted on each of the 4 days, compared with an average of 600 in winter (Table 2.1). Curlew numbers at individual sites in summer varied from zero to 174, with differences in flat area accounting for some of this variation.
Figure 2.1 shows the relationship between counts on different days and different months using a logarithmic scale to separate the large number of low counts (on smaller flats). The relative numbers of curlews on consecutive days corresponded closely \((r = 0.89–0.95, P < 0.0005\) for all; Figure 2.1A–D). There was also a high and significant correlation \((r = 0.87\) and 0.92, \(P < 0.0005\), between counts on different months within both seasons (Figure 2.1E, F).

**Table 2.1.** The total number of Eastern Curlews counted on each day of the low-tide survey of feeding grounds in Moreton Bay.

<table>
<thead>
<tr>
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<th>Winter Survey</th>
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<td><strong>Date of count</strong></td>
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</tbody>
</table>

The average summer count was also highly correlated with the average winter count \(r = 0.79, P < 0.0005\). Approximately one quarter of the summer population occurred in Moreton Bay during the winter (Table 2.1) but there were some sites where the numbers of curlews occurring remained similar in summer and winter (Figure 2.2). Table 2.2 shows the location, area and abundance for the 30 sites that supported the lowest and highest curlew counts. Those sites where the count was low were generally relatively small in area when compared with those sites where the count was high (Table 2.2).
Figure 2.1. Correspondence between counts across all sites (each a point on the graph) comparing: consecutive days within months (A, B, C, D), and different months within seasons (E, F). \( r \) is Pearson’s correlation coefficient.
Calculations of the curlew density (number of birds per ha of tidal flat) provide some control over the effects of variation in site area. Winter and summer densities were significantly correlated ($P < 0.0005$) although the relationship was weaker ($r = 0.45$) than the correlation in the counts. The curlew density also decreased from summer to winter across the majority of sites, although there were some sites where it remained similar between the seasons (Figure 2.3). There was one relatively small (16 ha) site, situated at Deception Bay, where the winter density was almost four times greater than the summer density (Figure 2.3). With this site removed from the analysis the strength of the correlation between winter and summer densities was greater ($r = 0.58$).

Figure 2.2. Relationship between the average (of four) curlew counts in summer versus winter, across 157 sites. $r$ is Pearson’s correlation coefficient.
Table 2.2. The 30 sites that supported the lowest and highest numbers of Eastern Curlews, ranked by count value.

<table>
<thead>
<tr>
<th>Low Counts of Eastern Curlew</th>
<th>High Counts of Eastern Curlew</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Location</strong></td>
<td><strong>Area (ha)</strong></td>
</tr>
<tr>
<td>Coochiemudlo I.</td>
<td>12</td>
</tr>
<tr>
<td>Hays Inlet 1</td>
<td>1</td>
</tr>
<tr>
<td>Redcliffe 2</td>
<td>16</td>
</tr>
<tr>
<td>Redcliffe 3</td>
<td>5</td>
</tr>
<tr>
<td>Redcliffe 5</td>
<td>3</td>
</tr>
<tr>
<td>Redcliffe 6</td>
<td>5</td>
</tr>
<tr>
<td>Redland Bay 4</td>
<td>6</td>
</tr>
<tr>
<td>Shorncliffe 2</td>
<td>22</td>
</tr>
<tr>
<td>Aquatic Paradise</td>
<td>1</td>
</tr>
<tr>
<td>Victoria Pt. 1</td>
<td>5</td>
</tr>
<tr>
<td>Cleveland Pt.</td>
<td>12</td>
</tr>
<tr>
<td>Redcliffe 4</td>
<td>3</td>
</tr>
<tr>
<td>Redland Bay 3</td>
<td>11</td>
</tr>
<tr>
<td>Wynnum</td>
<td>6</td>
</tr>
<tr>
<td>Brisbane Airport 4</td>
<td>2</td>
</tr>
<tr>
<td>N. Stradbroke I. 5</td>
<td>16</td>
</tr>
<tr>
<td>Ningi Ck. 2</td>
<td>8</td>
</tr>
<tr>
<td>Peel I. 1</td>
<td>4</td>
</tr>
<tr>
<td>Raby Bay 2</td>
<td>24</td>
</tr>
<tr>
<td>Redcliffe 7</td>
<td>26</td>
</tr>
<tr>
<td>Redland Bay 1</td>
<td>4</td>
</tr>
<tr>
<td>Manly Boat Harbour</td>
<td>2</td>
</tr>
<tr>
<td>N. Stradbroke I. 2</td>
<td>10</td>
</tr>
<tr>
<td>Redcliffe 1</td>
<td>25</td>
</tr>
<tr>
<td>Shorncliffe 1</td>
<td>26</td>
</tr>
<tr>
<td>Redland Bay 1</td>
<td>5</td>
</tr>
<tr>
<td>Brisbane Airport 3</td>
<td>27</td>
</tr>
<tr>
<td>Cleveland Pt. 1</td>
<td>46</td>
</tr>
<tr>
<td>Luggage Pt. 1</td>
<td>120</td>
</tr>
<tr>
<td>Raby Bay 1</td>
<td>3</td>
</tr>
</tbody>
</table>
Table 2.3 lists the 30 sites that supported the lowest and highest curlew densities in summer. Out of the 30 sites that had the lowest curlew count (Table 2.2), 21 also appeared in the 30 sites that had the lowest densities (Table 2.3). Locations that supported both low counts and densities included Redland Bay, Victoria Point, Cleveland, Wynnum, Brisbane Airport, Shorncliffe, and Redcliffe. In comparison, 17 of the 30 sites that supported the highest counts (Table 2.2) also appeared in the 30 sites that supported the highest densities (Table 2.3). Locations that supported both high counts and densities included Lota, North Stradbroke Island, Moreton Island, Fisherman Islands, Hays Inlet, Deception Bay, and Pumicestone Passage.

![Figure 2.3](image)

**Figure 2.3.** Relationship between the average (of four) curlew densities in summer versus winter, across 128 sites. $r$ is Pearson’s correlation coefficient.
Table 2.3. The 30 sites that supported the lowest and highest densities of Eastern Curlews, ranked by density.

<table>
<thead>
<tr>
<th>Location</th>
<th>Area (ha)</th>
<th>Density (No./100ha)</th>
<th>Count</th>
<th>Location</th>
<th>Area (ha)</th>
<th>Density (No./100ha)</th>
<th>Count</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aquatic Paradise</td>
<td>1</td>
<td>0.0</td>
<td>0.0</td>
<td>Empire Pt. 2</td>
<td>22</td>
<td>32.3</td>
<td>7.0</td>
</tr>
<tr>
<td>Coochiemudlo I.</td>
<td>12</td>
<td>0.0</td>
<td>0.0</td>
<td>Manly Boat Harbour</td>
<td>2</td>
<td>32.4</td>
<td>0.8</td>
</tr>
<tr>
<td>Hays Inlet 1</td>
<td>1</td>
<td>0.0</td>
<td>0.0</td>
<td>N. Stradbroke I. 4</td>
<td>82</td>
<td>32.4</td>
<td>26.5</td>
</tr>
<tr>
<td>Redcliffe 2</td>
<td>16</td>
<td>0.0</td>
<td>0.0</td>
<td>Hays Inlet 3</td>
<td>105</td>
<td>32.6</td>
<td>34.3</td>
</tr>
<tr>
<td>Redcliffe 3</td>
<td>5</td>
<td>0.0</td>
<td>0.0</td>
<td>Thoreside 2</td>
<td>22</td>
<td>37.7</td>
<td>8.3</td>
</tr>
<tr>
<td>Redcliffe 5</td>
<td>3</td>
<td>0.0</td>
<td>0.0</td>
<td>Pumicestone Passage 3</td>
<td>48</td>
<td>37.8</td>
<td>18.0</td>
</tr>
<tr>
<td>Redcliffe 6</td>
<td>5</td>
<td>0.0</td>
<td>0.0</td>
<td>Fisherman I.1</td>
<td>353</td>
<td>37.9</td>
<td>133.8</td>
</tr>
<tr>
<td>Redland Bay 4</td>
<td>6</td>
<td>0.0</td>
<td>0.0</td>
<td>Pumicestone Passage 10</td>
<td>316</td>
<td>40.5</td>
<td>127.8</td>
</tr>
<tr>
<td>Shorncliffe 2</td>
<td>22</td>
<td>0.0</td>
<td>0.0</td>
<td>Fisherman I. 2</td>
<td>280</td>
<td>41.1</td>
<td>115.0</td>
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<td>Victoria Pt. 1</td>
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<td>0.0</td>
<td>0.0</td>
<td>N. Stradbroke I. 7</td>
<td>191</td>
<td>42.5</td>
<td>81.0</td>
</tr>
<tr>
<td>Luggage Pt. 1</td>
<td>120</td>
<td>1.3</td>
<td>1.5</td>
<td>Fisherman I. 4</td>
<td>106</td>
<td>43.1</td>
<td>45.5</td>
</tr>
<tr>
<td>Redcliffe 7</td>
<td>26</td>
<td>1.9</td>
<td>0.5</td>
<td>Thoreside 1</td>
<td>69</td>
<td>43.6</td>
<td>30.0</td>
</tr>
<tr>
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<td>24</td>
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<td>0.5</td>
<td>Pumicestone Passage 1</td>
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<td>44.3</td>
<td>13.5</td>
</tr>
<tr>
<td>Cleveland Pt.</td>
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<td>0.3</td>
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<td>0.3</td>
<td>N. Stradbroke I. 8</td>
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<td>30.5</td>
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<td>Pumicestone Passage 6</td>
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<td>46.8</td>
<td>21.3</td>
</tr>
<tr>
<td>Shorncliffe 1</td>
<td>26</td>
<td>2.9</td>
<td>0.8</td>
<td>Ningi Ck. 1</td>
<td>44</td>
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<tr>
<td>N. Stradbroke I. 5</td>
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<td>3.1</td>
<td>0.5</td>
<td>Pumicestone Passage 5</td>
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<td>47.7</td>
<td>8.0</td>
</tr>
<tr>
<td>Redcliffe 1</td>
<td>25</td>
<td>3.1</td>
<td>0.8</td>
<td>Empire Pt. 1</td>
<td>10</td>
<td>51.8</td>
<td>5.0</td>
</tr>
<tr>
<td>Cleveland 1</td>
<td>46</td>
<td>3.3</td>
<td>1.5</td>
<td>Pumicestone Passage 11</td>
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<td>51.8</td>
<td>6.8</td>
</tr>
<tr>
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<td>5.0</td>
<td>Pumicestone Passage 4</td>
<td>255</td>
<td>51.8</td>
<td>132.3</td>
</tr>
<tr>
<td>Peel I. 7</td>
<td>58</td>
<td>3.9</td>
<td>2.3</td>
<td>Raby Bay 1</td>
<td>3</td>
<td>54.4</td>
<td>1.5</td>
</tr>
<tr>
<td>Bramble Bay 5</td>
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<td>4.3</td>
<td>Pumicestone Passage 13</td>
<td>9</td>
<td>55.1</td>
<td>4.8</td>
</tr>
<tr>
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<td>45</td>
<td>4.4</td>
<td>2.0</td>
<td>Hays Inlet 2</td>
<td>57</td>
<td>61.3</td>
<td>35.0</td>
</tr>
<tr>
<td>Wynnum</td>
<td>6</td>
<td>4.4</td>
<td>0.3</td>
<td>Ningi Ck. 4</td>
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<td>63.0</td>
<td>19.3</td>
</tr>
<tr>
<td>Peel I. 4</td>
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<td>4.5</td>
<td>4.0</td>
<td>Moreton I. 4</td>
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<td>71.9</td>
<td>156.5</td>
</tr>
<tr>
<td>Brisbane Airport 3</td>
<td>27</td>
<td>4.7</td>
<td>1.3</td>
<td>Lota 2</td>
<td>9</td>
<td>73.3</td>
<td>6.8</td>
</tr>
<tr>
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<td>4.8</td>
<td>5.3</td>
<td>Ormiston</td>
<td>12</td>
<td>97.6</td>
<td>12.0</td>
</tr>
<tr>
<td>Nudgee Beach</td>
<td>151</td>
<td>5.3</td>
<td>8.0</td>
<td>Deception Bay 1</td>
<td>45</td>
<td>134.9</td>
<td>61.3</td>
</tr>
<tr>
<td>Kippa Ring</td>
<td>127</td>
<td>5.7</td>
<td>7.3</td>
<td>Ningi Ck. 3</td>
<td>4</td>
<td>165.3</td>
<td>6.8</td>
</tr>
</tbody>
</table>
2.4 Discussion

2.4.1 Distribution of curlews among intertidal feeding flats in Moreton Bay

Almost half of the total Eastern Curlew population of south east Queensland, estimated at approximately 5,000 (Driscoll 1997), were counted during each of the low-tide surveys. The constancy of curlew numbers across sites suggests that short surveys (such as one count per season instead of four) can give useful results. Some tidal areas supported considerably higher counts and densities of curlews than others, and the fact that a substantial proportion of the sites with high counts also had high densities (and likewise for low counts) indicates that the variation in curlew numbers across sites was not due only to the effect of flat size.

Why these areas are important for curlews cannot be inferred from the count data obtained in this study. The distribution of shorebirds may be influenced by both the substrate type (Quammen 1982, Kelsey and Hassall 1989, Nehls and Tiedemann 1993, Yates et al. 1993), and disturbance by humans (Le Drean-Quenechdu et al. 1995, Bhuva and Soni 1998). These two factors are likely to be important determinants of the distribution of Eastern Curlews in Moreton Bay.

The substrate type at the preferred sites may offer a greater density and/or harvestability of prey. At all of the key areas for curlews within Moreton Bay (listed above) the substrate was either sand or sandy-mud as opposed to mud or coral. The particle size composition of a substrate affects its invertebrate biomass (Sanders 2000) and penetrability (Kelsey and Hassall 1989). The presence of coral would certainly reduce substrate penetrability and may be the reason why low abundances and densities of curlews were recorded at sites where coral occurred. Quammen (1982) found that shallow-probing shorebirds have a greater feeding efficiency on muddy
substrates with little sand. Large, deep-probing shorebirds such as curlews are likely to have different preferences. Soft mud may be difficult for large shorebirds to walk through. The results of these surveys suggest that the distribution of seagrass may also be an important factor as all of the key areas except one, Hays Inlet, support dense patches of seagrass, although Congdon and Catterall (1994) found no association between curlew density and seagrass occurrence at a local scale.

Moreton Bay is heavily utilised by both recreational and professional bait harvesters and fishers. Human interference reduces feeding efficiency in shorebirds (Smit et al. 1987, de Boer and Longamane 1996, Lord et al. 1997). De Boer and Longamane (1996) noted a 34% reduction in foraging time for Whimbrels due to human presence. Within all of the key areas mentioned above there is feeding habitat that is relatively inaccessible to humans. In areas where large scale professional bait harvesting takes place, such as the Fisherman Islands, the area is sufficiently large to provide some habitat well away from the commercial activities. Continued research, described in later chapters of this thesis, further elucidated the factors affecting curlew distribution in Moreton Bay at different spatial scales.

2.4.2 The utility of flat versus roost counts.

The total numbers of curlews counted on feeding flats during this study were comparable to the numbers counted on roost sites during independent surveys conducted by the Queensland Wader Study Group (QWSG). Flat counts gave similar results to roost counts for both total numbers of curlews and summer/winter differences in numbers (Table 2.1; Driscoll 1997). Other studies have also noted a high correspondence between flat and roost counts of shorebirds (e.g. Dominguez 1986, Yates and Goss-Custard 1991) however this result is not always expected (e.g. Kirby et al. 1988). The winter population of Eastern Curlews in Moreton Bay
remained at approximately 25% of the summer population (Table 2.1). This figure is not only supported by roost counts for Moreton Bay (Driscoll 1997), but is also similar to the percentage of winter to summer numbers obtained for Eastern Curlews elsewhere in Queensland (Houston and Mitchell 1997) and for other shorebirds that breed in the northern hemisphere (Thompson 1990a).

Counts on flats are useful for different reasons than counts on roosts. At roost sites, shorebirds are generally tightly packed into a relatively small area. In comparison, on feeding grounds, they are usually only loosely aggregated. Therefore, due to their spatial distribution, birds on roost sites may be harder to count accurately. Rappoldt et al. (1985) quantified an error of 37% in birds counted at roosts. This figure was not compared with counts on feeding grounds, but when compared to birds counted in flight, the error fell to 17% (Rappoldt et al. 1985). Although there may be a reduced error associated with counting birds on feeding grounds, due to their relatively sparse and wide distribution, a greater area must be surveyed to census a significant proportion of the total population. Therefore, roost counts may be preferable for population monitoring over years because less time and effort is involved to survey a significant proportion of the population. However, surveys of roost sites are of limited usefulness in identifying key intertidal feeding habitat. Although roost counts do provide an estimate of the numbers of birds that feed on nearby intertidal areas, low-tide counts are more appropriate for assessing the quality of these feeding areas.
Chapter 3

Eastern Curlew numbers at high-tide roosts versus low-tide feeding grounds: a comparison at three spatial scales

3.1 Introduction

Surveys of shorebird numbers and distribution patterns have been used for a variety of purposes. These include: determining the geographical distributions of species; obtaining population numbers that may lead to Ramsar listings; monitoring populations in order to detect changes over time; and understanding the environmental factors that underlie density differences and habitat preferences. Most shorebird surveys in Australia have focussed on either counts at roost sites (e.g. Close and Jaensch 1981, Thompson 1989, Houston and Mitchell 1997, Wilson 2000) or counts on feeding grounds (e.g. Garnett 1986, Thompson 1990a, b, Congdon and Catterall 1994, Gill and Crawford 1999). However, the degree of correspondence between these two types of count is not well understood. A few studies world wide have compared shorebird counts at roosts with those on feeding grounds (Goss-Custard 1981, Barrett and Barrett 1984, Dominguez 1986, Kirby et al. 1988, Yates and Goss-Custard 1991, Summers and Kalejta-Summers 1996), with no such studies in Australia. Some of these studies have noted a high correspondence between counts of roosting and feeding shorebirds (e.g. Goss-Custard 1981, Barrett and Barrett 1984, Dominguez 1986, Yates and Goss-Custard 1991) however this result is not always

The aim of this chapter is to determine the correspondence between roosting and feeding numbers of a single species, the Eastern Curlew (Numenius madagascariensis), across about 150 km of coastline in subtropical eastern Australia. This comparison is part of a broader study which aims at understanding Eastern Curlew habitat use in Moreton Bay, a Ramsar site that supports over 15% of the world’s population (estimated at 31,000) during the summer months and is therefore of international importance for the species (Watkins 1993, Thompson 1993a, Driscoll 1997). The Eastern Curlew has declined in numbers in Australia over recent decades (Close and Newman 1984) and is a species of particular concern (Garnett 1992, Watkins 1993).

3.2 Study site and methods

3.2.1 Moreton Bay

Moreton Bay extends north east and south east of the city of Brisbane, in south east Queensland (27° 20’ 01” S, 153° 17’ 35” E). At 300,177 ha, it is one of the largest estuarine bays in Australia, enclosed on its western side by the mainland and on its eastern side by two of the largest sand islands in the world (Moreton and North Stradbroke Islands; Blackman and Craven 1999). Moreton Bay extends 132 km along the coast in a north–south direction, reaches a maximum width and depth of 40 km and 40 m respectively, and contains a complex system of intertidal flats totaling 23,000 ha at low tide (Blackman and Craven 1999). Salinity is highest on the eastern side of the Bay because the western side receives an input of fresh water from coastal
drainage systems (Young 1978), mainly from the Coomera, Logan, Brisbane, Pine and Caboolture rivers (Blackman and Craven 1999). Substrate types within the Bay are diverse and have been broadly categorised into sand, coral, sandy-mud, and mud (Young 1978). There are extensive mangrove stands and seagrass meadows in certain areas (Hyland et al. 1989, Blackman and Craven 1999)

3.2.2 Low-tide surveys

The Eastern Curlew’s use of feeding grounds in Moreton Bay was assessed during a series of low-tide surveys covering 160 intertidal flats (sites). Sites spanned a north–south distance of approximately 115 km, from the northern end of Pumicestone Passage to the southern Moreton Bay islands, and varied in area from 0.68 to 474 ha. Individual sites typically comprised a section of intertidal flat from high water to low water, or a sandbank or collection of banks at low tide. Sites were defined on the basis of convenience of access and survey logistics. Site locations were predetermined to achieve maximum coverage of the Bay’s intertidal flats and their varying characteristics (e.g. size, substrate, topography). An effort was made to delineate sites based on natural disjunctions. On the western side of the Bay observers using cars and gaining access from the shore covered the majority of sites, many of which were small in area. On the eastern and southern islands, along inlets, creeks, and rivers, and in Pumicestone Passage, the majority of sites were surveyed by boat and some sites were very large in area.

A total of approximately 9,500 ha or 41.3% of the intertidal habitat within Moreton Bay was surveyed. Within major sections of the Bay: the north west (western Bay sites from Pumicestone Passage to the Brisbane River), the south west (western Bay sites from the Brisbane River to Redland Bay), the eastern islands, and the southern islands, the intertidal area surveyed was 37%, 35%, 25% and 3% of the
total surveyed area respectively. In the western section of the Bay, where intertidal habitat coverage was the greatest, sites formed an almost continuous length of coastline for about 115 km. The main gaps in coverage were confined to the eastern and southern islands and the north west section (northern half of Pumicestone Passage).

Eastern Curlew counts were conducted on 8 days, four in each of summer and winter. Summer counts took place during the weekends of November 28–29, 1998 and January 30–31, 1999. Winter counts were on the weekends of June 26–27, 1999 and July 24–25, 1999. For various reasons some sites could not be surveyed on the allocated count days. These sites were surveyed as close as possible to the allocated days and were usually restricted to four areas: Pumicestone Passage, Peel Island, Moreton Island, and North Stradbroke Island. During summer and winter respectively, 125 and 108 of the 160 sites were surveyed on the allocated count days. Data were collected by 60 experienced volunteers. Counts were made using spotting scopes of at least 20× magnification.

3.2.3 High-tide surveys

Since 1991 members of the Queensland Wader Study Group (QWSG) have documented shorebird use of high-tide roosts in Moreton Bay. To date, a total of 170 shorebird roost sites have been identified and monitored over at least 2 years between 1991 and 1999. Roost sites were surveyed within 2 hours either side of a suitable high tide in each month of the year. However, not all roost sites were surveyed in each month and some were not surveyed for several months at a time, because QWSG volunteers moved on or stopped counting a site for various reasons. Surveys were conducted, using spotting scopes of at least 20× magnification, to count all the shorebird species utilising these roosts, not only Eastern Curlews. Many of the
volunteers who regularly counted at high-tide roosts were also involved in the Eastern Curlew counts at low tide described above.

Out of the total 170 roost sites, 30 were selected for comparison between roosting and feeding Eastern Curlew numbers (Table 3.1). Several criteria were used to select these roost sites. First, the roost site had to be utilised by Eastern Curlews. Second, each roost site had to have been surveyed at least five times during summer months between 1991 and 1999. This criterion was relaxed for one roost site (Newport Waterways creek mouth) which had been visited only once, but for which background knowledge indicated that this site was important to Eastern Curlews and that the count of 27 birds, made by P.V. Driscoll in November 1998, was a reasonable representation for this site. Roost sites that had been counted frequently were those considered important by experienced members of the QWSG. Third, roost sites were selected only if they corresponded with extensive coverage of feeding habitat in nearby areas during the broadscale survey. Where only a small proportion of the total feeding area had been covered, comparisons with numbers on adjacent roost sites would be ambiguous. Therefore, three feeding areas covered during the low-tide surveys (northern end of Pumicestone Passage, southern end of Moreton Island and northern end of North Stradbroke Island) and nearby roost sites were excluded from the comparison.

Summer numbers of Eastern Curlews were used for all comparisons between roost and feeding counts, because more areas were counted and there was a greater number of birds. The numbers on roost sites were represented by the average of all counts made between mid November and mid March from 1991 to 1999 (Table 3.1). It was necessary to average roost site counts over years to control for the between-count variation in Eastern Curlew numbers due to variation in environmental
Chapter 3. Curlew numbers at roosts and feeding grounds

conditions, coupled with the patchy record of within-year observer visits at some sites. The numbers on feeding grounds were represented by the average of a total of four counts carried out during the months of November 1998 and January 1999 (see also Chapter 2).

3.3 Results

3.3.1 Distribution of Eastern Curlews among intertidal feeding flats in Moreton Bay

The total number of Eastern Curlews counted during the low-tide surveys of feeding grounds on each of 4 days in summer were 2,388, 2,357, 2,221 and 2,080 and in winter were 528, 550, 661, and 679. The average winter count (604) was 27% of the average summer count (2,261).

The relative numbers of Eastern Curlews on consecutive days corresponded closely (Pearson’s correlation coefficient $r = 0.89–0.95$, $P < 0.0005$ for all; Table 3.2). There was also a high and significant correlation between counts on different months within both seasons ($r = 0.87$ and 0.92, $P < 0.0005$; Table 3.2) and between counts during summer and winter ($r = 0.79$, $P < 0.0005$; Table 3.2). Eastern Curlew numbers at individual flats varied between zero and 174 in summer and zero and 82 in winter with a wide range of variation in the area of individual flats (0.68 to 474 ha).

3.3.2 Relationship between counts on roost sites and counts on feeding grounds

In total, the average summer count at the 30 selected roost sites (Table 3.1) was 1,851 and the corresponding average summer count on adjacent feeding grounds was 1,728; a difference between counts of 6.6%. Counts at roost sites from 1991–1997 were highly correlated with those from 1998–1999 (Figure 3.1). This validates

Figure 3.1. Correspondence between the summer counts of Eastern Curlews averaged within roost sites across nine roost site groups in 1991–1997 versus 1998–1999 ($r = 0.79$, $r^2 = 0.62$).
Table 3.1. The names and locations of the 30 selected roost sites with their average summer count of Eastern Curlews (\( n \) = the number of times each site was surveyed). This table also shows which roost sites were grouped together for each analysis (A, B, and C).

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Site Name</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Average summer count</th>
<th>( n )</th>
</tr>
</thead>
<tbody>
<tr>
<td>a a a</td>
<td>Donnybrook claypan</td>
<td>27 00 46</td>
<td>153 04 06</td>
<td>46</td>
<td>18</td>
</tr>
<tr>
<td>a a b</td>
<td>Toorbul north</td>
<td>27 03 00</td>
<td>153 06 20</td>
<td>1</td>
<td>26</td>
</tr>
<tr>
<td>a a b</td>
<td>Toorbul</td>
<td>27 02 30</td>
<td>153 06 30</td>
<td>11</td>
<td>27</td>
</tr>
<tr>
<td>a a b</td>
<td>Dux Creek Bribie Island</td>
<td>27 03 25</td>
<td>153 08 20</td>
<td>409</td>
<td>32</td>
</tr>
<tr>
<td>a a c</td>
<td>Sandstone Point</td>
<td>27 05 00</td>
<td>153 08 00</td>
<td>5</td>
<td>28</td>
</tr>
<tr>
<td>a b d</td>
<td>Caboolture River mouth</td>
<td>27 09 06</td>
<td>153 02 15</td>
<td>17</td>
<td>18</td>
</tr>
<tr>
<td>a b e</td>
<td>Deception Bay claypan</td>
<td>27 10 30</td>
<td>153 01 30</td>
<td>71</td>
<td>11</td>
</tr>
<tr>
<td>a b e</td>
<td>Deception Bay south</td>
<td>27 12 00</td>
<td>153 02 30</td>
<td>2</td>
<td>25</td>
</tr>
<tr>
<td>a b f</td>
<td>Newport Waterways creek mouth</td>
<td>27 12 30</td>
<td>153 05 20</td>
<td>27</td>
<td>1</td>
</tr>
<tr>
<td>b c g</td>
<td>Pine Rivers Wetland Reserve</td>
<td>27 17 30</td>
<td>153 02 30</td>
<td>95</td>
<td>16</td>
</tr>
<tr>
<td>b c g</td>
<td>Pine Rivers north</td>
<td>27 17 40</td>
<td>153 01 30</td>
<td>27</td>
<td>14</td>
</tr>
<tr>
<td>c d h</td>
<td>Dynah Island</td>
<td>27 20 05</td>
<td>153 05 05</td>
<td>7</td>
<td>25</td>
</tr>
<tr>
<td>c d h</td>
<td>Dynah Island mangrove/claypan</td>
<td>27 20 24</td>
<td>153 05 17</td>
<td>4</td>
<td>15</td>
</tr>
<tr>
<td>c d i</td>
<td>Jackson Creek Point</td>
<td>27 21 03</td>
<td>153 06 47</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>c d i</td>
<td>Kedron Brook Floodway</td>
<td>27 21 40</td>
<td>153 06 20</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>c d i</td>
<td>Luggage Point</td>
<td>27 22 40</td>
<td>153 09 00</td>
<td>31</td>
<td>16</td>
</tr>
<tr>
<td>d e j</td>
<td>Bishop Island</td>
<td>27 21 42</td>
<td>153 10 30</td>
<td>41</td>
<td>28</td>
</tr>
<tr>
<td>d e j</td>
<td>Fisherman Island claypan</td>
<td>27 23 35</td>
<td>153 10 30</td>
<td>152</td>
<td>26</td>
</tr>
<tr>
<td>d e k</td>
<td>Lytton north</td>
<td>27 24 55</td>
<td>153 09 40</td>
<td>77</td>
<td>26</td>
</tr>
<tr>
<td>d e k</td>
<td>Lytton</td>
<td>27 25 25</td>
<td>153 09 52</td>
<td>49</td>
<td>32</td>
</tr>
<tr>
<td>e f l</td>
<td>Manly Harbour</td>
<td>27 27 22</td>
<td>153 11 25</td>
<td>51</td>
<td>30</td>
</tr>
<tr>
<td>e f l</td>
<td>Manly Lota Esplanade</td>
<td>27 28 00</td>
<td>153 11 00</td>
<td>3</td>
<td>17</td>
</tr>
<tr>
<td>e f m</td>
<td>Acacia Street Wellington Point</td>
<td>27 28 43</td>
<td>153 14 03</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td>e f m</td>
<td>West Geoff Skinner Reserve</td>
<td>27 29 11</td>
<td>153 14 35</td>
<td>45</td>
<td>11</td>
</tr>
<tr>
<td>e f m</td>
<td>East Geoff Skinner Reserve</td>
<td>27 29 30</td>
<td>153 15 10</td>
<td>162</td>
<td>11</td>
</tr>
<tr>
<td>e f n</td>
<td>Empire Point</td>
<td>27 30 12</td>
<td>153 15 41</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>f g o</td>
<td>Nandeebie Park Cleveland</td>
<td>27 32 00</td>
<td>153 16 45</td>
<td>33</td>
<td>14</td>
</tr>
<tr>
<td>f g p</td>
<td>Thornlands Road Thornlands</td>
<td>27 33 30</td>
<td>153 16 58</td>
<td>304</td>
<td>17</td>
</tr>
<tr>
<td>g h q</td>
<td>South Stradbroke Island tip</td>
<td>27 44 30</td>
<td>153 26 25</td>
<td>144</td>
<td>9</td>
</tr>
<tr>
<td>h i r</td>
<td>Peel Island north west corner</td>
<td>27 30 00</td>
<td>153 20 00</td>
<td>23</td>
<td>5</td>
</tr>
</tbody>
</table>
Table 3.2. Correspondence between counts across all sites (n) comparing consecutive days within months, different months within seasons (average of two counts) and different seasons (average of four counts). $P < 0.0005$ for all comparisons.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Pearson’s $r$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>November 28 vs. 29</td>
<td>0.93</td>
<td>159</td>
</tr>
<tr>
<td>January 30 vs. 31</td>
<td>0.89</td>
<td>159</td>
</tr>
<tr>
<td>June 26 vs. 27</td>
<td>0.93</td>
<td>157</td>
</tr>
<tr>
<td>July 24 vs. 25</td>
<td>0.95</td>
<td>157</td>
</tr>
<tr>
<td>November vs. January</td>
<td>0.92</td>
<td>159</td>
</tr>
<tr>
<td>June vs. July</td>
<td>0.87</td>
<td>157</td>
</tr>
<tr>
<td>Summer vs. Winter</td>
<td>0.79</td>
<td>157</td>
</tr>
</tbody>
</table>

To enable the comparison of roosting and feeding numbers, groups of feeding sites were matched against a nearby roost site or group of roost sites, using three different rules of association (Table 3.3). For example, in analysis ‘B’, roost sites within a 5 km radius were grouped together (forming nine groups) and associated with adjacent feeding sites (Table 3.3). These rules were intended to allow a comparison of alternative objective systems for matching roosting and feeding areas at different spatial scales. Sites were grouped over a larger spatial scale in analyses ‘A’ and ‘B’ than in analysis ‘C’.

There was a high correlation between roosting and feeding Eastern Curlew numbers using all three methods of association ($r = 0.65–0.91$, $P < 0.005$ for all; Table 3.3, Figure 3.2). The two larger-area (around 5 km radius) groupings of continuous feeding habitat gave similar, high levels of association, with 83% and 76% of the variation in roost site numbers explained by variation in feeding site numbers for grouping methods ‘A’ and ‘B’ respectively (Figure 3.2, Table 3.3). When the sites were grouped at the finer scale of around 500 m, the association was weakened,
although it remained statistically significant (42% of variation explained; Figure 3.2, Table 3.3).

The average difference between roosting and feeding counts using rule ‘A’ for associating feeding grounds with roost sites (Table 3.3) was 31.0% (range: 11.8% to 64.6%); and the difference was 29.7% (range: 7.1% to 64.6%) using rule ‘B’; and 45.4% (range: 4.1% to 93.8%) using rule ‘C’. These percentage differences were calculated by subtracting the smallest count from the largest count and then dividing this figure by the largest count. Out of the nine groups defined using grouping method ‘B’, four showed greater average counts on feeding grounds compared with roost sites.

3.4 Discussion

3.4.1 Relationship between counts on roost sites and counts on feeding grounds

Counts of Eastern Curlews at high-tide roosts in Moreton Bay closely matched counts on low-tide feeding grounds. Summers and Kalejta-Summers (1996) found shorebird counts at low tide to be less than those at high tide at Langebaan Lagoon, South Africa, and suggested that failing to count high density feeding areas or over-estimating numbers on roosts were the most likely explanations. The high degree of correspondence between counts at roosts and on feeding grounds found in the present study suggests that it is unlikely that any feeding areas of high density were overlooked or that numbers on roost sites were over-estimated. This result is also encouraging in terms of the apparent consistency between different types of observations by volunteers, probably facilitated by the fact that Eastern Curlews are large and relatively conspicuous. Yates and Goss-Custard (1991) found the greatest
Table 3.3. The three methods used to associate feeding areas with roost sites (A, B, C, as in Table 3.1) and the resulting total number of groups compared (n), Pearson’s correlation coefficient (r), slope of the regression line, and statistical probability (P).

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Method of association</th>
<th>n</th>
<th>r</th>
<th>r²</th>
<th>slope</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>The intertidal feeding area was subdivided at breaks in continuous feeding habitat (a break constituted approximately 500 m of non-feeding habitat) and then associated with adjacent roost sites or site groupings.</td>
<td>8</td>
<td>0.91</td>
<td>0.83</td>
<td>0.78</td>
<td>0.001</td>
</tr>
<tr>
<td>B</td>
<td>Roost sites within a 5 km radius were grouped together and associated with grouped adjacent intertidal feeding sites, which were separated at the midpoint between the roost groupings.</td>
<td>9</td>
<td>0.87</td>
<td>0.76</td>
<td>0.84</td>
<td>0.002</td>
</tr>
<tr>
<td>C</td>
<td>Single roost sites or small-scale groups (roost sites within 500 m being grouped together) were associated with grouped immediately adjacent intertidal feeding sites; separated at the midpoint between the roost sites.</td>
<td>18</td>
<td>0.65</td>
<td>0.42</td>
<td>1.04</td>
<td>0.003</td>
</tr>
</tbody>
</table>

Figure 3.2. Eastern Curlew numbers on feeding flats versus roost sites in Moreton Bay during summer, using three different rules (A, B, C; see Table 3.3 for explanation) for associating groups of adjacent roost sites with groups of feeding flats. A and B are groups of around 5 km radius, C is around 500 m.
correspondence between high- and low-tide counts in Shelducks (*Tadorna tadorna*) and Eurasian Oystercatchers (*Haematopus ostralegus*), the two most conspicuous species of their study, compared with Ringed Plovers (*Charadrius hiaticula*), Grey Plovers (*Pluvialis squatarola*), Red Knots (*Calidris canutus*), Dunlins (*Calidris alpina*), Bar-tailed Godwits (*Limosa lapponica*), Eurasian Curlews (*Numenius arquata*), Redshanks (*Tringa totanus*), and Ruddy Turnstones (*Arenaria interpres*).

The comparison of high- and low-tide counts of ten shorebird species on the Wash in England revealed that in 45 comparisons: 13 ‘corresponded well’, differing by less than 25%; 20 ‘corresponded moderately well’, differing by between 25% and 50%; while the remaining 12 ‘corresponded poorly’, differing by at least 50% (Yates and Goss-Custard 1991). The average difference between high- and low-tide counts of Eurasian Curlews in Yates and Goss-Custard’s (1991) study was 43.2%. In an earlier study, Goss-Custard (1981) found that there was good correspondence between high- and low-tide counts of Eurasian Oystercatchers (*Haematopus ostralegus*), the two counts differing by an average of 6% on the River Exe in England and an average of 15% on the Wash. Similarly, on the Ortigueira estuary in Spain, Dominguez (1986) found an average difference between high- and low-tide counts of 19.2% in Eurasian Curlews (*Numenius arquata*) and 14% in Eurasian Oystercatchers. In the present study, the average difference between high- and low-tide counts was 29.7% when sites within a 5 km radius were grouped together. For Moreton Bay as a whole, the difference between average summer counts at high- and low-tide was 6.6%.

Goss-Custard (1981) proposed that the size of the intertidal area, the number of counters involved and the time lag between high- and low-tide counts can affect the correspondence between the counts, and as these factors increase so should the discrepancy between high- and low-tide counts. Dominguez (1986) reported greater
average shorebird counts at high-tide roosts than on low-tide feeding grounds in a
discrete estuary where both counts were made on the same days by one observer and
attributed the differences to an ‘area error’, where scarce species (<100 birds/site) are
consistently underestimated due to the observer overlooking individual birds isolated
from the main flocks. Yates and Goss-Custard (1991) also found deficits in low-tide
counts compared with high-tide counts, conversely, when numbers were high
(>10,000) and suggested that at high feeding densities birds dispersed to uncounted
areas.

Good correspondence between high- and low-tide shorebird counts is likely to
occur only on discrete estuaries (Dominguez 1986). Kirby et al. (1988) attributed
dissimilar counts between roosting and feeding areas to the high mobility of
populations within the system of estuaries studied, the exact bird distributions
depending on the tide height and prevailing weather conditions. Barrett and Barrett
(1984) and Yates and Goss-Custard (1991) also suggest that low similarities between
roosting and feeding shorebird numbers in some species were due to the high mobility
of those species.

The high correspondence between total roosting and feeding numbers found in
the present study indicates that a high proportion of Eastern Curlews roosting within
certain areas of Moreton Bay also feed there. A very good correspondence between
roost and feeding counts occurred when sites within about a 5 km radius were
grouped. When a scale of 500 m was used for the grouping, the resulting
correspondence was much looser, and there were some roosts of 100–400 Eastern
Curlews whose nearby flats contained half of those numbers (Figure 3.2). Some
roosts were clearly drawing birds from a wide area of feeding habitat. Also, the
average difference between roosting and feeding counts increased from 29.7% at the
scale of 5 km to 45.4% at the scale of 500 m. It is likely that some movement between different roost sites and feeding flats takes place within and/or between days, due to variation in prevailing physical and ecological conditions. For example, alternative feeding flats may be used if preferred areas are affected by strong winds or left unexposed during a neap tide, and alternative roost sites may be used if a preferred site is disturbed, or inundated during spring tides. However, it is also likely that Eastern Curlews are reluctant to change roost site or feeding flat if the alternative is too far away, as substantially more energy would need to be expended in travel. Within Moreton Bay, the distance over which the Eastern Curlew typically operate appears to be in the order of 5–10 km.

Counts on feeding flats are useful for different reasons than counts at roosts. At roost sites, shorebirds are generally tightly packed into a relatively small area. In comparison, on feeding grounds, they are usually loosely aggregated. Therefore, due to their spatial distribution, birds at roost sites may be harder to count accurately. In a study quantifying errors in large scale shorebird counts, estimated numbers were compared with known flock sizes and the resulting average counting error of birds at the roost (37%) was considerably higher than that for birds counted in flight (17%; Rappoldt et al. 1985). There may be a similarly reduced error associated with counting birds on feeding grounds, however a greater area must be surveyed to census a significant proportion of the total population. Therefore, roost counts may be preferable for population monitoring over years because less time and effort is involved to survey a significant proportion of the population. However, surveys of roost sites are of limited usefulness in identifying important intertidal feeding habitat (e.g. Barrett and Barrett 1984). Although roost counts do provide an estimate of the
numbers of birds that feed on nearby intertidal areas, low-tide counts are more appropriate for assessing the quality of these feeding areas.

3.4.2 Distribution of Eastern Curlews among intertidal feeding flats in Moreton Bay

Almost half of the total Eastern Curlew population of south east Queensland, estimated at approximately 5,000 (Driscoll 1997), were counted during each of the summer low-tide surveys. Low-tide surveys during winter revealed that the number of Eastern Curlews in Moreton Bay was approximately 25% of the number present in summer. This figure is not only supported by roost counts for Moreton Bay (Driscoll 1997), but is also similar to the ratio of winter to summer numbers obtained for Eastern Curlews elsewhere in Queensland (Houston and Mitchell 1997) and for other shorebirds that breed in the northern hemisphere (Thompson 1990a).

Individual sites on feeding grounds varied considerably in both size and the number of Eastern Curlews counted. Some intertidal areas supported considerably higher counts and densities of Eastern Curlews than others, and the fact that a substantial proportion of the sites with high counts also had high densities (and likewise for low counts) indicates that the variation in Eastern Curlew numbers across sites was not due only to the effect of flat size (Chapter 2). Where numbers of Eastern Curlews on low-tide feeding flats were high, the numbers at adjacent high-tide roosts were also large (Figure 3.2, Table 3.3). There are certain areas within Moreton Bay that are used more intensively than others; these key areas for Eastern Curlews are detailed in Chapter 2. Why these areas are important for Eastern Curlews cannot be inferred from the count data obtained in this study. However, both the substrate type and disturbance by humans are likely to be important determinants of the distribution of Eastern Curlews in Moreton Bay. The substrate types at the key Eastern Curlew feeding areas, sand or sandy-mud as opposed to mud or coral, may offer a greater
density and/or harvestability of prey (Chapter 2). The highest density Eastern Curlew feeding areas are also either relatively inaccessible to humans, or sufficiently large to provide some habitat well away from human activities (Chapter 2).
Chapter 4

Determinants of preferred intertidal feeding habitat for Eastern Curlews: a study at two spatial scales

4.1 Introduction

When in their coastal non-breeding habitats, shorebirds generally feed on intertidal flats at low tide, while at high tide they roost in nearby areas above the high water mark (Evans and Harris 1994, Dann 1999, Rogers 2003; Chapter 3). Their intertidal feeding techniques range from pecking at the substrate surface in response to visual stimuli to deep tactile probing of the sediment well below its surface (Schneider 1983, Pienkowski 1983, Zwarts 1985, Ntiamo-Baidu et al. 1998). Studies of the factors that influence shorebirds’ choice of feeding habitat have identified a variety of potentially important environmental attributes (Pienkowski 1978, Zwarts 1981, Ntiamo-Baidu et al. 1998). The most frequent determinants of habitat choice and local density in shorebirds appear to be: prey density (Goss-Custard et al. 1977a, Piersma et al. 1993b, Cabral et al. 1999); the properties of the substrate (Piersma 1986, Yates et al. 1993); proximity to roost sites (Rehfisch et al. 1996); and human disturbance (Lord et al. 1997, de Boer and Prins 2002, Smart and Gill 2003). However, there has been relatively little work on habitat use by shorebirds in the southern hemisphere. An understanding of habitat requirements will assist in predicting the impacts of environmental changes on shorebird numbers, and will also help to identify possible actions to manage or limit such changes in numbers.
Studies of local-scale habitat use within intertidal flats have frequently shown that feeding shorebirds use some substrates more often than others (Harrington 1982, Mouritsen and Jensen 1992, Kalejta and Hockey 1994, Riak et al. 2003). However, descriptions of the frequency of use cannot reveal whether any substrates are actively selected or avoided. Some studies have demonstrated active habitat selection, by showing that certain substrates are used more frequently than they occur (Grant 1984, Gerritse and van Heezik 1985, Kelsey and Hassall 1989). However, there has been little research into the strength of habitat selection at broader spatial scales, or the factors that influence it.

Studies at different spatial scales require different methods. At a broad spatial scale (i.e. regional), one method is to compare shorebird densities across many intertidal flats. Because shorebirds are very mobile, comparisons of the density of feeding birds among flats with differing environmental characteristics can provide a test of whether there is selection or avoidance of particular habitats (Kelsey and Hassall 1989, Nehls and Tiedemann 1993, Yates et al. 1993, Piersma et al. 1993b, Congdon and Catterall 1994, Thompson 1998). At a finer spatial scale (i.e. local), preferred feeding microhabitats within a tidal flat may be identified by comparing the relative frequencies at which the birds use different microhabitats (e.g., substrate types within a flat) with the relative areas occupied by these microhabitats (Evans and Harris 1994, Kalejta and Hockey 1994, Warnock and Takekawa 1995, Arthur et al. 1996).

This chapter investigates the habitat preferences of the Eastern Curlew (Numenius madagascariensis, hereafter “curlew”) in Moreton Bay, at both regional and local scales. Moreton Bay lies adjacent to Brisbane city, at the centre of a wider region which is undergoing a very high rate of human population increase. There is
some evidence that changing foreshore conditions are impacting on the local
distribution of shorebirds in the Bay (Thompson 1993b). Congdon and Catterall
(1994) showed that the density of curlews varied greatly among different intertidal
flats in Moreton Bay, and concluded that further study was needed to determine the
factors underlying habitat selection across spatial scales. Here I assess and compare a
wide range of environmental factors which have the potential to influence the bird’s
spatial patterns of habitat choice. These include properties of the substrate, the state
of the tidal cycle, the height of the tide, width and area of the flat, position within the
flat, proximity to roost sites, the level of human disturbance and the occurrence of
seagrass and mangroves.

4.2 Study site and methods

4.2.1 The Eastern Curlew in Moreton Bay

Moreton Bay extends approximately 132 km in a north–south direction along
the coast of subtropical eastern Australia, at 27–28° S and 153°–153°30’ E (Figure
4.1), covering around 300,000 ha (Blackman and Craven 1999). The bay reaches a
maximum width of 40 km and depth of 40 m, and contains a complex system of
intertidal flats totalling some 23,000 ha at low tide (Blackman and Craven 1999).
Salinity is highest on the eastern side of the Bay because the western side receives an
input of fresh water from coastal drainage systems (Young 1978). Substrate types
within the Bay are diverse and have been broadly categorised into sand, coral, sandy-
mud, and mud (Young 1978).
Figure 4.1. Map of the 32 broadscale sites in Moreton Bay.
Moreton Bay is also an important Ramsar site, and supports over 15% of the world’s Eastern Curlew population (estimated at 31,000) during the austral summer months (Watkins 1993, Thompson 1993a, Driscoll 1997). The curlews’ breeding grounds range from north east China to north east Russia (Gerasimov et al. 1997, Ueta and Antonov 2000, Driscoll and Ueta 2002, Ueta et al. 2002). Numbers in Moreton Bay during the breeding season (the austral winter) are approximately 25% of those occurring in the non-breeding season (the austral summer; Chapter 2).

4.2.2 Broadscale distribution

The curlew’s use of feeding grounds in Moreton Bay was assessed during a series of low-tide surveys of total curlew numbers within 160 intertidal flats. These flats spanned a north–south distance of approximately 115 km, from the northern end of Pumicestone Passage to the southern Moreton Bay islands. An individual flat typically comprised either a section of the intertidal zone from high water to low water adjacent to the shoreline, or a similar area which was separated from the shore by deeper channels of water (an outlying intertidal bank). The flats were chosen to achieve a wide ranging and extensive coverage of the Bay’s intertidal area and its varying characteristics (e.g. width of flat and type of substrate). In total, an area of approximately 9,500 ha or 41% of the intertidal habitat within Moreton Bay was surveyed.

Because shorebird habitat selection may vary temporally from day to day and season to season (Warnock and Takekawa 1995, Rompre and McNeil 1996, Thompson 1998), the surveys were repeated on 8 days, four in each of summer and winter. Summer counts took place on November 28–29, 1998 and January 30–31, 1999. Winter counts were on June 26–27, 1999 and July 24–25, 1999. For various reasons some flats could not be surveyed on the allocated count days. These flats
were surveyed within 7 days of the designated times. Data were collected by 60 volunteers who all had previous experience observing shorebirds. All counts were made with the aid of telescopes of at least 20× magnification. Curlew densities (number of birds per ha) were calculated for summer and winter by dividing the average of the four counts in each season by the flat area. The surveyed flats varied greatly in area (0.7–474 ha), and many of those on the Bay’s western side were small and arbitrarily delineated for convenience of data collection.

For analyses, 137 of the 160 individually-surveyed flats were amalgamated into 32 broadscale sites (Figure 4.1), having a more restricted range of flat area (64–544 ha, approximately 70% were 200–400 ha). The number of individually-surveyed flats contributing to each analysed site ranged from one to nine. Natural discontinuities of substrate type and geographical features (such as waterway entrances) contributed to decisions concerning site boundaries. The remaining 23 individually-surveyed flats were either too small (and not situated where they could be aggregated with other sites) or their area could not be calculated accurately (hence no curlew density estimate could be made), and these were excluded from analyses.

4.2.3 Broadscale habitat assessment

For each of the 32 broadscale sites within Moreton Bay, 11 environmental variables (Table 4.1) were measured as follows.

Area. A digital map of Moreton Bay (obtained from the Australian Hydrographic Office of the Royal Australian Navy) was set up as a base layer within a GIS (‘MapInfo’) and a combination of hard copy maps and GPS coordinates of site boundaries were used to digitise site areas on screen. The intertidal area was defined at its potential maximum, from highest water to zero datum.
Table 4.1. Environmental variables measured at each of 32 intertidal sites and their strength of correlation (Pearson’s $r$) with curlew density (*** $P < 0.001$, ** $P < 0.005$, * $P < 0.05$).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Units</th>
<th>Mean</th>
<th>Range</th>
<th>$r$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area</td>
<td>Site area from highest astronomical tide to zero datum.</td>
<td>ha</td>
<td>294.45</td>
<td>64–544</td>
<td>-0.01</td>
</tr>
<tr>
<td>Width</td>
<td>Average width of site from highest astronomical tide to zero datum.</td>
<td>m</td>
<td>648.70</td>
<td>129–1563</td>
<td>0.04</td>
</tr>
<tr>
<td>Seagrass</td>
<td>Seagrass cover derived from the BFND report (Dennison et al. 1998).</td>
<td>% cover</td>
<td>31.81</td>
<td>0–70</td>
<td>0.42*</td>
</tr>
<tr>
<td>Mangroves</td>
<td>Mangrove presence/absence derived from Dennison and Abal (1999).</td>
<td>proportion</td>
<td>0.54</td>
<td>0–1</td>
<td>0.54**</td>
</tr>
<tr>
<td>Droost</td>
<td>Average distance to the nearest roost site.</td>
<td>km</td>
<td>2.24</td>
<td>0.73–4.63</td>
<td>0.03</td>
</tr>
<tr>
<td>Durban</td>
<td>Average distance to the nearest urban development.</td>
<td>km</td>
<td>2.41</td>
<td>0.10–9.06</td>
<td>0.13</td>
</tr>
<tr>
<td>Humans</td>
<td>Degree of human disturbance.</td>
<td>proportion</td>
<td>0.11</td>
<td>0–0.67</td>
<td>-0.001</td>
</tr>
<tr>
<td>Wc clarity</td>
<td>Water clarity (related to secchi depth in meters) derived from Dennison and Abal (1999).</td>
<td>relative score</td>
<td>3.99</td>
<td>2.5–6.0</td>
<td>0.22</td>
</tr>
<tr>
<td>Pindex</td>
<td>Pollution index: sum of scores for total phosphorus and nitrogen (mg/L), chlorophyll a (μg/L), and delta 15N (ppt); derived from Dennison and Abal (1999).</td>
<td>relative score</td>
<td>8.94</td>
<td>5.0–15.8</td>
<td>-0.29</td>
</tr>
<tr>
<td>Resistance</td>
<td>Degree of substrate resistance.</td>
<td>proportion</td>
<td>0.52</td>
<td>0–1</td>
<td>-0.67***</td>
</tr>
<tr>
<td>Substrate</td>
<td>Broad substrate type (sand, mud, sandy-mud, coral) derived from Young (1978).</td>
<td>category</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Width. Using the GIS, five evenly spaced measurements were taken from each flat included in each site, and the average of all measurements then calculated. The intertidal flat width was defined at its potential maximum, from highest water to zero datum.

Seagrass. Dennison et al. (1998) mapped the percentage seagrass cover across Moreton Bay using six categories: 0; 1–20; 20–40; 40–60; 60–80; 80–100. Each of the 32 sites defined in the present study was divided into two to eight equal subareas, each approximately 800 m in length (following the natural contour of the coastline). Each component subarea was allocated the midpoint percentage seagrass cover (0, 10,
30, 50, 70, 90) from Dennison et al. (1998), and the average percent score across all subareas within a site was calculated.

**Mangroves.** From Dennison and Abal (1999), a score of one (present) or zero (absent) was given for each of the same component subareas as for seagrass. These scores were then averaged.

**Distance to nearest roost.** Using the same component subareas as for seagrass, distance was measured from the midpoint of each subarea to the nearest high-tide roost. Thirty roost sites used by curlews were identified (Chapter 3).

**Distance to nearest urban development.** As for distance to nearest roost, using the nearest extremity of an urban area. The map used was Queensland Department of Transport Boating Safety Chart Number One, ‘Moreton Bay – Southport to Caloundra’, third edition – revised December 1991, scale 1:100,000. Urban areas were used as marked on this map regardless of their size; the smallest (Kooringal on Moreton Island) consisted of approximately 120 houses.

**Human disturbance.** During each broadscale survey, counters recorded the presence or absence of humans on the intertidal flat. Thus, for each of the 160 flats in the broadscale survey, eight records of ‘yes’ or ‘no’ to human disturbance were obtained. For each flat I calculated the proportion of counts during which the birds were disturbed. For each of the 32 sites (groups of flats) I also calculated the proportion of the total area that each flat contributed, and the proportion of ‘yes’ to human disturbance at a flat was multiplied by the proportion of the area of that flat to the total site area. The adjusted ‘yes’ proportions were then summed to give an overall disturbance score for the site.
Chapter 4. Intertidal feeding habitat of curlews

_**Water clarity.**_ Dennison and Abal (1999) mapped six categories of secchi depth (measured in March 1998) in meters: 0–0.25; 0.25–0.5; 0.5–1.0; 1.0–1.7; 1.7–4.0; 4.0+. I assigned each a score from one to six respectively, and averaged them over the same component subareas as for seagrass.

_**Pollution index.**_ Scores for total phosphorus and nitrogen, phytoplankton biomass and sewage plumes were summed. All pollution measures were obtained from Dennison and Abal (1999) with the exception of sewage plumes, which was obtained directly from the Queensland Environmental Protection Agency, Ecosystem Health Monitoring Program. Each of the components had six categories (total phosphorus, mg/L: 0–0.02, 0.02–0.03, 0.03–0.1, 0.1–0.3, 0.3–1.0, and 1.0+; total nitrogen, mg/L: 0–0.07, 0.07–0.14, 0.14–0.3, 0.3–0.6, 0.6–1.0, and 1.0+; phytoplankton biomass, chlorophyll a μg/L: 0–0.5, 0.5–1.0, 1–2, 2–5, 5–10, and 10+; and sewage plumes, delta15N (ppt): 0–3, 3–4, 4–5, 5–7, 7–9, and 9+), and was scored from one to six respectively and then averaged over the same component subareas as for seagrass. Phytoplankton biomass data were collected in March 1998 and total phosphorus and nitrogen data were collected in October 1997 (Dennison and Abal 1999). Sewage plume data were collected in August 1998.

_**Substrate resistance.**_ In an associated study of curlew feeding ecology, I sampled intertidal sediment for fauna at 20 sites, using benthic coring. During this sampling, the presence of resistant (hard) material such as coral, rocks, shells, wood and other debris within the cored substrate was recorded. The proportion of randomly positioned core samples, out of 20 taken at each site, which had resistant material making up more than a quarter of their total volume, was calculated. These sampling sites were geographically scattered across the study region and had been chosen to encompass much of Moreton Bay’s natural variability in both substrate type and
curlew density. The 20 cored sites were within or immediately adjacent to 24 out of the 32 broadscale sites considered in the present study, and shared their mapped substrate types. This gave measures of substrate resistance for 24 sites. Of the remainder, four sites were specially sampled with benthic coring (as described) to allow resistance measures to be calculated. Based upon published substrate maps (Young 1978) or the author’s field experience, the other four sites were known to be predominantly coral. These sites were allocated scores of 1.0 and 0.85 (two of each) depending on the general prevalence of coral, relative to the two coral sites where benthic coring was performed (both had scored 1.0).

**Substrate type.** Young (1978) mapped substrate types of Moreton Bay’s intertidal areas, using categories (sand, coral, sandy-mud, and mud), and these categories were allocated to each of my sites.

### 4.2.4 Fine-scale habitat selection

Between November 16, 1999 and March 7, 2000 an in-depth study was made of 12 intertidal flats, chosen on the basis of accessibility and coverage of different habitat features (e.g. width of flat and type of substrate). Count data from the broadscale survey were used in selecting flats, to ensure that there was a reasonable chance of occurrence of curlews. Flats were also spaced throughout the north, south, east and west extremities of the Bay. Focal flats ranged in length from 500 to 1,500 m, in width from 200 to 1,000 m, and in area from 23 to 97 ha.

Each flat was visited either eight or 12 times (see below). During each visit, the behaviours of ten curlews (or all present if ten or fewer) were observed. The focal birds were chosen, out of all birds counted on the flat, using sets of random numbers specifically generated to reflect the number of curlews present. Each focal bird was
observed for 3 minutes, and the following information was spoken and recorded on audiotape.

1. The substrate used, recorded at the start of each minute (giving three point records): coral; sand; sandy-mud; mud; seagrass; seagrass pool; other pools; water (tidal/ocean water as opposed to a pool above low tide on the flat); and air (bird flying).

2. The bird’s distance (m) to the moving low water line at the start of each observation period.

3. The time each of the following activities commenced: standing; walking; running; resting; preening; flying. Transcription of the tape allowed measurement of the duration of each activity, in seconds.

A count of each focal flat, recording the total number of curlews, was made before and after each observation period. Flat area was measured and curlew density calculated in the same way as previously described for the boadscale survey.

The observations at six flats were repeated on 12 different days, six during neap and six during spring tides. The other six flats in the study were visited on 8 different days, four during neap and four during spring tides. The low-tide observation period, defined by preliminary observations of the daily tide cycle, was limited to 1.5 hours before (early low tide) and 1.5 hours after (late low tide) the time of dead low tide. Each flat received an equal number of visits during both the early and late low-tide periods (i.e. either four or six in each). The lower numbers of repeat visits at six flats was a consequence of the limited total availability of diurnal low-tide periods during the season. There were 120 different observation periods in total, giving a maximum possible number of focal birds of 1,200. In fact 970 focal bird
observations were obtained due to low curlew numbers at some flats. Of these, 950 were used in the present study due to 20 of the focal birds not being visible for the full 3 minutes observed. For analysis of curlew habitat preference in relation to distance to low water, 924 focal bird observations were used as the distance to the low-water line was not recorded in 26 cases. Of these 924 records, 628 birds were walking and 82 birds were resting or preening for at least 2.5 of the 3.0 minutes observed, and all the other birds \((n = 215)\) were engaged in a variety of activities. I have used the activity of ‘walking’ to equate with feeding in curlews. Of all activities recorded, ‘walking’ was the only one reliably associated with actively searching for prey.

To assess patterns of fine-scale habitat selection, focal observations were only used if the bird remained on a single substrate throughout the 3 minutes \((n = 732)\). For investigations of feeding preferences I used a subset of these records \((n = 474)\) in which the birds walked for at least 2.5 of the 3.0 minutes observed. For investigations of habitat preferences when resting or preening I only used the subset of records in which the birds were resting or preening for at least 2.5 of the 3.0 minutes observed \((n = 79)\).

4.2.5 Fine-scale assessment of substrate

The proportions of each substrate type (coral, sand, sandy-mud, mud, seagrass, seagrass pool, other pools and water) present at each of the 12 focal flats were estimated between November 9 and December 17, 2000, during spring low tides \((<0.56 \text{ m})\), 1.5 hours before and after dead low.

A series of transects was evenly spaced along the length of the flat and orientated perpendicular to the shoreline from high water to low water. The spacing varied from between 50 to 200 m apart depending upon the length of the flat. The
number of transects, varying from three to nine, was also determined by the length of the flat. Along each transect, sampling points were established every 30 or 50 m depending on the width of the flat (50 m in three broad sites and 30 m in the other nine). The number of sample points per transect varied from six to 20 and transect length varied from 180 m (6 points, 30 m apart) at the narrowest flat to 1,000 m (20 points, 50 m apart) at the broadest flat. The aim was to obtain between 50 and 100 substrate data points for each focal flat that were more or less evenly distributed across the entire flat. The achieved number of substrate data points per site ranged from 60 to 99. Across all sites, the total number of points was 895.

At each sampling point the substrate type and relative position on the flat were recorded. The substrate was scored in accordance with the categories used in the curlew feeding observations.

4.2.6 Data analyses

The dependent variable, curlew density, was calculated as the average number of birds in eight counts (four in both summer and winter) divided by the site area. Summer and winter counts were combined (rather than using only summer counts), in order to assess the curlew’s year-round utilisation of feeding habitat and to maximise the sample sizes on which the density estimates were based. Consistent across sites, winter numbers of curlews were approximately 25% of summer numbers (Chapter 2).

To produce an ordination showing the patterns of environmental similarity among 32 broadscale sites, principal components analysis (PCA) was performed using SAS statistical software (SAS Institute Inc. 1999). There were ten environmental variables: Area; Width; Seagrass; Mangroves; Droost; Durban; Humans; Wclarity; Pindex; and Resistance (Table 4.1). A correlation matrix was used in the PCA to standardise for the substantially different scales at which each variable was measured.
To assess the broadscale preferences of curlews, I used correlation and all-subsets multiple regression (Quinn and Keough 2002) of curlew density against the same ten environmental variables and 32 sites, using SAS (SAS Institute Inc. 1999). As the broadscale, substrate type was the only categorical variable, its effect on curlew density was analysed separately through an analysis of variance (ANOVA), using SPSS statistical software (SPSS Inc. 2003), with and without substrate resistance as a covariate.

For the finer-scale assessment, Pearson’s correlation coefficient ($r$) was used to explore the relationship between the proportional availability of the eight different substrate types within flats and the proportional use of those substrate types by feeding curlews. The sample size was the 60 combinations of focal flat and substrate type for which these proportions were available (omitting the cases where a given substrate was not present in either the feeding or the habitat measurements).

### 4.3 Results

#### 4.3.1 Broadscale habitat selection

The 32 sites varied from two to 47 birds/100 ha in the density of curlews (Table 4.2). The mean was 14.5. Most sites (75%) supported between five and 25 individuals/100 ha (Table 4.2). The sites also varied greatly in other environmental features (Table 4.1). In the principal components analysis (Figure 4.2A), sites with great distances to urban development and high water clarity grouped together: the Moreton and North Stradbroke Island areas (adjacent eastern Bay sites: MI1, MI2,
Table 4.2. The code and corresponding place name, the area (ha), the average summer (ASD) and winter (AWD) curlew density (birds/100 ha) and the overall average density (AvgDen = [ASD+AWD]/2), at all sites (*n* = 32) ranked by density.

<table>
<thead>
<tr>
<th>No. of Flats¹</th>
<th>Code</th>
<th>Place Name</th>
<th>Area</th>
<th>ASD</th>
<th>AWD</th>
<th>AvgDen</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>MI3</td>
<td>Moreton Island</td>
<td>218</td>
<td>71.89</td>
<td>22.05</td>
<td>46.97</td>
</tr>
<tr>
<td>5</td>
<td>PP1</td>
<td>Pumicestone Passage</td>
<td>414</td>
<td>46.31</td>
<td>19.59</td>
<td>32.95</td>
</tr>
<tr>
<td>3</td>
<td>HAY</td>
<td>Hays Inlet</td>
<td>164</td>
<td>42.34</td>
<td>16.81</td>
<td>29.58</td>
</tr>
<tr>
<td>9</td>
<td>SBI</td>
<td>Southern Bay Islands</td>
<td>259</td>
<td>49.02</td>
<td>4.50</td>
<td>26.76</td>
</tr>
<tr>
<td>4</td>
<td>NSI2</td>
<td>North Stradbroke Island</td>
<td>296</td>
<td>39.70</td>
<td>10.56</td>
<td>25.13</td>
</tr>
<tr>
<td>6</td>
<td>PP2</td>
<td>Pumicestone Passage</td>
<td>544</td>
<td>37.49</td>
<td>10.52</td>
<td>24.00</td>
</tr>
<tr>
<td>1</td>
<td>F12</td>
<td>Fisherman Islands</td>
<td>280</td>
<td>41.09</td>
<td>6.52</td>
<td>23.80</td>
</tr>
<tr>
<td>6</td>
<td>ORM</td>
<td>Ormiston</td>
<td>113</td>
<td>28.20</td>
<td>13.76</td>
<td>20.98</td>
</tr>
<tr>
<td>5</td>
<td>PP3</td>
<td>Pumicestone Passage</td>
<td>199</td>
<td>29.08</td>
<td>10.28</td>
<td>19.68</td>
</tr>
<tr>
<td>1</td>
<td>W1</td>
<td>Whyte Island</td>
<td>353</td>
<td>37.93</td>
<td>1.35</td>
<td>19.19</td>
</tr>
<tr>
<td>5</td>
<td>DB</td>
<td>Deception Bay</td>
<td>317</td>
<td>27.16</td>
<td>11.21</td>
<td>19.19</td>
</tr>
<tr>
<td>5</td>
<td>NSI1</td>
<td>North Stradbroke Island</td>
<td>221</td>
<td>31.69</td>
<td>6.00</td>
<td>18.84</td>
</tr>
<tr>
<td>9</td>
<td>LOTH</td>
<td>Lota and Thoreside</td>
<td>349</td>
<td>30.20</td>
<td>6.46</td>
<td>18.33</td>
</tr>
<tr>
<td>1</td>
<td>VP2</td>
<td>Victoria Point</td>
<td>117</td>
<td>22.44</td>
<td>12.61</td>
<td>17.53</td>
</tr>
<tr>
<td>2</td>
<td>FI1</td>
<td>Fisherman Islands</td>
<td>403</td>
<td>28.79</td>
<td>5.03</td>
<td>16.91</td>
</tr>
<tr>
<td>1</td>
<td>MI2</td>
<td>Moreton Island</td>
<td>469</td>
<td>17.50</td>
<td>8.53</td>
<td>13.01</td>
</tr>
<tr>
<td>9</td>
<td>VP1</td>
<td>Victoria Point</td>
<td>270</td>
<td>19.25</td>
<td>5.92</td>
<td>12.58</td>
</tr>
<tr>
<td>4</td>
<td>BEA2</td>
<td>Beachmere</td>
<td>432</td>
<td>15.98</td>
<td>3.18</td>
<td>9.58</td>
</tr>
<tr>
<td>2</td>
<td>BEA1</td>
<td>Beachmere</td>
<td>331</td>
<td>13.35</td>
<td>1.28</td>
<td>7.32</td>
</tr>
<tr>
<td>2</td>
<td>WP2</td>
<td>Wellington Point</td>
<td>381</td>
<td>12.15</td>
<td>2.36</td>
<td>7.26</td>
</tr>
<tr>
<td>2</td>
<td>MI1</td>
<td>Moreton Island</td>
<td>542</td>
<td>10.42</td>
<td>2.49</td>
<td>6.46</td>
</tr>
<tr>
<td>3</td>
<td>CLE2</td>
<td>Cleveland</td>
<td>348</td>
<td>10.91</td>
<td>1.65</td>
<td>6.28</td>
</tr>
<tr>
<td>4</td>
<td>PI2</td>
<td>Peel Island</td>
<td>410</td>
<td>11.57</td>
<td>0.49</td>
<td>6.03</td>
</tr>
<tr>
<td>6</td>
<td>WYN</td>
<td>Wynnum</td>
<td>195</td>
<td>10.89</td>
<td>1.02</td>
<td>5.96</td>
</tr>
<tr>
<td>6</td>
<td>RB</td>
<td>Redland Bay</td>
<td>64</td>
<td>10.51</td>
<td>0.00</td>
<td>5.25</td>
</tr>
<tr>
<td>3</td>
<td>WP1</td>
<td>Wellington Point</td>
<td>191</td>
<td>8.11</td>
<td>0.78</td>
<td>4.45</td>
</tr>
<tr>
<td>5</td>
<td>PI1</td>
<td>Peel Island</td>
<td>226</td>
<td>7.86</td>
<td>0.22</td>
<td>4.04</td>
</tr>
<tr>
<td>3</td>
<td>BB1</td>
<td>Bramble Bay</td>
<td>292</td>
<td>4.03</td>
<td>3.85</td>
<td>3.94</td>
</tr>
<tr>
<td>7</td>
<td>BALP</td>
<td>Brisbane Airport and Luggage Point</td>
<td>421</td>
<td>6.00</td>
<td>0.59</td>
<td>3.29</td>
</tr>
<tr>
<td>5</td>
<td>BB2</td>
<td>Bramble Bay</td>
<td>268</td>
<td>5.88</td>
<td>0.37</td>
<td>3.12</td>
</tr>
<tr>
<td>4</td>
<td>CLE1</td>
<td>Cleveland</td>
<td>223</td>
<td>4.03</td>
<td>0.22</td>
<td>2.13</td>
</tr>
<tr>
<td>8</td>
<td>RED</td>
<td>Redcliffe</td>
<td>114</td>
<td>3.71</td>
<td>0.22</td>
<td>1.97</td>
</tr>
</tbody>
</table>

¹Number of individual flats grouped for each site.
Figure 4.2. Principal components analysis of 32 sites on the basis of site environmental characteristics. (A) See codes in Table 4.2. (B) Size of points shows curlew density (large points >19.0 birds/100 ha, n = 11; medium 6.5–19.0, n = 10; small <6.5, n = 11). Environmental characteristics (see Table 4.1) with greatest contribution to site values on each axis are also shown (position indicates + or − association).
Sites with both broad intertidal flats and high levels of human disturbance also grouped together: the Fisherman Islands and White Island areas (adjacent sites immediately south of the Brisbane River: FI1, FI2 and WI). The human disturbance on these broad flats was due mostly to bait-diggers (commercial and recreational fishers digging for the bloodworm, *Marphysa sanguinea*, and crustacean, *Trypaea australis*). Although there was no strong relationship between the grouping of sites based on their environmental attributes and curlew density, there was a greater proportion of low density sites on the left hand side of the plot where pollution was high, the substrate was more resistant, water clarity was low, and there were shorter distances to urban development (Figure 4.2B).

Substrate resistance showed a strong negative correlation with curlew density ($r = -0.67$, $P < 0.001$; Table 4.1, Figure 4.3). The mean curlew density at the 11 flats with zero resistance was 22 birds/100 ha, whereas at the 12 flats with maximum resistance it was seven birds/100 ha. Substrate resistance alone explained 45% of the variation in curlew density among the 32 sites (Table 4.3). In an all-subsets multiple regression comparing curlew density with the ten environmental variables, substrate resistance contributed the most to the explained variance in curlew density, was present in all of the better models, and models without it were consistently less efficient predictors (most efficient models are those with relatively low BIC values; Table 4.3). Mangroves and width also contributed to the best model (lowest BIC). Of ten possible pair-wise correlations among the five variables that were the most important predictors of curlew density (resistance, mangroves, width, seagrass, pindex; Table 4.3), four were statistically significant. Resistance was significantly correlated with mangroves ($r = -0.39$, $P < 0.05$), seagrass ($r = -0.45$, $P < 0.01$) and pindex ($r = 0.38$, $P < 0.05$), and seagrass was correlated with pindex ($r = -0.56$, $P <$
Width was not correlated with either mangroves \((r = 0.32, P = 0.08)\) or resistance \((r = -0.25, P = 0.17)\).

**Figure 4.3.** Substrate resistance versus curlew density (birds/100 ha) across 32 sites (see also Table 4.1). Three pairs of points coincide at maximum resistance (1.0) and low density (1.97 and 2.13, 3.12 and 3.29, 7.26 and 7.32).

Multiple regression analyses run on summer and winter curlew densities separately gave very similar results to the analyses using the average densities across seasons. To test whether the extent of avoidance of resistant flats differed between summer and winter I conducted a repeated measures two-factor ANOVA with the main effects resistance and season (summer, winter), and sites as subjects. Sites were grouped into resistant (range 0.85–1.00, \(n = 15\)) and non-resistant (range 0.00–0.15, \(n = 15\)), two sites with medium level resistance were excluded. There were significant effects of resistance \((F = 34.5, \text{df} = 1, 28, P < 0.0001)\) and season \((F = 161.3, \text{df} = 1,\)
Chapter 4. Intertidal feeding habitat of curlews

28, \( P < 0.0001 \) but no interaction between resistance and season \( (F = 0.5, \text{df} = 1, 28, \ P = 0.49) \).

| Table 4.3. Selected results of an all-subsets multiple regression comparing curlew density (dependant variable) with ten environmental characteristics (Table 4.2) across 32 intertidal sites. The best models for 1–5 predictors with and without resistance are presented as well as the full model. The table also shows the Adjusted \( r^2 \) (Adj \( r^2 \)), Mallow's Cp (\( C_p \)), Akaike Information Criterion (AIC) and Schwarz Bayesian Information Criterion (BIC) for each model. |

<table>
<thead>
<tr>
<th>No. of predictors</th>
<th>Model</th>
<th>( r^2 )</th>
<th>Adj ( r^2 )</th>
<th>( C_p )</th>
<th>AIC</th>
<th>BIC</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Models with resistance:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Resistance</td>
<td>0.45</td>
<td>0.44</td>
<td>4.08</td>
<td>135.90</td>
<td>137.89</td>
</tr>
<tr>
<td>2</td>
<td>Resistance + Mangroves</td>
<td>0.54</td>
<td>0.51</td>
<td>0.72</td>
<td>132.04</td>
<td>135.15</td>
</tr>
<tr>
<td>3</td>
<td>Resistance + Mangroves + Width</td>
<td>0.59</td>
<td>0.55</td>
<td>-0.10</td>
<td>130.48</td>
<td>134.96</td>
</tr>
<tr>
<td>4</td>
<td>Resistance + Mangroves + Seagrass + Width</td>
<td>0.61</td>
<td>0.55</td>
<td>0.94</td>
<td>131.16</td>
<td>136.80</td>
</tr>
<tr>
<td>5</td>
<td>Resistance + Mangroves + Pindex + Durban + Width</td>
<td>0.62</td>
<td>0.55</td>
<td>2.09</td>
<td>131.96</td>
<td>138.94</td>
</tr>
<tr>
<td>10</td>
<td>Resistance + Mangroves + Seagrass + Pindex + Wclarity + Durban + Width + Droost + Area + Humans</td>
<td>0.64</td>
<td>0.47</td>
<td>11.00</td>
<td>140.34</td>
<td>153.31</td>
</tr>
<tr>
<td><strong>Models without resistance:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Mangroves</td>
<td>0.29</td>
<td>0.27</td>
<td>13.69</td>
<td>144.28</td>
<td>145.24</td>
</tr>
<tr>
<td>2</td>
<td>Mangroves + Pindex</td>
<td>0.39</td>
<td>0.35</td>
<td>9.63</td>
<td>141.25</td>
<td>142.62</td>
</tr>
<tr>
<td>3</td>
<td>Mangroves + Seagrass + Width</td>
<td>0.42</td>
<td>0.36</td>
<td>10.16</td>
<td>141.91</td>
<td>143.39</td>
</tr>
<tr>
<td>4</td>
<td>Mangroves + Seagrass + Pindex + Width</td>
<td>0.44</td>
<td>0.36</td>
<td>10.71</td>
<td>142.52</td>
<td>144.30</td>
</tr>
<tr>
<td>5</td>
<td>Mangroves + Seagrass + Pindex + Wclarity + Droost</td>
<td>0.46</td>
<td>0.36</td>
<td>11.53</td>
<td>143.35</td>
<td>145.52</td>
</tr>
</tbody>
</table>

Curlew density varied significantly among substrate types, being greatest on sand and least on coral (ANOVA \( F = 3.1, \text{df} = 3, 28, \ P = 0.043 \); Figure 4.4A). However, the ultimate predictor was the resistance of the substrate, as sand was significantly less resistant than coral and sandy-mud (ANOVA \( F = 5.4, \text{df} = 3, 28, \ P = 0.005 \); Figure 4.4B). When resistance was used as a covariate in the substrate analysis, the ANOVA \( P \) value was not significant (ANOVA \( F = 6.6, \text{df} = 3, 27, \ P = \))
0.551). Therefore the apparent substrate effect was due to the variation in the resistance of the substrate. These results were not caused by spatial autocorrelation patterns, since the high density (and high resistant) sites were spread throughout the Moreton Bay study area (Figure 4.1, Table 4.2).

Figure 4.4. Effect of substrate type on (A) curlew density (birds/100 ha) and (B) substrate resistance (bars show means and standard errors; sample sizes from left to right are 10, 3, 12 and 7). Means with the same letter are not significantly different (LSD tests).
4.3.2 Fine-scale habitat selection

Most (74%) of the variation in use of different substrates by feeding curlews was explained by the availability of those substrates ($r = 0.86$, $P < 0.001$, $n = 60$ site/substrate combinations; Figure 4.5A). However, the curlews also showed a preference for feeding on sand (Table 4.4). While curlews were resting or preening, only 23% of the variation in their use of different substrates was explained by the availability of those substrates ($r = 0.48$, $P < 0.001$, $n = 60$ site/substrate combinations; Figure 4.5B), and seagrasses were avoided (Table 4.4).

Table 4.4. The mean proportion of random points where each substrate type occurred (across different flats, SE in parentheses), and the mean proportion of curlew observations on each substrate, separately for feeding and resting/preening (see also Figure 4.5). $P(t)$ shows the results of paired $t$-tests, comparing curlew proportions with random occurrences.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>$n^{(1)}$</th>
<th>Random presence$^{(2)}$</th>
<th>Curlew feeding$^{(3)}$</th>
<th>$P(t)$ feeding</th>
<th>Curlew resting/preening$^{(4)}$</th>
<th>$P(t)$ rest/preen</th>
</tr>
</thead>
<tbody>
<tr>
<td>coral</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>sand</td>
<td>5</td>
<td>0.45 (0.08)</td>
<td>0.75 (0.07)</td>
<td>&lt;0.00001</td>
<td>0.56 (0.15)</td>
<td>0.493</td>
</tr>
<tr>
<td>sandy-mud</td>
<td>6</td>
<td>0.21 (0.10)</td>
<td>0.27 (0.14)</td>
<td>0.191</td>
<td>0.17 (0.11)</td>
<td>0.058</td>
</tr>
<tr>
<td>mud</td>
<td>7</td>
<td>0.21 (0.08)</td>
<td>0.22 (0.09)</td>
<td>0.603</td>
<td>0.24 (0.10)</td>
<td>0.804</td>
</tr>
<tr>
<td>seagrass</td>
<td>10</td>
<td>0.22 (0.06)</td>
<td>0.19 (0.06)</td>
<td>0.470</td>
<td>0.12 (0.05)</td>
<td>0.004</td>
</tr>
<tr>
<td>seagrass pool</td>
<td>10</td>
<td>0.25 (0.07)</td>
<td>0.18 (0.08)</td>
<td>0.116</td>
<td>0.06 (0.02)</td>
<td>0.057</td>
</tr>
<tr>
<td>pools</td>
<td>10</td>
<td>0.12 (0.03)</td>
<td>0.05 (0.02)</td>
<td>0.106</td>
<td>0.26 (0.10)</td>
<td>0.100</td>
</tr>
<tr>
<td>water</td>
<td>11</td>
<td>0.10 (0.02)</td>
<td>0.07 (0.04)</td>
<td>0.508</td>
<td>0.07 (0.04)</td>
<td>0.483</td>
</tr>
</tbody>
</table>

$^{(1)}$Number of flats where either substrate frequency or curlew feeding >0.

$^{(2)}$Proportion of random points, at a site, at which the substrate occurred.

$^{(3)}$Proportion of records, at a site, during which feeding curlews used the substrate.

$^{(4)}$Proportion of records, at a site, during which resting/preening curlews used the substrate.
Figure 4.5. The proportion of records where curlews used a given substrate versus the proportion of a site’s area at which the substrate occurs, for 60 site/substrate combinations (COR = coral, SAN = sand, SMU = sandy-mud, MUD = mud, SGR = seagrass, SGP = seagrass pool, PLS = pools, WTR = water); (A) while feeding and (B) while resting or preening. The line depicts $y = x$. 

Chapter 4. Intertidal feeding habitat of curlews
Chapter 4. Intertidal feeding habitat of curlews

Most curlews fed at between zero and 50 m from the low-water line and numbers steadily declined as the distance to low water increased (Figure 4.6). Within zero and 50 m from low water, the majority of curlews fed at 0–10 m (Figure 4.6). The intensity of use of low-tide feeding areas by curlews did not differ between neap and spring tidal types (paired \( t \)-test of densities across 12 focal flats \( t = 0.15, P = 0.88 \)) or early and late tidal states (\( t = 1.08, P = 0.30 \)).

Figure 4.6. The numbers of curlews in relation to the position of the low water line; between -200 and 500 m (\( n = 924 \)) and between -10 and 60 m (\( n = 472 \)). The focal birds’ activities are also shown.
4.4 Discussion

4.4.1 Broadscale habitat selection

Substrate resistance was the best predictor of curlew density at the regional scale. Sites with the least resistant substrates had curlew densities three times those with the most resistant substrates. A possible reason is that more resistant substrates might contain a lower prey supply. Solid structures such as rocks and dense shell grit within the sediment may reduce the numbers of infaunal prey items present per unit of substrate volume. However the measurement of prey density, and its relationship with substrate resistance, was beyond the scope of this chapter. Several studies in other regions have concluded that the supply of prey strongly influences shorebird communities within particular intertidal feeding areas (Grant 1984, Gerritsen and van Heezik 1985, Kelsey and Hassall 1989, Zwarts and Wanink 1993, Piersma et al. 1993a, b, Backwell et al. 1998).

Curlews may also prefer less resistant substrates because they present a lower risk of bill damage during foraging. Curlews have extremely long decurved bills (around 15 cm in males and 18 cm in females; Barter 1990, Rogers 1995a), which allow them to probe deeply and catch crabs, ghost shrimps and worms (Piersma 1986). In the intertidal feeding grounds, crustaceans are a frequent prey item (Piersma 1986, Zharkov and Skilleter 2003). To capture large, deep-burrowing crustaceans, a curlew may push its whole head into the substrate (Piersma 1986), reaching a depth of over 20 cm (Barter 1990, Rogers 1995a). The presence of rocks and other obstructions within the sediment can reduce prey capture rates by preventing curlews inserting their bills, and also cause bill damage if they do attempt
it (Urfi et al. 1996). At least one curlew with evidence of a previously damaged bill has been recorded in Moreton Bay (personal observation 1998).

The bills of some shorebirds contain pressure-sensitive receptors which detect solid objects embedded in the wet substrate (Piersma et al. 1998). Quammen (1982) found that sand interferes with the feeding of small shorebirds in mud substrates because the sand grains were similar in diameter to their annelid prey. Rocks or other inanimate objects buried within the sediment could likewise confuse curlews as they probe for their (larger) prey items.

My results also indicate that any apparent preference of curlews for broadscale substrate types (sand, mud, sandy-mud or coral) is an indirect consequence of variation in the resistance of these substrates. Sand was less resistant than mud, sandy-mud or coral. It might be expected that mud and sandy-mud would be less resistant than sand. However, in Moreton Bay, substrates consisting of mud and sandy-mud frequently had layers with higher proportions of resistant material such as rocks, coral or shells, located less than 40 cm below the surface. For example, a site at Cleveland (CLE1) had a maximum of approximately 10 cm of mud, under which was coral. At a site adjacent to the Brisbane Airport (BALP) the sandy-mud substrate generally had a high proportion of shell grit, which also formed a harder, compacted layer at a depth of about 15 cm. There is a need to look below the substrate surface to assess the suitability of feeding habitat for curlews.

Many of the other environmental variables measured in the present study were poor predictors of curlew density. These included flat area, seagrass abundance, distance to roost sites and urban development, human disturbance, water clarity and pollution indices. Congdon and Catterall (1994) suggested that curlews in Moreton Bay prefer broader tidal flats, in part because these flats showed highest local curlew
densities near the water’s edge. However, interpreting the role of flat width is fraught with complexity. Some of the broader flats which contained many curlews in their study correspond with flats shown here to have the least resistant substrates, so resistance may also have been an important causal factor. In the present study, I measured average density across the whole flat, and simple correlation analyses indicated that flats of larger area contained most curlews ($r = 0.48, n = 32, P < 0.005$), but when densities rather than total counts were used the relationship disappeared ($r = 0.01, n = 32, P > 0.5$). However, flat width (but not area) did emerge as a predictor of increasing curlew density in the best multiple regression model. Even if flat width has little influence on average across-flat density, feeding curlews should reach highest local densities within broad flats, because they tend to concentrate in a more-or-less linear band near the water’s edge.

4.4.2 Fine-scale habitat selection

Some intertidal flats contained many feeding curlews at all seasons and tidal states, and individual birds probably show a high degree of site fidelity (Congdon and Catterall 1994, Zharikov and Skilleter 2004a; Chapters 2 and 3). Within each flat, feeding curlews used most substrates in roughly the same proportions as they occurred. Baker (1979) suggested that an increase in bill length increases feeding versatility in shorebirds, and the range of habitats that can be used. Consistent with this, both the present study and previous work have showed that curlews are versatile foragers that use a wide variety of habitats (Zwarts and Esselink 1989, Congdon and Catterall 1994, Ferns and Siman 1994, Thompson 1998).

However, the curlews also showed a fine-scale preference for feeding on sand. It is clear that this preference was associated with the needs of foraging birds, because it did not occur in birds which were resting or preening. Substrate resistance probably
also contributes to this fine-scale feeding preference (Grant 1984, Gerritsen and van Heezik 1985, Kelsey and Hassall 1989). While seagrass frequently occurred on sandy substrates, it was not a preferred feeding substrate (and tended to be avoided). Bare substrates would be less resistant than substrates of the same sediment composition which are covered in seagrass, and many shorebird species are known to avoid densely-vegetated substrates (Cabral et al. 1999, Raffaelli et al. 1999).

Curlews preferred to feed close to the low-water line, but not in the water itself. Prey may be both more abundant close to the surface in this zone, and also more accessible, because the wet substrate is likely to be less resistant. Several studies of curlews (N. madagascariensis and N. arquata) and Whimbrels (N. phaeopus) have reported a preference for feeding on wet substrates (Piersma 1986, Zwarts and Esselink 1989, Riak et al. 2003), especially at night, when tactile foraging is possibly their only option (Rohweder and Baverstock 1996). Other small to medium shorebirds also exhibit strong preferences for the wettest areas of intertidal flats (Burger et al. 1977), and this may be correlated with higher feeding rates in these areas (Milsom et al. 2002).

4.4.3 Determinants and management of feeding habitat

In general terms, the availability of invertebrate prey to shorebirds is largely dependant on the physical properties of the substrate (Myers et al. 1980, Quammen 1982, Esselink and Zwarts 1989, Kelsey and Hassall 1989, Mouritsen and Jensen 1992). Substrate resistance has been identified as an important proximal factor determining the feeding distributions of many small, short-billed, shorebird species worldwide (Kelsey and Hassall 1989, Mouritsen and Jensen 1992, Mouritsen 1994). In this context, it is not surprising that habitat selection by the curlew, the largest and
longest-billed shorebird in the world, is also strongly influenced by substrate resistance.

The curlew is a conspicuous species on intertidal flats of eastern Australia, but has declined in numbers over recent decades (Close and Newman 1984, Reid and Park 2003), and is listed as a species of conservation concern (Garnett 1992, Watkins 1993). While the reasons for this decline are not clear, it would be prudent to avoid human impacts which degrade or destroy the curlews’ preferred feeding habitats. Intertidal flats of eastern Australia are important to curlews because they provide food resources which support adult birds outside of the breeding season, as well as year-round feeding grounds for immatures (Wilson 2000; Chapter 2). My results suggest that substrate resistance is the best surrogate factor for identifying the most important areas. Environmental changes which lead to increased substrate resistance (such as the development of intertidal oyster farms) would be expected to cause local decreases in curlew density. However, further research is required to clarify the relationship between substrate resistance and the supply and availability of prey.
Chapter 5

Prey versus substrate as determinants of habitat choice in feeding Eastern Curlews

5.1 Introduction

Migratory shorebirds generally utilise very different habitats, great distances apart, during breeding and non-breeding seasons (Hale 1980, Lane 1987, Piersma 1997). On the non-breeding grounds their primary concern is fuelling up in recovery from, and preparation for, long distance migration (Dann 1987, Piersma 1997, Battley et al. 2003, Kvist and Lindstrom 2003, Battley et al. 2004). Migratory shorebirds have a relatively high metabolic rate and the largest daily food requirement relative to body weight of any marine predator (Schneider 1983).

It is widely suggested that shorebirds should choose to feed in places where they can get the most food in the shortest time (Goss-Custard 1970, Hale 1980, Quammen 1982, Dann 1987, Colwell and Landrum 1993, Barbosa 1996, Rippe and Dierschke 1997, Van Gils et al. 2005b). A number of studies have reported that the distribution of feeding shorebirds is directly correlated with the density of their main prey, and this relationship occurs spatially at both large scales (between-flat: Goss-Custard 1970, et al. 1977a, Bryant 1979, Kalejta and Hockey 1994, Mercier and McNeil 1994) and fine scales (within-flat: Colwell and Landrum 1993, Meire 1996, Ribeiro et al. 2004). However, the availability of prey may be more important than prey density, particularly for substrate-probing shorebirds that locate and capture prey from beneath the substrate surface using tactile methods (Quammen 1982, Grant
Chapter 5. Determinants of habitat choice in curlews

1984, Gerritsen and van Heezik 1985, Kelsey and Hassall 1989, Mouritsen and Jensen 1992, Danufsky and Colwell 2003). The availability of prey to tactile, probing shorebirds depends on how close the prey are to the substrate surface, which may vary with prey behaviour (Zwarts and Esselink 1989, Piersma et al. 1993b), and the penetrability of the substrate (Myers et al. 1980, Grant 1984, Gerritsen and van Heezik 1985, Kelsey and Hassall 1989, Mouritsen and Jensen 1992). The less resistant the substrate, the deeper the birds’ bill can penetrate in search of prey (Myers et al. 1980, Mouritsen and Jensen 1992), and the lower the foraging costs (Myers et al. 1980, Grant 1984, Gerritsen and van Heezik 1985, Kelsey and Hassall 1989, Mouritsen and Jensen 1992).

Substrate penetrability has been identified as a proximal factor influencing the feeding distributions of small, short-billed, probing shorebird species, at a within-flat scale (Grant 1984, Kelsey and Hassall 1989, Mouritsen and Jensen 1992, Mouritsen 1994). The choice of feeding area for large, long-billed shorebirds, which may depend on obtaining prey from deep within the sediment, could be expected to be even more strongly affected by substrate penetrability. However, this has not been previously investigated.

It has been suggested that prey density is likely to be an important factor in shorebird habitat selection at a large (between-flat) spatial scale (Colwell and Landrum 1993, Kalejta and Hockey 1994), whereas properties of the substrate may be more important at a fine (within an intertidal flat) spatial scale (Grant 1984). I found substrate resistance to be a good predictor of Eastern Curlew distribution at a between-flat scale in Moreton Bay, Australia, whereas distance to the nearest roost, level of human disturbance and intertidal area and width were relatively poor predictors (Chapter 4). However, prey density was not measured. The present study
tests whether the between-flat feeding distribution of a large, long-billed shorebird, the Eastern Curlew *Numenius madagascariensis*, is explained better by prey density or by substrate resistance.

### 5.2 Study site and methods

#### 5.2.1 The Eastern Curlew in Moreton Bay

Moreton Bay extends approximately 132 km in a north–south direction along the coast of subtropical eastern Australia, at 27°–28° S and 153°–153°30' E (Figure 5.1), covering around 300,000 ha (Blackman and Craven 1999). The bay reaches a maximum width of 40 km and contains a complex system of intertidal flats totalling some 23,000 ha at low tide (Blackman and Craven 1999). Substrate types within the Bay are diverse and have been broadly categorised into sand, coral, sandy-mud, and mud (Young 1978).

Moreton Bay supports around 5,000 of the global population of 31,000 Eastern Curlews (hereafter ‘curlews’) during the austral summer months (Watkins 1993, Thompson 1993a, Driscoll 1997; Chapter 2). Numbers in Moreton Bay during the breeding season (the austral winter) are approximately 25% of those occurring in the non-breeding season (the austral summer; Chapter 2). Curlews are the largest migratory shorebird in the world. An extremely long, decurved bill (around 15 cm in males and 18 cm in females: Barter 1990, Rogers 1995a) allows curlews to probe deeply and catch crabs, ghost shrimps and worms (Piersma 1986). In their intertidal feeding grounds, crustaceans are a frequent prey item (Piersma 1986, Zharikov and Skilleter 2003). To capture large, deep-burrowing crustaceans, a curlew may push its
whole head into the substrate (Piersma 1986), reaching a depth of over 20 cm (Barter 1990, Rogers 1995a).

5.2.2 Curlew density

The curlews’ broadscale use of feeding grounds in Moreton Bay was assessed through a series of low-tide surveys covering a total of approximately 9,500 ha or 41% of the intertidal habitat within Moreton Bay during the austral summer of 1998–1999. The results, and detailed description of the survey and habitat assessment methods are reported in Chapters 2, 3 and 4. Ancillary curlew density estimates were also made, as part of the feeding observations and benthic fauna assessments, as noted below.

5.2.3 Curlew feeding observations

To identify the curlews’ prey, between November 16, 1999 and March 7, 2000 a study of curlew feeding behaviour was made at 12 intertidal flats (sites), chosen on the basis of accessibility and coverage of different habitat features (e.g. width of flat and type of substrate). Count data from the broadscale assessment of low-tide feeding grounds (Chapter 2) were used to select flats in which the density of curlews ranged from six to 135 birds/100 ha. Flats with very low curlew density were not used, as the aim was to acquire feeding data. Flats were also spaced throughout the Bay (Figure 5.1). Focal flats ranged in length from 500 to 1,500 m, in width from 200 to 1,000 m, and in area from 23 to 97 ha.

Each flat was visited either eight or 12 times (see below). During each visit, the behaviours of ten curlews (or all present if less than ten) were sequentially observed. The focal birds were randomly chosen, using a prior count and a random
number table. During a 3-minute observation, all feeding attempts were recorded, together with:

1. The substrate utilised, recorded at the start of each minute (giving three point records), within nine categories: coral; mud; sandy-mud; sand; seagrass; seagrass pool; other pools; water (tidal or ocean water as opposed to a pool above low tide on the flat); and air (bird flying).

2. The size and nature of any prey item captured. Identification of prey type was only possible for larger items, or if the feeding bird was sufficiently close to the observer. Categories of prey type were: Gastropoda, Polychaeta; Caridea; Thalassinidea; Brachyura; Mictyridae; fish; unidentified; and, small and unseen. Size categories for all prey types except polychaetes were estimated in relation to the depth of the curlews’ bill (i.e. 1, 2, 3, 4 and 5 depth/s); polychaetes were sized in relation to the length of the bill (1/4, 1/3, 1/2 and 1 length). Bill depth (8.57 mm), obtained from nine Queensland Museum specimens, was calculated as the average for male \( (n = 3) \) and female \( (n = 6) \) combined, taking three measures from each bill (near gape, middle, and tip; so as to obtain an average bill width over its entire length). Bill length (167.65 mm), obtained from Barter (1990) and Rogers (1995a), was also calculated as the average for male and female combined \( (n = 469) \).

A count of the total number of curlews on each focal flat was made before and after each observation period. Flat area was measured as described in Chapter 4 and curlew density was calculated by dividing the average of the two counts from each observation period by the flat area.
**Figure 5.1.** Sites in Moreton Bay used for observations of curlew feeding and for substrate coring to sample their prey (sites marked with ‘*’ or ‘†’ were only used for coring or feeding observations respectively). Symbols represent: □ low curlew density (<7 birds/100 ha); ● high curlew density (>12 birds/100 ha).
Focal birds were observed through 20–60× zoom telescopes, by a single observer at each site, from a vantage point 50–1,000 m from the bird, and level with, or slightly above it. Green- or sand-coloured clothing was worn to blend in with the background, and focal observations began after the observer had been in position and relatively still for at least 10 minutes. The observations at six flats were repeated on 12 different days, six during neap and six during spring tides. The other six flats in the study were visited on 8 different days, four during neap and four during spring tides. The low-tide observation period was limited to 1.5 hours before (early low tide) and 1.5 hours after (late low tide) the time of dead low tide. Each flat received an equal number of visits during both the early and late low-tide periods (i.e. either four or six in each). This resulted in a total of 970 focal bird observations.

5.2.4 Benthic fauna sampling

Sampling of benthic fauna was conducted at a total of 19 intertidal flats (sites), to assess differences in prey density and composition between areas of high and low curlew use. A count of curlews was made before the sampling was conducted at each site, to enable a comparison of densities with broadscale surveys completed in previous years.

Eleven sites were high (>12 birds/100 ha) and eight were low (<7 birds/100 ha) in terms of intensity of use by feeding curlews (Figure 5.1; Chapter 2). The precise location of sites was also determined on the basis of accessibility and coverage of the Bay and its varying characteristics (e.g. width of flat and type of substrate). Seven of these sites were also used for the curlew feeding observations; the differences in sites used for fauna and feeding observations is due to the constraint of accessibility and presence of curlews for obtaining feeding records. The average and minimum distances between sites were 9 and 2 km, respectively. Sites ranged from
between 350–3,200 m long by 20–1,000 m wide. Intertidal benthic fauna were sampled between the 24th of January and the 28th of February 2001, on spring low tides (<0.56 m) and confined to 1.5 hours before and after dead low tide.

Each site had ten sampling stations where two paired core samples were taken, making a total of 20 cores for each site. Sampling stations were located along a series of transects that ran perpendicular to the shoreline and were evenly spaced along its length. The number of transects, varying from two to five, was determined by the length and width of the site. The transects were divided evenly into two to five sections from high water to low water, with the number of sections determined by the length and width of the site. The outcome was ten similarly-sized transect sections, evenly-spaced across each site. Within each section, one sampling station was positioned at a random distance from the start of the section. A minimum distance of 10 m separated any two sampling stations. The two cores at each of the ten sampling stations were taken at points 0.5–1.0 m either side of a transect, but on the same substrate. A compass was used to maintain a certain bearing along a transect across the flat and a GPS was used to approximate distances.

The substrate was sampled with a large corer which was a modified version of that used by Esselink and Zwarts (1989) and Zwarts and Wanink (1991, 1993). It comprised a PVC cylinder, 15 cm in diameter, with a handle. One end was sealed with a cap, containing a pluggable air-hole. For sampling the corer was thrust rapidly 40 cm into the substrate (or as far as it could go if <40 cm), the air-hole was plugged to create a vacuum and the corer hauled out at an angle after being twisted 180° to sever the core at its base. The plug was then removed, and the substrate core carefully manoeuvred into a plastic bag. The corer was marked with graduations at 10 cm intervals so that the depth of a core could be recorded.
Each core sample (usually 0.007 m$^3$ in volume, but less if there was a solid rock layer within 40 cm of the substrate surface) was washed through a 2 mm sieve (diameter 40 cm). This occurred either within 12 hours from extraction, or after being stored at 2 °C for up to 5 days. All sieved fauna were placed immediately into a plastic vial filled with 75% ethanol. Any other material left over after sieving (seagrass, rocks, shells, etc.) was stored temporarily in 75% ethanol and later picked over with the aid of a magnifying lamp, in a white photographic tray. Difficult samples were stained with Rose Bengal to assist in spotting the fauna. Any of these organisms that were smaller than 2 mm were discarded through re-sieving.

All fauna over 2 mm were sorted to their lowest easily identifiable taxonomic classification (at least Class except for Bryozoans, and often Infraorder or Family), and were measured to the nearest 5 mm along their longest dimension, with the largest (Polychaeta) recorded at 220 mm. For example, short-bodied individuals such as crabs were measured across the width of their carapace, but fish, shrimp-like and elongated prey were measured from head to tail. The smallest size classes were generally made up of amphipods and bivalves whereas the largest size classes generally comprised thalassinids and polychaetes.

The volume of hard material such as coral, rocks, shells, wood and other debris was also measured. A given sample was classed as “resistant” to probing if the volume of hard material exceeded 25% of the full core volume. For each site, the proportion of core samples (out of 20) which were “resistant” was then calculated.

Substrate resistance is usually measured by a penetrometer which either measures the pressure (kg/cm$^2$) needed to push a standard object a standard depth into the substrate, or the depth (mm) to which a standard object penetrates the substrate with a standard amount of pressure. In this study I measured substrate resistance as
the proportion of the substrate core composed of hard material (rocks, coral, etc.). Curlews are able to thrust their bills about 20 cm into the substrate and it is not only the force required to insert their bill that may be important but the chance of hitting something impenetrable (either by accident or when mistaken as a prey item; see Section 5.4.2). Therefore, the entire 20 cm depth is relevant to curlews and this is difficult to measure by any normally used penetrometer. One possible bias in my study was that high substrate resistance may have inhibited my benthic fauna sampling (because it was more difficult to insert the corer, allowing more opportunity for fauna to escape), however escape from probing curlews is also more likely within these substrates.

5.2.5 Data analyses

The counts of curlews made during the curlew feeding observations and benthic fauna sampling provided curlew density estimates that were independent of those obtained during the previous more intensive broadscale low-tide surveys (Chapters 2, 3 and 4). Curlew density estimates for the sites that were surveyed during all three field components were highly correlated (broadscale survey versus curlew feeding: \( r = 0.88, n = 12, P < 0.001 \); broadscale survey versus benthic fauna sampling: \( r = 0.87, n = 19, P < 0.001 \); and, curlew feeding versus benthic fauna sampling: \( r = 0.96, n = 7, P < 0.001 \)). The curlew density estimates from the broadscale survey are used in subsequent analyses, as these were based on most counts made over the largest temporal scale, using a consistent method for all sites. The intertidal areas used for both the curlew feeding observations and benthic fauna sampling were covered during the broadscale low-tide surveys.

The approximate biomass of fauna and prey were estimated with reference to an assumed quantitative relationship between biomass and linear size (along each prey
item’s maximum dimension) for each of five groupings of prey types (Figure 5.2). A relative “base” biomass index value was assigned to each prey type, at the size of one curlew bill depth (8.6 mm) for the four “non-elongated” fauna groups and one-quarter curlew bill length (41.9 mm) for elongated taxa (Table 5.1, Figure 5.2). The baseline values were based on the authors’ experience, published papers (McKinney et al. 2004, Zharikov and Skilleter 2004b, Van Gils et al. 2005a) and in consultation with Y. Zharikov (personal communication), who had measured energy values of some curlew prey items in Moreton Bay. This base biomass index value was intended to reflect the relative energy value of the prey to curlews (i.e. amongst “non-elongated” fauna, hard-bodied taxa, fauna category ‘A’, scored 1; non-mictyrid crabs, fauna category ‘B’, scored 2; mictyrid crabs, fauna category ‘C’, scored 3; shrimp-like taxa and fish, fauna category ‘D’, scored 4; Figure 5.2). Shrimp-like taxa and fish have a high proportion of soft flesh per total body mass compared with crabs which have more indigestible skeletal material (Zharikov and Skilleter 2004b). Mictyrid crabs likewise have a higher proportion of soft flesh than other crabs (Y. Zharikov, personal communication). Hard-bodied taxa were grouped together and were considered to have low energy value for curlews because they contain a large proportion of indigestible material. The base biomass index value was then multiplied by the prey’s size class cubed. The multiplication factors for these size classes were 1, 2, ..., 5 from smallest to largest size for non-elongated taxa, and 0.25, 0.33, 0.5, and 1.0 for elongated taxa (as estimated in relation to bill depth or length during feeding observations). The total biomass index was calculated by summing the biomass index values across all prey items consumed during feeding records or all fauna sampled in substrate cores.
**Figure 5.2.** Relationship between prey size and biomass index for each fauna group eaten by curlews (A = hard-bodied taxa, B = non-mictyrid crabs, C = mictyrid crabs and unidentified prey, D = shrimp-like taxa and fish, and E = elongated taxa). See Table 5.1 for taxonomic composition. The points on the graph represent the size classes: 1–5 × curlew bill width (A–D); and 1/4, 1/3, 1/2 and 1 × curlew bill length (E). The starting values of the biomass index at size class one for each fauna group are: A = 1; B = 2; C = 3; and, D and E = 4.
For “elongated” fauna, by comparing size dimensions (volume) of real specimens, polychaetes were deemed equivalent to thalassinids one quarter their length (i.e. a thalassinid 8.6 mm long had a similar biomass value (4) as a polychaete 34.4 mm long). The biomass index values for different sizes of polychaetes and other elongated prey (i.e. Pennatulacea and Anoplida) were scaled accordingly (fauna category ‘E’; Figure 5.2). All items smaller than size class one (i.e. <8 mm for fauna categories A–D; <35 mm for fauna category E; Figure 5.2) were given a minimal biomass index value (A = 0.3, B = 0.5, C = 0.8, D and E = 1.0). Prey items that were recorded as ‘unseen’ (small, all <8 mm) or ‘unidentified’ during focal curlew observations were included in fauna category C (mictyrid crabs), because mictyrid crabs were an average prey item in terms of biomass index value to curlews and were the most frequently consumed category of identified prey items (46%).

Prey groupings used in analyses were: (1) crustacean prey (Tanaidacea, Isopoda, Amphipoda, Stomatopoda, Penaeidea, Caridea, Thalassinidea, Anomura, Brachyura and Mictyridae); and (2) potential prey (crustacean prey plus Anoplida, Polychaeta, Gastropoda, Bivalvia and fish). The fauna selected for these two groups were those fauna sampled during substrate coring that were considered plausible prey for curlews, based on what was recorded during the curlew feeding observations. I calculated six measures of the benthic fauna and prey abundance; the density (number of individuals per core) and biomass index per core for each of: total fauna, potential prey, and crustacean prey. Values per core were used, rather than values per unit of sediment volume, so as to include solid coral and other hard material as part of the “core”. These six measures and the measure of curlew density were log-transformed (\log(x + 1)) to improve normality. Substrate resistance was not transformed for statistical analyses because angular transformation (arcsin) did not greatly improve
the distribution of the data or alter the statistical results. Substrate resistance and
arcsin-transformed substrate resistance were highly correlated ($r = 0.995$).

Pearson’s correlations were used to explore the relationships between substrate
resistance and each of the six fauna density and biomass index measures, and between
curlew density, substrate resistance, fauna density and biomass indices. Multiple
regression analyses were used to relate curlew density (as the dependent variable) to
substrate resistance together with each of the six fauna density and biomass index
measures, using SPSS statistical software (SPSS Inc. 2003).

A two-dimensional ordination of sites by multidimensional scaling was used
to assess patterns of between-site similarity in fauna biomass indices, using total fauna
biomass index data (square-root transformed to improve normality) for each taxon
identified during the substrate core sampling, with the Bray-Curtis dissimilarity
measure, using PRIMER statistical software (Clarke and Warwick 2001). The
associations between the ordination pattern, the biomass index of each contributing
fauna taxon and eight extrinsic factors (substrate resistance, curlew density and the six
fauna density and biomass index measures) was assessed by multiple regression of
each factor value on the $x$ and $y$ ordination values for each site, using the Pop Tools
Excel add-in (Hood 2003), and their significance levels were calculated using a
randomisation test (Edgington 1980). Biplot vectors (Jongman et al. 1995) for fauna
taxa or extrinsic factors which had a significant ($P \leq 0.05$) multiple regression with
the ordination axes were added to the ordination plot, to show the increasing trend for
that taxon or extrinsic factor in the ordination space. Coordinates of each vector’s
terminal point were defined by Pearson’s correlations (Anderson and Willis 2003)
between the taxon biomass index or extrinsic factor and the $x$ and $y$ ordination scores.
Differences in the combined relative contributions of different taxa to the biomass
index between sites with high (>12 birds/100 ha) and low (<7 birds/100 ha) curlew density were tested using Analysis of Similarity (ANOSIM: Clarke and Green 1988).

**Table 5.1.** Composition of fauna from curlew feeding observations (prey) and intertidal substrate core sampling (benthic). The biomass-value reference category is related to the energy value of each fauna type to curlews (see Figure 5.2).

<table>
<thead>
<tr>
<th>Taxonomic classification</th>
<th>Biomass-value reference category</th>
<th>% prey items</th>
<th>% total prey biomass</th>
<th>Average biomass / prey item</th>
<th>% benthic individuals</th>
<th>% total benthic biomass</th>
<th>Average benthic biomass / item</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polyplacophora</td>
<td>A</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.0</td>
<td>0.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>A</td>
<td>0.2</td>
<td>0.1</td>
<td>8.0</td>
<td>2.0</td>
<td>0.4</td>
<td>3.7</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>A</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>17.3</td>
<td>8.0</td>
<td>8.4</td>
</tr>
<tr>
<td>Anomura</td>
<td>A</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.7</td>
<td>0.0</td>
<td>1.1</td>
</tr>
<tr>
<td>Bryozoa</td>
<td>A</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.3</td>
<td>0.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Ophiuroidea</td>
<td>A</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>3.7</td>
<td>0.1</td>
<td>0.3</td>
</tr>
<tr>
<td>Asteroidea</td>
<td>A</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.1</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Ascidiacea</td>
<td>A</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.0</td>
<td>0.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Brachyura</td>
<td>B</td>
<td>9.8</td>
<td>17.7</td>
<td>40.8</td>
<td>7.7</td>
<td>1.4</td>
<td>3.4</td>
</tr>
<tr>
<td>Mictyridae</td>
<td>C</td>
<td>15.4</td>
<td>13.8</td>
<td>20.2</td>
<td>7.4</td>
<td>1.7</td>
<td>4.1</td>
</tr>
<tr>
<td>Unseen</td>
<td>C</td>
<td>36.1</td>
<td>1.3</td>
<td>0.8</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Unidentified</td>
<td>C</td>
<td>30.2</td>
<td>26.6</td>
<td>19.8</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Tanaidacea</td>
<td>D</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.3</td>
<td>0.3</td>
<td>16.0</td>
</tr>
<tr>
<td>Isopoda</td>
<td>D</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.9</td>
<td>0.1</td>
<td>1.3</td>
</tr>
<tr>
<td>Amphipoda</td>
<td>D</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.5</td>
<td>0.1</td>
<td>2.1</td>
</tr>
<tr>
<td>Stomatopoda</td>
<td>D</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.0</td>
<td>1.2</td>
<td>500.0</td>
</tr>
<tr>
<td>Penaeidea</td>
<td>D</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.5</td>
<td>5.0</td>
<td>182.5</td>
</tr>
<tr>
<td>Caridea</td>
<td>D</td>
<td>4.7</td>
<td>14.1</td>
<td>68.0</td>
<td>1.9</td>
<td>9.1</td>
<td>84.9</td>
</tr>
<tr>
<td>Thalassinidea</td>
<td>D</td>
<td>2.8</td>
<td>18.5</td>
<td>151.3</td>
<td>1.9</td>
<td>27.0</td>
<td>253.2</td>
</tr>
<tr>
<td>Fish</td>
<td>D</td>
<td>0.2</td>
<td>0.6</td>
<td>82.7</td>
<td>0.6</td>
<td>10.0</td>
<td>288.6</td>
</tr>
<tr>
<td>Pennatulacea</td>
<td>E</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.2</td>
<td>4.0</td>
<td>322.4</td>
</tr>
<tr>
<td>Anoplacelae</td>
<td>E</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.4</td>
<td>0.0</td>
<td>1.3</td>
</tr>
<tr>
<td>Polychaeta</td>
<td>E</td>
<td>0.7</td>
<td>7.3</td>
<td>243.7</td>
<td>53.4</td>
<td>31.7</td>
<td>10.8</td>
</tr>
</tbody>
</table>
Chapter 5. Determinants of habitat choice in curlews

5.3 Results

Crustaceans were a relatively small component of the benthic fauna, however they were numerically dominant in the curlews’ diet (Table 5.1). In particular, Mictyridae (soldier crabs), Brachyura (other crabs), Caridea (shrimp) and Thalassinidea (yabbies) made up 15.4, 9.8, 4.7 and 2.8 percent of food items consumed respectively (Table 5.1). These are under-estimates of the frequency in the curlews’ diet, because 66% of prey items consumed could not be identified, because of their small size and/or distance from the observer. Of all identified prey items, thalassinids made up the greatest percentage of the total ingested biomass index. In contrast, polychaetes and bivalves were the most common fauna sampled during substrate coring, making up 53.4 and 17.3 percent of the total number of individuals sampled respectively (Table 5.1), and polychaetes contributed most to the benthic biomass index, followed by Thalassinidea. Although curlews did not eat many polychaetes, the average biomass index per polychaete ingested by curlews was much greater than the average biomass index per polychaete sampled in the substrate cores, 243.7 compared with 10.8 (Table 5.1). Similarly, crabs (Mictyridae and Brachyura) ingested by curlews had a much greater biomass index than those sampled in the substrate cores. Conversely the average biomass index per shrimp (Caridea and Thalassinidea), although greater than crabs in both curlew diet and benthos, was greater in the substrate cores compared with those ingested by curlews (Table 5.1).

All six measures of fauna density and biomass index were correlated to varying degrees: out of 15 correlations, eight coefficients were above 0.8 and only two were below 0.6, and all correlation coefficients were 0.5 or above and statistically significant. Examination of the total fauna and crustacean biomass index values for all site-substrate combinations at which four or more benthic core samples were
available revealed that the highest biomass values were found on sand, but this and other substrates were also very variable (Figure 5.3).

![Figure 5.3](image)

**Figure 5.3.** Total fauna biomass index (A) and crustacean prey biomass index (B) per unit substrate surface area (core) sampled during benthic coring on each identified substrate within each site (COR = coral, MUD = mud, SMU = sandy-mud, SAN = sand, SGR = seagrass, SGP = seagrass pool, PLS = other pools, and WTR = tidal/ocean water). Means are depicted as dark circles. Number of sites at which each substrate was measured is shown in parentheses.
Substrate resistance alone explained 67% of the variation in curlew density among the 19 sites \((r = -0.82, P < 0.001; \text{Figure } 5.4)\). Curlew density also showed a strong positive correlation with all six fauna density and biomass index measures (Figure 5.4, Table 5.2). In a multiple regression, around 71% of the variation in curlew density among the 19 sites was explained by substrate resistance together with each of the six individual alternative measures of benthic fauna density or biomass index \((r = 0.83 \text{ or } 0.84; \text{Table } 5.2)\). With the effect of each fauna density or biomass index variable statistically removed, substrate resistance remained highly significant \((P < 0.005)\) in all six tests (Table 5.2). However, with the effect of substrate resistance statistically removed, curlew density was not significantly correlated with any of the six fauna variables (Table 5.2). The main variable driving the multiple regression result was substrate resistance, and hence the additional inclusion of different fauna variables made little difference to the correlation coefficient (Table 5.2), especially since the fauna variables were also correlated with one another. When the effect of substrate resistance was removed by focusing on the seven most penetrable sites only (Table 5.2), there was also no statistically significant relationship between curlew density and any of the six measures of fauna density and biomass index, although there were moderately high positive correlations (range of \(r\) values = 0.41–0.53) for most fauna variables. Substrate resistance was also negatively correlated with all six fauna density and biomass index measures (Figure 5.4, Table 5.2), and with both total fauna density per unit soft-sediment volume \((r = -0.50, n = 19, P < 0.05)\) and biomass index per unit soft-sediment volume \((r = -0.54, n = 19, P < 0.02)\).
Figure 5.4. Relationship between curlew density (birds/100 ha) and (A) total fauna density per unit substrate surface area (core), (B) substrate resistance, and (C) total fauna biomass index per unit substrate surface area (core); and (D) between total fauna biomass index per unit substrate surface area (core) and substrate resistance; across all 19 sites.
Ordination of sites based on the total fauna biomass index within each taxon revealed clear differences between high and low curlew density sites (Figure 5.5). Factors associated with the ordination space occupied by high curlew density sites included all six fauna density and biomass index measures (total fauna, potential prey and crustacean prey) as well as the biomass index of Bivalvia, Polychaeta, Penaeidea, Caridea, Thalassinidea, Brachyura, Mictyridae and fish. Low curlew density sites were characterised by high substrate resistance. The difference in the fauna biomass index composition across taxa between high (>12 birds/100 ha) and low (<7 birds/100 ha) curlew density sites was statistically significant (ANOSIM $R = 0.56$, $P < 0.001$).

Table 5.2. Strength of correlation of curlew density and substrate resistance with various measurements of benthic fauna per unit substrate surface area (core) and per unit soft-sediment volume: Pearson's $r$-values with and without controlling for the effect of substrate resistance ($*** = P < 0.001$, $** = P < 0.005$, $* = P < 0.05$).

<table>
<thead>
<tr>
<th>Fauna measurement</th>
<th>Substrate resistance versus fauna</th>
<th>fauna plus substrate resistance$^1$</th>
<th>fauna not substrate resistance$^2$</th>
<th>substrate resistance not fauna$^3$</th>
<th>fauna per volume soft-sediment</th>
<th>Curlew density versus fauna at low-resistance sites ($n = 7$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density of:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total fauna</td>
<td>-0.72***</td>
<td>0.70***</td>
<td>0.84***</td>
<td>0.26</td>
<td>-0.65**</td>
<td>0.50*</td>
</tr>
<tr>
<td>Potential prey</td>
<td>-0.75***</td>
<td>0.73***</td>
<td>0.84***</td>
<td>0.30</td>
<td>-0.62*</td>
<td>0.54*</td>
</tr>
<tr>
<td>Crustacean prey</td>
<td>-0.59*</td>
<td>0.60*</td>
<td>0.83***</td>
<td>0.25</td>
<td>-0.73**</td>
<td>0.37</td>
</tr>
<tr>
<td>Biomass of:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total fauna</td>
<td>-0.67**</td>
<td>0.67**</td>
<td>0.84***</td>
<td>0.28</td>
<td>-0.69**</td>
<td>0.56*</td>
</tr>
<tr>
<td>Potential prey</td>
<td>-0.66**</td>
<td>0.67**</td>
<td>0.84***</td>
<td>0.28</td>
<td>-0.69**</td>
<td>0.55*</td>
</tr>
<tr>
<td>Crustacean prey</td>
<td>-0.55*</td>
<td>0.60*</td>
<td>0.84***</td>
<td>0.31</td>
<td>-0.74**</td>
<td>0.50*</td>
</tr>
</tbody>
</table>

$^1$ From multiple regression analysis.

$^2$ Partial correlation (removing effect of resistance).

$^3$ Partial correlation (removing effect of fauna).
Figure 5.5. Ordination by multidimensional scaling of sites on the basis of total fauna biomass index per unit substrate surface area (core) of each taxon sampled during substrate coring, and biplot vectors for significantly associated extrinsic factors (top) and benthic taxa (bottom). Symbols represent: □ low curlew density (<7 birds/100 ha); ● high curlew density (>12 birds/100 ha).
5.4 Discussion

5.4.1. Prey consumed by curlews in Moreton Bay

Although the sediment infauna was dominated by small worms, curlews in my study mainly consumed different types of crustacean, similar to their conspecifics on intertidal feeding flats in other parts of Australia (Tulp and de Goeij 1994, Zharikov and Skilleter 2004b). Piersma (1986) conducted the only non-Australian intertidal study of the diet of Eastern Curlews: in South Korea, where they solely ate crabs, mostly obtained by using deep probes into their burrows and in the lower, wetter areas of the intertidal zone. Polychaetes are more common than crustaceans in the diet of the Eurasian Curlew (Numenius arquata) in northern Europe (Zwarts and Esselink 1989, Ens et al. 1990, Rippe and Dierschke 1997).

Thalassinid shrimps were among the largest and most energy-rich prey consumed by curlews. Zharikov and Skilleter (2004b) concluded that thalassinids were preferred by curlews during the pre-migratory period because of their high digestive quality. In my study the curlews showed less dependence on thalassinids, and consumed a wide range of prey. This difference is probably because Zharikov and Skilleter (2004b) confined their observations to a single sandflat of high curlew density and two discrete time periods (mid-nonbreeding and pre-migratory), whereas the present study included many more sites of varying curlew density and a broader time scale (entire overwintering period), during which energy-rich prey may be less important. Pre-migratory shorebirds may rely on high-energy prey because their digestive organs are reduced (Van Gils et al. 2003). Crabs were the most common identified prey item consumed by curlews in this study, consistent with the findings of Zharikov and Skilleter (2004b) during the mid-nonbreeding period.
5.4.2 Substrate resistance as a determinant of feeding distribution

Sites with high curlew density had substrates with low resistance and a greater density and biomass of most types of intertidal fauna. Although crustaceans made up the majority of the curlew diet, they were a relatively small component of the total benthic fauna and not the best predictor of curlew density. Instead, substrate resistance was by far the best predictor of curlew density. At resistant sites, both the curlew density and benthic fauna density and biomass were lower than at non-resistant sites.

Low substrate resistance has been associated with higher foraging success in several sandpipers capturing prey by tactile probing of the sediment (Myers et al. 1980, Grant 1984, Gerritsen and van Heezik 1985, Kelsey and Hassall 1989, Mouritsen and Jensen 1992). This is also likely to be the case for curlews, the largest and deepest probing shorebird in the world. There are several reasons why resistant substrates in the present study may lead to lower foraging success and hence been used by fewer curlews.

First, resistant substrates have a lower prey density. Resistant substrates negatively affect prey density and biomass by providing less available habitat for prey, thereby restricting density. Prey growth to maximum size may also be limited and species composition possibly affected if there is insufficient space for larger types of prey. In this study, there were not simply fewer prey because there was less available habitat for them. Resistant substrates also had a significantly lower prey density and biomass per unit of soft sediment compared to substrates of low resistance (Table 5.2). Sediment characteristics have been shown to greatly influence invertebrate densities (Yates et al. 1993) and Sanders (2000) found that the experimental addition of stones to newly constructed, shorebird-feeding ponds caused
a lowered invertebrate biomass per unit sediment volume. However in the present study the density of curlews was still greater at less resistant sites even when the effect of differences in prey density or biomass were statistically removed.

Second, they may be more costly to probe. Substrate resistance potentially affects prey availability directly as substrates of low resistance may allow deeper probing (Myers et al. 1980, Mouritsen and Jensen 1992) and lower foraging costs (Grant 1984, Gerritsen and van Heezik 1985, Kelsey and Hassall 1989), including a lower risk of bill damage (see below). Probe depth and prey detection by sandpipers were reduced in more resistant substrates, as shown both in aviary conditions (Myers et al. 1980) and on intertidal flats in the Danish Wadden Sea (Mouritsen and Jensen 1992). Pressure-sensitive receptors in the bills of some probing shorebirds allow for the detection of solid objects embedded in the wet substrate (Piersma et al. 1998) but inanimate objects buried within the substrate could also interfere with prey detection by shorebirds. Rocks or other hard objects buried within the sediment could confuse curlews as they probe for similar-sized prey items, thus reducing their foraging success. Hard objects and hard substrates could also cause physical damage to the bills of probing birds (see also Chapter 4). If birds with long, decurved bills are probing into homogenous sediment, hard substrates may cause bill breakage (Davidson et al. 1986). If they are probing into prey burrows, hard objects may cause abrasions to the bill. Several species have been shown to switch between tactile hunting on soft substrates and visual hunting on hard substrates (e.g. Gerritsen and van Heezik 1985, Rompre and McNeil 1996).

Third, prey availability may decrease if large sediment particles or obstacles affect prey behaviour in a way that makes them less accessible to probing shorebirds. The high substrate resistance and low water retention capacity of coarse sediments
(Botto and Iribarne 2000) may affect the behaviour of intertidal invertebrates. The faster that water drains through the sediment after tidal exposure, the faster invertebrates retreat deep into their burrows and out of the reach of shorebirds (Kalejta and Hockey 1991, Dierschke et al. 1999). The burial depth of many intertidal invertebrates increases with body size (Zwarts and Wanink 1993) and can be affected by sediment type (Esselink and Zwarts 1989). Esselink and Zwarts (1989) found in the Dutch Wadden Sea that marine worms of similar size buried deeper in harder sediments. Some resistant substrates identified in the present study may have had low water retention capabilities, however, they were generally characterised by a wet layer of mud or sandy-mud with a resistant layer of rock, coral or shell grit just beneath (c. 10–15 cm) the surface. This hard layer is likely to restrict the burrowing by prey and the probing by shorebirds alike, and hence the “prey behaviour” hypothesis seems unlikely to be a major cause of habitat choice by curlews in Moreton Bay.

5.4.3 Factors involved in choice of feeding area

Chapter 4 showed that curlews select feeding habitat more strongly at the between-flat than the within-flat scale and concluded that substrate resistance was the reason for this pattern of selection. Within flats, curlews tend to concentrate their foraging effort close to the moving low-water line (Chapter 4), where resistance would be lower because of the higher water content.

The curlews’ choice of feeding habitat seems more strongly influenced by the physical nature of the substrate than by the composition or abundance of their prey. Intertidal invertebrates vary considerably in space and time (Underwood 1996) and thus it would arguably be prudent for curlews to simply select habitats across a large area that offer the greatest potential availability of prey. Although curlews seem to be
selecting feeding habitat by its physical nature, this is also a good predictor of prey availability for deep-probing shorebirds. Curlews which choose to feed in areas of low resistance will get the indirect benefit of a greater food abundance, even if this was not their proximal trigger for choice of feeding area. Prey abundance may be an ultimate factor which has affected the evolution of habitat choice, through the proximal cue of physical properties. Nevertheless, prey availability, in terms of the probability of the prey being successfully captured when a long-billed shorebird probes the substrate, is arguably at least as important as prey abundance, providing that the increased availability does not correlate with decreased density of preferred prey items.

5.4.5 Conclusions

The results of this study indicate that choice of feeding area by a large, long-billed shorebird (the Eastern Curlew) was more strongly affected by substrate resistance than prey density or biomass, across a broad range of intertidal habitats on the non-breeding grounds. This confirms that properties of the substrate can be an important driver of habitat selection by large-bodied shorebirds at the large (between-flat) spatial scale. Both the birds and their prey were most abundant on substrates with little to no hard material (rocks, coral, shell grit), and such a preference would confer a probing and burrowing advantage to both birds and prey, respectively. The Eastern Curlew is listed as near-threatened globally (Collar et al. 1994) and my results suggest that habitat management to avoid further declines in this species should include minimising physical modifications of their soft-substrate feeding grounds. Any physical modifications that increased the resistance of the substrate may be detrimental to curlews.
Chapter 6

Does foraging success explain choice of feeding sites by Eastern Curlews on their non-breeding grounds?

6.1 Introduction

Food is of primary importance for survival in animals such as migratory shorebirds where energy expenditure is extremely high (Kersten and Piersma 1987). Migratory shorebirds on their non-breeding grounds are utilising habitat primarily for its foraging potential (Evans 1976; Chapter 1). Here foraging success is of crucial importance for them in terms of maintaining healthy body condition and in fuelling up before long-distance migration and breeding (Evans and Dugan 1984, Dann 1987, Kersten and Piersma 1987, Piersma 1997, Battley et al. 2003, Kvist and Lindstrom 2003, Battley et al. 2004). Therefore, foraging success could be expected to influence shorebird distributions on non-breeding grounds.

et al. 2004). Substrate type can affect prey density through the preferences of invertebrate prey for certain substrates (Yates et al. 1993). It can also affect prey availability (i.e. the ability of prey to be captured), either through physical impedance when the birds probe for prey with their bills (Myers et al. 1980, Grant 1984, Kelsey and Hassall 1989) or by affecting the prey’s behaviour making them more or less susceptible to predation (Esselink and Zwarts 1989). The density of conspecifics can affect both prey density (through depletion from current predation: Sanchez et al. 2006), and prey availability (through a depressive effect where prey are alerted to the presence of predators and retreat deep into their burrows: Goss-Custard 1977b, Yates et al. 2000). Conspecifics can also have a direct negative effect on each other through agonistic interactions such as fighting or kleptoparasitism (Ens et al. 1990, Triplet et al. 1999, Leeman et al. 2001).

It is likely that the suitability of a habitat for non-breeding shorebirds is determined by the potential foraging success that a bird may gain from the habitat, rather than the overall density of prey that it contains (Piersma et al. 1993a). There are many different ways to measure foraging success, and different studies have used a variety of different measures, including: feeding rate (the number of feeding attempts made per unit time); success or capture rate (the number of prey items consumed per unit time); and intake rate (the biomass or energy gained from prey consumption per unit time). Previous research has identified many factors that affect intake rate in shorebirds (Goss-Custard 1984) but relatively few studies have found or even looked for a direct relationship between intake rate and shorebird density (e.g. Goss-Custard 1970, Sutherland 1982). It has often been assumed that shorebirds seek habitats where they maximise their intake rates (e.g. Goss-Custard et al. 1995) and low intake rates in otherwise apparently good quality habitats have consequently been
attributed to a negative effect of high bird density on the availability of prey (Masero and Perez-Hurtado 2001). In contrast, research on habitat selection in shorebirds has focused on factors that may affect prey availability (Myers et al. 1980, Quammen 1982) or the relationship between intake rate and prey density (i.e. the functional response: Goss-Custard et al. 2006).

Furthermore, the vast majority of research into the relationship between food acquisition and habitat selection in shorebirds has focused on a small number of species consuming one or two prey types (Guillemette et al. 1992). Large, deep-probing shorebirds are poorly represented. These birds are able to capture and eat large, deep-burrowing prey (Goss-Custard 1977b, Reading and McGrorty 1978, Esselink and Zwarts 1989, Zwarts and Wanink 1993, Leeman et al. 2001) and hence may consume a wider variety of prey (Goss-Custard and Jones 1976, Zwarts and Esselink 1989, Ferns and Siman 1994) than smaller shorebird species.

Previous studies (Chapters 4 and 5) found that low substrate resistance was a good predictor of high density in a large, deep-probing shorebird (the Eastern Curlew, Numenius madagascariensis) on their non-breeding grounds, and that less-resistant flats had relatively higher prey abundances. However, these previous studies did not assess the birds’ foraging success. The present study asks the question: does any aspect of foraging success explain choice of feeding site by non-breeding Eastern Curlews? Foraging success is measured in three main ways: feeding rate, success rate and biomass intake rate. I also investigate the relationship between these measurements of foraging success and substrate characteristics, and test whether foraging success is a better predictor of curlew density than substrate characteristics themselves. Curlews are sexually dimorphic with respect to bill length so I also test
Chapter 6. Curlew distribution and foraging success

the effects of bill size dimorphism between sexes, to assess whether the longer bill of females confers any advantage or disadvantage on the non-breeding grounds.

6.2 Methods

6.2.1 The Eastern Curlew in Moreton Bay

Moreton Bay extends approximately 132 km in a north–south direction along the coast of subtropical eastern Australia, at 27–28° S and 153°–153°30’ E (Figure 6.1), covering around 300,000 ha (Blackman and Craven 1999). The bay reaches a maximum width of 40 km and contains a complex system of intertidal flats totalling some 23,000 ha at low tide (Blackman and Craven 1999). Substrate types within the Bay are diverse and have been broadly categorised into sand, coral, sandy-mud, and mud (Young 1978).

Moreton Bay supports around 5,000 of the global population of 31,000 Eastern Curlews (hereafter ‘curlews’) during the austral summer months (Watkins 1993, Thompson 1993a, Driscoll 1997; Chapter 2). These curlews are the largest migratory shorebirds in the world. They have extremely long decurved bills (around 15 cm in males and 18 cm in females: Barter 1990, Rogers 1995a), which allow them to probe deeply and catch crabs, ghost shrimps and worms (Piersma 1986). In their intertidal feeding grounds, crustaceans are a frequent prey item (Piersma 1986, Zharikov and Skilleter 2003). To capture large, deep-burrowing crustaceans, a curlew may push its whole head into the substrate (Piersma 1986), reaching a depth of over 20 cm (Barter 1990, Rogers 1995a).
Figure 6.1. Map of the 11 sites in Moreton Bay used for focal Eastern Curlew feeding observations.
6.2.2 Study design

To identify the curlews’ prey and foraging success, curlew feeding was recorded at 11 intertidal flats (sites), chosen on the basis of accessibility and coverage of different habitat features (e.g. width of flat and type of substrate) across Moreton Bay (Figure 6.1). Count data from a broadscale assessment of low-tide feeding grounds (Chapters 2, 3 and 4) were used to select flats in which the density of curlews ranged from moderately low to high (6–72 birds/100 ha). Flats with very low curlew density were not used, as the aim was to acquire feeding data. The minimum distance between sites was approximately 2 km. Focal flats ranged in length from 500 to 1,500 m, in width from 200 to 1,000 m, and in area from 23 to 97 ha.

The observations at five flats were repeated on 12 different days, six during neap and six during spring tides, between 16 November 1999 and 7 March 2000. The other six flats were visited on 8 different days (four neap and four spring). The observation period was between 1.5 hours before (early low tide) and 1.5 hours after (late low tide) the time of dead low tide. Each flat received an equal number of visits during both the early and late low-tide periods (i.e. either four or six in each).

A count of each focal flat, recording the total number of curlews, was made before and after each observation period. Flat area was measured as described in Chapter 4 and curlew density was calculated by dividing the average of the two counts from each observation period by the flat area.

Each site was assigned a macro-substrate type (i.e. sand, mud, sandy-mud or coral), obtained from Young (1978) who mapped the broadscale substrate types across the whole of Moreton Bay. A measure of substrate resistance, derived from the amount of hard material such as coral, rocks and shells within the substrate, was
Chapter 6. Curlew distribution and foraging success

calculated for each site; according to the method reported in Chapter 4. Similar to macro-substrate type, substrate resistance was a broadscale (between-flat) measure and did not change with the tide level within sites. Substrate resistance could not be predicted from the macro-substrate type. Some mud sites had high substrate resistance due to layers of coral, rock or shells just below (10–15 cm) the surface.

6.2.3 Curlew feeding observations

Focal birds were observed through 20–60× zoom telescopes, by a single observer at each site, from a vantage point 50–1,000 m from the bird, and level with, or slightly above it. Green- or sand-colored clothing was worn to blend in with the background, and focal observations began after the observer had been in position and relatively still for at least 10 minutes. During each visit, the behaviours of ten curlews (or all present if less than ten) were sequentially observed, resulting in a total of 831 focal bird observations. The focal birds were randomly chosen, using a prior count and a random number table. The age/sex of the birds was determined by the length of the bill (male = short, female = long and unknown = intermediate). Many of the birds with bills of intermediate length were probably juvenile females.

Data were recorded on the birds feeding location and activities within sites during 3-minute observation periods. The micro-substrate that the birds’ were situated on was recorded at the start of each minute (giving three point records), within the categories: coral, mud, sandy-mud, sand, seagrass, seagrass pool, other pools, water (tidal/ocean water as opposed to a pool above low tide on the flat) and air (bird flying). The birds’ distance (m) to the moving low water level (excluding pools) was recorded at the start of the observation period. The birds’ activities that were recorded during the 3-minute observation periods included: the number and types of feeding attempts made (types were pecks and probes – divided into half-, full- and
multiple-probes); whether each feeding attempt was successful and the size and broad
taxonomic classification (as far as possible, see below) of any prey item consumed;
the time (seconds) spent on all possible activities (i.e. standing, walking, running,
resting, preening, flying); and the occurrence of agonistic interactions including
distance to conspecifics.

Identification of prey type was only possible for larger items, or if the feeding
bird was sufficiently close to the observer. Categories of prey type were: Gastropoda,
Polychaeta; Caridea; Thalassinidea; Brachyura; Mictyridae; fish; unidentified; and
small and unseen. Size categories for all prey types except polychaetes were assigned
in relation to the depth of the curlews’ bill (1, 2, 3, 4 and 5 depth/s); polychaetes were
sized in relation to the length of the bill (1/4, 1/3, 1/2, and 1 length). Bill depth (8.57
mm), obtained from nine Queensland Museum specimens, was calculated as the
average for male \((n = 3)\) and female \((n = 6)\) combined, taking three measures from
each bill (near gape, middle, and tip). Bill length (167.65 mm), obtained from Barter
(1990) and Rogers (1995a), was also calculated as the average for male and female
combined \((n = 469)\).

Five components of foraging success (feeding rate, percent attempts
successful, success rate, average biomass per prey item and biomass intake rate) were
calculated. Feeding rate is the total number of feeding attempts (pecks and probes)
made per bird per minute. Percent attempts successful was calculated by dividing the
number of feeding attempts that resulted in prey consumption per bird per minute by
the total number of feeding attempts made per bird per minute and then multiplying
by 100. Success rate is the number of prey items consumed per bird per minute. The
approximate biomass of each prey item consumed was estimated with reference to an
assumed quantitative relationship between biomass and linear size for each of five
groupings of prey type (gastropods, brachyuran crabs, mictyrid crabs and unidentified prey, shrimp-like taxa and fish, and polychaetes). The average biomass per prey item was calculated by adding up the biomass value across all prey items consumed and dividing by the number of prey items consumed (per bird per minute). The biomass intake rate was calculated by adding up the biomass value across all prey items consumed in 3 minutes and then divided by three to give a rate per minute foraging time.

The biomass values reflect the relative energy values of different prey types and sizes to curlews, and Chapter 5 provides a detailed description of its calculation. Broadly, its basis was as follows. Shrimp-like taxa and fish have a high proportion of soft flesh per total body mass compared with crabs which have more indigestible skeletal material (Zharikov and Skilleter 2004b). Mictyrid crabs likewise have a higher proportion of soft flesh than brachyuran crabs (Y. Zharikov, personal communication). Gastropods were considered to have low energy value for curlews because they contain a large proportion of indigestible material. By comparing size dimensions (volume) of real specimens, polychaetes were deemed equivalent to thalassinids one quarter their length (i.e. a thalassinid 8.6 mm long had a similar biomass value as a polychaete 34.4 mm long). Prey items that were recorded as ‘unseen’ (small, all < 8 mm) or ‘unidentified’ during curlew feeding observations were included in the fauna category of mictyrid crabs, because they were an average prey item in terms of biomass value to curlews and were the most frequently consumed category of identified prey items (46%).

6.2.4 Data analyses

A number of two-factor analyses of variance were used to test whether feeding rates, success rates and biomass intake rates differed significantly between age/sex
categories and among different levels of each of four environmental factors (site, macro-substrate, micro-substrate and distance to low water). Focal observations were only used if the bird was actively foraging (i.e. walked for at least 2.5 of the 3.0 minutes observed; \( n = 542 \)). There were 11 sites, four macro-substrate types, seven micro-substrate types and nine categories of distance to low water. The categories of distance to the moving low water level (at the time of observation) were: -50–0, 0–50, 50–100, 100–150, 150–200, 200–250, 250–300, 300–350, and >300 (for this analysis 530 focal curlew observations were used because the distance to low water was not recorded in 12 cases). Seven micro-substrate categories were used (only for 400 observations in which the bird remained on the same micro-substrate during the full 3-minute period): mud, sandy-mud, sand, seagrass, seagrass pool, other pools, and water (tidal/ocean water as opposed to a pool above low tide on the flat); coral and air (bird flying) were omitted because there were no 3-minute records of birds on these substrates. Age/sex categories (males, females and unknowns) were used in each analysis of variance to see how they affected the three main components of foraging success and interacted with the four environmental factors.

Pearson’s correlation coefficients (across the 11 individual flats) were used to assess the relationships among the five components of curlew foraging success (feeding rate, percent attempts successful, success rate, average biomass per prey item and biomass intake rate), and also to compare each of three components of foraging success (feeding rate, success rate and biomass intake rate) with substrate resistance and curlew density. Due to some differences in feeding measurements between age/sex categories, and different proportions of males across all environmental variables, feeding data for the age/sex categories were averaged (i.e. (males + females
+ unknown)/3) for each of the five components of foraging success in all correlations so as to give them equal weighting.

Differences in diet, micro-substrate preference and feeding technique between the age/sex categories were tested using chi-squared contingency table analyses. I compared males with others (females and those of unknown sex) in terms of the number of individual prey items consumed within six categories of prey type (small and unseen, unidentified, Mictyridae, Brachyura, Caridea, and Thalassinidea), nine categories of prey type and size (small and unseen, small unidentified, large unidentified, small Mictyridae, large Mictyridae, small Brachyura, large Brachyura, small Caridea, Thalassinidea and fish, and large Caridea, Thalassinidea and fish), and five categories of prey biomass (0.8, 2–16, 24–81, 108–192, and 250–500). Prey items were divided into small and large based on their size category from curlew feeding observations (small \( \leq 2 \times \) bill width for all non-polychaete prey and \( \leq 0.5 \times \) bill length for polychaete prey, large \( \geq 3 \times \) bill width for all non-polychaete prey and \( >0.5 \times \) bill length for polychaete prey). Polychaetes and gastropods were not included in the chi-squared analyses due to their small sample sizes. I also compared males with others in terms of which micro-substrate they preferred within seven categories (mud, sandy-mud, sand, seagrass, seagrass pool, other pools and tidal water). To test whether sexual dimorphism affected feeding behaviour, I compared males with females in terms of the feeding technique they employed within two categories (pecks and probes).

To test whether curlew foraging success differed between early versus late tidal states and neap versus spring tidal types I used two-factor analyses of variance with age/sex and tidal state/type.
6.3 Results

Of 831 focal curlew observations, 542 curlews were actively feeding and 436 were successful in consuming a total of 1,238 prey items. Across 542 curlew feeding observations the average feeding rate was 11.8 feeding attempts per minute and the average success rate was 0.76 prey items consumed per minute (Table 6.1). Analyses of variance revealed some statistically significant differences in feeding and success rates among sites (Table 6.2, Figure 6.2) and substrates (macro and micro; Table 6.2, Figures 6.3 and 6.4) but not with distance to low water (Table 6.2). The significant effects of site and macro- and micro-substrate are not due to one or two sites only, because when the sites associated with the highest feeding and success rates (PP2 and VPT) were removed from the analyses, the main effects of site or substrate remained statistically significant. In comparison, differences in biomass intake rate were not as clear cut, partly because this measure was associated with large standard errors. Biomass intake rate did differ significantly among sites but this relationship was relatively weak, and biomass intake rate did not differ significantly among substrates (macro and micro) or distances to low water (Table 6.2). Feeding and success rates were not correlated among sites, macro- or micro-substrates ($r = 0.17, n = 11, P = 0.63; r = -0.32, n = 4, P = 0.68$; and, $r = -0.04, n = 7, P = 0.94$ respectively).

Males exhibited higher feeding rates and greater success and biomass intake rates than other birds (females and those of unknown sex; Table 6.1) across most sites and substrates. However, this was only statistically significant for success rate at the two broadscale (between-flat) environmental factors (site and macro-substrate; Table 6.2, Figures 6.2 and 6.3), and the significant result was driven by the large difference between males and others at one site (VPT). With ‘VPT’ removed from the analyses, the statistical significance of age/sex disappeared. Males had a higher biomass intake
rate at mud and sandy-mud macro-substrates than did females, particularly at sites VPT, FI1 and FI2 (Figures 6.2 and 6.3), but due to large standard errors this was not statistically significant.

### Table 6.1
Feeding, success and biomass intake rates (all per bird per minute, means and standard errors), average biomass per prey item consumed, and percent pecks and probes for Eastern Curlews across 11 sites in Moreton Bay. *n* comprises all focal curlews that were walking for at least 2.5 of 3.0 minutes (i.e. actively foraging).

<table>
<thead>
<tr>
<th>Sex</th>
<th>n</th>
<th>Feeding rate mean (SE)</th>
<th>Success rate mean (SE)</th>
<th>Biomass intake rate mean (SE)</th>
<th>Average biomass per prey item mean (SE)</th>
<th>Percent pecks</th>
<th>Percent probes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>197</td>
<td>12.8 (0.42)</td>
<td>0.90 (0.06)</td>
<td>20.1 (3.39)</td>
<td>22.4 (3.83)</td>
<td>49.0</td>
<td>51.0</td>
</tr>
<tr>
<td>Female</td>
<td>145</td>
<td>11.4 (0.44)</td>
<td>0.67 (0.06)</td>
<td>17.6 (2.77)</td>
<td>24.8 (4.26)</td>
<td>36.5</td>
<td>63.5</td>
</tr>
<tr>
<td>Unknown</td>
<td>200</td>
<td>11.2 (0.37)</td>
<td>0.68 (0.04)</td>
<td>16.0 (2.01)</td>
<td>23.2 (3.44)</td>
<td>38.1</td>
<td>61.9</td>
</tr>
<tr>
<td>All</td>
<td>542</td>
<td>11.8 (0.24)</td>
<td>0.76 (0.03)</td>
<td>17.9 (1.62)</td>
<td>23.3 (2.20)</td>
<td>41.9</td>
<td>58.1</td>
</tr>
</tbody>
</table>

1. Age/sex categories were determined by bill length: female = long, male = short, unknown = intermediate.
Table 6.2. Analyses of variance comparing Eastern Curlew feeding, success and biomass intake rates (all per bird per minute) among different categories of site, distances (m) to low water (DLW) and macro- and micro-substrate type across 11 sites in Moreton Bay. For site and macro-substrate, $n = 542$ focal birds; for DLW, $n = 530$; for micro-substrate type, $n = 400$.

<table>
<thead>
<tr>
<th>Environmental factor</th>
<th>df</th>
<th>Feeding rate</th>
<th></th>
<th>Success rate</th>
<th></th>
<th>Biomass intake rate</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$F$</td>
<td>$P$</td>
<td>$F$</td>
<td>$P$</td>
<td>$F$</td>
<td>$P$</td>
</tr>
<tr>
<td><strong>Site</strong></td>
<td>10</td>
<td>6.32</td>
<td>$&lt;0.0001$</td>
<td>6.71</td>
<td>$&lt;0.0001$</td>
<td>1.89</td>
<td>0.044</td>
</tr>
<tr>
<td>Age/sex</td>
<td>2</td>
<td>1.40</td>
<td>0.25</td>
<td>5.70</td>
<td>0.004</td>
<td>2.49</td>
<td>0.08</td>
</tr>
<tr>
<td>Site × Age/sex</td>
<td>20</td>
<td>1.16</td>
<td>0.29</td>
<td>1.78</td>
<td>0.020</td>
<td>0.923</td>
<td>0.56</td>
</tr>
<tr>
<td><strong>Macro-substrate</strong></td>
<td>3</td>
<td>6.88</td>
<td>$&lt;0.0001$</td>
<td>12.23</td>
<td>$&lt;0.0001$</td>
<td>0.84</td>
<td>0.47</td>
</tr>
<tr>
<td>Age/sex</td>
<td>2</td>
<td>1.53</td>
<td>0.22</td>
<td>6.36</td>
<td>0.002</td>
<td>0.85</td>
<td>0.43</td>
</tr>
<tr>
<td>Macro-substrate × Age/sex</td>
<td>6</td>
<td>0.88</td>
<td>0.51</td>
<td>1.41</td>
<td>0.21</td>
<td>0.28</td>
<td>0.95</td>
</tr>
<tr>
<td><strong>Micro-substrate</strong></td>
<td>6</td>
<td>3.05</td>
<td>0.006</td>
<td>5.96</td>
<td>$&lt;0.0001$</td>
<td>1.45</td>
<td>0.20</td>
</tr>
<tr>
<td>Age/sex</td>
<td>2</td>
<td>2.98</td>
<td>0.05</td>
<td>0.88</td>
<td>0.42</td>
<td>0.12</td>
<td>0.89</td>
</tr>
<tr>
<td>Micro-substrate × Age/sex</td>
<td>12</td>
<td>1.65</td>
<td>0.08</td>
<td>0.91</td>
<td>0.54</td>
<td>0.86</td>
<td>0.59</td>
</tr>
<tr>
<td><strong>Distance to low water</strong></td>
<td>8</td>
<td>0.61</td>
<td>0.77</td>
<td>1.13</td>
<td>0.34</td>
<td>0.70</td>
<td>0.49</td>
</tr>
<tr>
<td>Age/sex</td>
<td>2</td>
<td>0.77</td>
<td>0.47</td>
<td>1.35</td>
<td>0.26</td>
<td>1.96</td>
<td>0.09</td>
</tr>
<tr>
<td>Distance to low water × Age/sex</td>
<td>16</td>
<td>1.03</td>
<td>0.43</td>
<td>0.75</td>
<td>0.75</td>
<td>0.75</td>
<td>0.75</td>
</tr>
</tbody>
</table>
Figure 6.2. Eastern Curlew feeding, success and biomass intake rates (all per bird per minute) for each of 11 sites in Moreton Bay (means and standard errors); males (dark bars) versus others (females and unknown). Sites are ordered from highest to lowest average feeding rate. The numbers above the bars on the top graph indicate the number of males (top) and others (bottom) observed at each site. The letters above the bars on the middle graph indicate the macro-substrate type of each site (SA = sand, SM = sandy-mud, MU = mud, and CO = coral).
Figure 6.3. Eastern Curlew feeding, success and biomass intake rates (all per bird per minute) against macro-substrate (at the whole-flat level) across 11 sites in Moreton Bay (means and standard errors); males (dark bars) versus others (females and unknown); s-mud = sandy-mud. Substrates are ordered from highest to lowest average feeding rate. The numbers above the bars on the top graph indicate the number of males and others observed on each macro-substrate.
Figure 6.4. Eastern Curlew feeding, success and biomass intake rates (all per bird per minute) against micro-substrate (within-flat: PLS = pools, SGR = seagrass, SGP = seagrass pools, SAN = sand, MUD = mud, SMU = sandy-mud, and WTR = tidal water) across 11 sites in Moreton Bay (means and standard errors); males (dark bars) versus others (females and unknown). Substrates are ordered from highest to lowest average feeding rate. The numbers above the bars on the top graph indicate the number of males and others observed on each micro-substrate.
Chapter 6. Curlew distribution and foraging success

Of the ten possible correlations among the five components of foraging success across the 11 tidal flats (feeding rate, percent attempts successful, success rate, average biomass per prey item and biomass intake rate), three were statistically significant (Table 6.3). As the average biomass per prey item increased, the biomass intake rate increased but the success rate declined (Table 6.3). Of the three main feeding characteristics measured (feeding, success and biomass intake rates), biomass intake rate showed the best relationship with substrate resistance \( r = -0.28, P = 0.41; \) \( r = -0.10, P = 0.78; \) and, \( r = -0.65, P = 0.03 \) respectively), being higher at sites with low substrate resistance (Figure 6.5). Biomass intake rate was also a much better predictor of curlew density \( r = 0.75, P = 0.007; \) Figure 6.6A) than was either feeding or success rate \( r = -0.02, P = 0.96; \) and, \( r = -0.03, P = 0.93 \) respectively). A negative correlation between substrate resistance and the percent of probes made during feeding (as opposed to pecks) was not statistically significant \( r = -0.24, n = 11, P = 0.47).\)

There was a non-significant negative correlation between substrate resistance and curlew density based on the focal scan counts from the present study across the 11 sites \( r = -0.53, P = 0.097; \) Figure 6.6B). Very similar values were obtained when substrate resistance and the density in summer 1999–2000 from a study of the curlews’ broadscale distribution (Chapter 4) were compared across the same 11 sites \( r = -0.53, P = 0.092).\) However, across the total 32 sites used in the broadscale study (where there was a greater range of curlew densities; Chapter 4), there was a strong negative correlation between substrate resistance and summer curlew density \( r = -0.69, P < 0.0001).\)
Table 6.3. Correlations among the five different components of foraging success in Eastern Curlews across 11 sites in Moreton Bay (*$P < 0.05$; **$P < 0.005$).

<table>
<thead>
<tr>
<th></th>
<th>Feeding rate</th>
<th>Success rate</th>
<th>Percent successful</th>
<th>Average biomass per prey item</th>
</tr>
</thead>
<tbody>
<tr>
<td>Success rate</td>
<td>0.16</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent successful</td>
<td>-0.42</td>
<td>0.75*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average biomass per prey item</td>
<td>-0.03</td>
<td>-0.80**</td>
<td>-0.58</td>
<td></td>
</tr>
<tr>
<td>Biomass intake rate</td>
<td>-0.23</td>
<td>-0.32</td>
<td>-0.09</td>
<td>0.61*</td>
</tr>
</tbody>
</table>

Since females and those of unknown sex did not differ in foraging technique or success (Table 6.1) they were combined for analyses of prey type and size. There were some differences in diet between male and other curlews in terms of prey type alone ($\chi^2 = 12.4$, df = 5, $P = 0.029$), prey type and size combined ($\chi^2 = 21.7$, df = 8, $P = 0.005$; Table 6.4), and prey biomass ($\chi^2 = 28.4$, df = 4, $P < 0.0001$). Males consumed fewer of the lowest biomass items and more mictyrid crabs. The average biomass intake per prey item for females was not significantly different from that of males ($t = 0.41$, $P = 0.34$; Table 6.1). In terms of feeding micro-substrate males preferred mud and sand, while other birds (females and those of unknown sex) preferred seagrass, seagrass pools and tidal water ($\chi^2 = 15.6$, df = 6, $P = 0.016$). There were statistically significant differences between males and females with respect to the feeding techniques employed: males pecked as often as they probed, whereas
females probed almost twice as often as they pecked ($\chi^2 = 190$, df = 1, $P < 0.0001$; Table 6.1).

Success rate was significantly greater during spring tides (0.83, standard error ± 0.04) than neap tides (0.68, standard error ± 0.04; ANOVA $F = 4.88$, df = 1, 541, $P = 0.028$), but feeding and biomass intake rates did not differ significantly (ANOVA $P$ values = 0.48 and 0.88 respectively). Feeding rate was significantly higher early (12.38, standard error ± 0.34) compared with late (11.25, standard error ± 0.33) in the tidal cycle (ANOVA $F = 5.68$, df = 1, 541, $P = 0.018$), but success and biomass intake rates did not differ significantly (ANOVA $P$ values = 0.09 and 0.90 respectively). There were no significant interactions between age/sex and tide type or state (ANOVA $P$ values ranged from 0.10 to 0.90).

![Graph](image)

**Figure 6.5.** Relationship between substrate resistance and biomass intake rate (per minute) across 11 sites in Moreton Bay ($r$ = Pearson's correlation coefficient). Symbols denote the macro-substrate type at each site (s-mud = sandy-mud).
Chapter 6. Curlew distribution and foraging success

**Figure 6.6.** Relationships between (A) biomass intake rate (per minute) and (B) substrate resistance and Eastern Curlew density (no. birds/100 ha, from focal scan counts) across 11 sites in Moreton Bay ($r = $ Pearson's correlation coefficient).

**A** ($r = 0.75, P = 0.007$)

**B** ($r = -0.53, P = 0.097$)

- mud
- s-mud
- sand
- coral
I recorded a total of eight agonistic interactions and 27 cases where curlews fed in close proximity to each other (0.5–3 m). The agonistic interactions comprised four cases of aggressive posturing and calling, and four cases of chasing.

Table 6.4. The percent of prey items consumed within each of 11 categories of prey type and size, compared between male and other (females and those of unknown sex) Eastern Curlews. Biomass is the range of biomass values assigned for each category (see Chapter 5). Prey items are divided into small (sm) and large (lg) based on their size category (sm ≤2 × bill width for all non-polychaete prey and ≤0.5 × bill length for polychaete prey, lg ≥3 × bill width for all non-polychaete prey and >0.5 × bill length for polychaete prey).

<table>
<thead>
<tr>
<th>Prey type and size</th>
<th>Biomass</th>
<th>% in males’ diet</th>
<th>% in others’ diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unseen sm</td>
<td>0.8</td>
<td>32.1</td>
<td>38.5</td>
</tr>
<tr>
<td>Unidentified sm</td>
<td>3–24</td>
<td>31.4</td>
<td>25.0</td>
</tr>
<tr>
<td>Unidentified lg</td>
<td>81–192</td>
<td>1.5</td>
<td>4.7</td>
</tr>
<tr>
<td>Mictyrid crabs sm</td>
<td>3–24</td>
<td>16.4</td>
<td>12.8</td>
</tr>
<tr>
<td>Mictyrid crabs lg</td>
<td>81–192</td>
<td>1.5</td>
<td>1.4</td>
</tr>
<tr>
<td>Brachyuran crabs sm</td>
<td>2–16</td>
<td>5.6</td>
<td>6.8</td>
</tr>
<tr>
<td>Brachyuran crabs lg</td>
<td>54–250</td>
<td>2.8</td>
<td>3.1</td>
</tr>
<tr>
<td>Shrimp and fish sm</td>
<td>4–32</td>
<td>4.3</td>
<td>3.4</td>
</tr>
<tr>
<td>Shrimp and fish lg</td>
<td>108–256</td>
<td>3.4</td>
<td>3.7</td>
</tr>
<tr>
<td>Polychaetes sm</td>
<td>32–108</td>
<td>0.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Polychaetes lg</td>
<td>500</td>
<td>0.7</td>
<td>0.1</td>
</tr>
<tr>
<td>No. of prey items</td>
<td>—</td>
<td>535</td>
<td>701</td>
</tr>
<tr>
<td>No. of focal birds</td>
<td>—</td>
<td>170</td>
<td>266</td>
</tr>
</tbody>
</table>
6.4 DISCUSSION

6.4.1 Components of foraging success and their measurement

Foraging success has different components that may vary in ways that counteract one another. The success rate combines the feeding rate and the percent of feeding attempts that are successful, and the biomass intake rate combines the success rate and the average biomass per prey item (Figure 6.7). In this study I found some significant variation in feeding and success rates with site, feeding habitat and age/sex, but the specific pattern of variation differed between feeding rates and success rates. For example, sites where there was a high feeding rate can offer a low success rate and vice versa: at FI1 where curlews exhibited the second highest average feeding rate, they had the lowest average success rate; and at VPT curlews had the second lowest average feeding rate but the second highest average success rate (Figure 6.2). Similarly, contrasting patterns also occurred across macro- and micro-substrates: on mud, curlews fed at the lowest rate but experienced the greatest success (Figure 6.3); and in pools of water, curlews fed at the highest rate but experienced the least success (Figure 6.4). Therefore, the biomass intake rate arguably provides the best measure of the actual importance of different sites and substrates to curlews, as it best represents the net energy outcome to curlews feeding at different sites. The biomass intake rate was strongly influenced by the average biomass per prey item at a site (Table 6.3).
Success rate alone can be a poor predictor of intake rate, especially when comparing different habitats and prey types (Goss-Custard 1970, Kalejta and Hockey 1994, Durell *et al.* 1996, Barbosa 1997). This is because shorebirds may capture and consume items at a higher rate when prey are small than when they are large (due to greater handling time of larger prey) and larger prey have a greater biomass value. Intake rates have the potential to be much higher when birds consume large prey, even though the feeding rate may be lower (Goss-Custard 1970). For example in this study, as the average biomass per item increased, the biomass intake rate increased but the success rate declined, presumably because of the longer handling times involved with larger items. *Wong et al.* (2000) recorded statistically significant differences in feeding and capture rates in Little Egrets (*Egretta garzetta*) between two mudflats approximately 20 km apart in Hong Kong, but energy intake rates were
almost identical. Small shorebirds, feeding on small and relatively uniform prey may tend to show a greater correspondence between feeding and intake rates (for example, as assumed by Masero 2003) than large, deep-probing shorebirds such as the curlew. This is because larger prey generally bury deeper (Esselink and Zwarts 1989, Zwarts and Wanink 1991, Piersma et al. 1993a) and therefore are more likely to be captured by larger birds with longer bills (Goss-Custard et al. 1977b, Reading and McGrorty 1978, Esselink and Zwarts 1989, Zwarts and Wanink 1993). However, even among Masero’s (2003) small sandpipers, Little Stints (*Calidris minuta*) had a higher feeding rate than the other three calidrid species but their intake rate was lower due to consuming a lower average prey size.

Biomass or energy intake rates take into account the size, type and quality of the prey consumed and therefore are arguably the most meaningful way of assessing the relative importance of feeding habitats to shorebirds (Zwarts et al. 1996, Wong et al. 2000, Goss-Custard et al. 2006). In this study, biomass intake rate (in spite of its high variability between individuals observed) was a far better predictor of curlew density at the site (between-flat) scale than feeding or success rates. Over the non-breeding period, each curlew mostly consumes relatively small prey but occasionally (10–15% of the time) obtains a large item, which has a substantial effect on its overall intake.

### 6.4.2 Differences between the sexes

Bill morphology is intimately linked with foraging behaviour, diet choice and habitat selection (Baker 1979, Barbosa and Moreno 1999, Nebel et al. 2005). Many shorebird species are sexually dimorphic and males and females of these species have been found to exhibit marked differences in feeding characteristics, hypothesised to be an evolutionary mechanism designed to reduce intraspecific competition (Gerritsen
and van Heezik 1985, Durell 2000, Zharikov and Skilleter 2002, Mathot and Elner 2004, Nebel 2005). Shorebirds with long bills have a higher propensity to probe than those with shorter bills (Puttick 1981, Barbosa and Moreno 1999, Zharikov and Skilleter 2002, Nebel et al. 2005). For Eurasian Curlews (N. arquata), almost identical to Eastern Curlews, the female bill (3 cm longer on average than that of the male) allows deeper penetration into the sediment and greater efficiency at extracting prey from deep burrows, whereas the male bill is more manoeuvrable and more adept at catching prey from in and around rocks and small cavities (Ferns and Siman 1994).

In the present study, although the overall feeding rate did not differ significantly between males and females, there were statistically significant differences in feeding techniques used by the different sexes: males pecked as often as they probed whereas females probed twice as many times as they pecked. Male curlews had a significantly greater success rate compared with that of females, even if driven by one or two sites only. Males appeared to be most advantaged at sites broadly categorised as mud and sandy-mud, which in this study contained higher proportions of under-surface obstacles such as rocks, coral or shells (Chapter 4). Also, of those curlews utilising sites predominantly made up of coral, 56% were male, compared with 44%, 24% and 21% at sand, sandy-mud and mud respectively. Males may do better in coral habitats because their shorter bill is better suited to avoiding physical obstructions than the longer female bill, whereas females may be disadvantaged because there are fewer burrows to probe. In addition, at a finer scale (within-flat) females showed a preference for wet micro-substrates (seagrass pools and tidal water) whereas males preferred dry substrates (mud and sand). Wet substrates are more penetrable (Myers et al. 1980, Mouritsen and Jensen 1992) and this result may reflect the females’ higher propensity to probe and/or the males’
greater ability in dealing with less penetrable substrates. Eurasian Curlews (*N. arquata*) tend to probe more often on wet substrates and peck more often on dry substrates (Esselink and Zwarts 1989).

Although the biomass intake of female curlews in Moreton Bay did not differ significantly from that of males, the longer female bill may give a foraging advantage on the breeding grounds. Breeding Eastern Curlews prefer to feed on sphagnum bogs (Ueta and Antonov 2000), but their sex-specific feeding patterns in these habitats have not been described. Berg (1993) in a study of Eurasian Curlews (*N. arquata*) on breeding grounds in Sweden, found that shorter-billed males caught significantly more surface-living invertebrates, whereas longer-billed females caught more earthworms. This was an advantage considering the mean dry weight of earthworms was about 20 times greater than that of surface-living invertebrates and males did not catch enough of the surface-living invertebrates to make up for it (Berg 1993).

6.4.3 Does foraging success determine variation in curlew density?

Previous work (Chapters 4 and 5) in Moreton Bay found that substrate resistance (the inverse of penetrability) was a better predictor of variation in curlew density than either prey density, prey biomass per unit substrate area, or any of a wide range of physical and habitat characteristics of sites. These habitat characteristics that were poor predictors of curlew density included distance to the nearest roost, level of human disturbance (a form of predation risk) and distance to urban settlement (Chapter 4). The present study has found that the relationship between biomass intake rate and curlew density is stronger than the relationship between substrate resistance and curlew density found in this and in my previous study (Chapter 4). This is consistent with the proposition that a high biomass intake rate is the ultimate desirable outcome for migratory shorebirds on their non-breeding grounds.
Although it is often assumed that shorebirds should seek areas in which they may maximise their intake rate, this is not always the case (Kalejta and Hockey 1994, Norris 1999). There are three correlation possibilities between intake rate and bird density. A negative correlation can arise from severe effects of intraspecific competition (prey depletion or interference: Vahl et al. 2005) or the birds’ choosing habitat on the basis of some factor that may be negatively associated with intake rate (Kalejta and Hockey 1994). The absence of a correlation between intake rate and bird density can arise where individuals form an ideal-free distribution (arranging themselves so that resources are evenly distributed: Parker and Sutherland 1986, Stillman et al. 1996, Santos et al. 2005) or when other important factors (such as variation in travel costs: Van Gils et al. 2006) obscures the relationship. A positive correlation between intake rate and bird density is more likely to occur in situations where there is negligible intraspecific competition relative to the available resources (Goss-Custard 1970, Sutherland 1982). There are few studies testing the relationship between intake rate and bird density in the field. I found only two studies on shorebirds that documented empirical evidence of a statistically significant positive relationship between intake rate and bird density among different intertidal flats (Goss-Custard 1970, Sutherland 1982). The present study provides further empirical evidence that biomass intake rate can predict the density of a large, deep-probing shorebird on their non-breeding grounds. In Moreton Bay, curlew density increased with increasing biomass intake rate. The birds tended to congregate where they did better, and the low incidence of agonistic interactions suggests that there was negligible intraspecific competition at good quality (high intake rate) sites.

This raises the question of why so many birds chose to feed in the poorer quality sites. Although the rate of aggression recorded in this study was low, could it
have been enough to deter some birds (for example, leading to an ideal-despotic distribution: Oro 2008)? This is unlikely unless the effects of the recorded aggression were greater than was apparent, or there were more subtle aggressive interactions that were overlooked. Alternatively the occurrence of substantial numbers of curlews in poorer sites could be explained by the birds’ need to sample feeding areas repeatedly (Sutherland 1982). However, this seems unlikely since biomass intake rate is influenced more by substrate resistance and being able to probe effectively than by prey density, and the former is unlikely to change over time. Some individuals may simply have a greater ability to select good quality sites, for example older birds or those in better physical condition (Stamps 2006). It is also possible that success rate could be adequate at most sites and therefore even at poor quality sites, the biomass intake rate did not fall below a critical departure threshold (Van Gils et al. 2003). There may be particular times (such as during bad weather or in the immediate pre-migratory period) when birds in poorer sites would be more disadvantaged, and competition at higher quality sites may be more intense. Longer-term research into the foraging and movement patterns of known individuals of varying age are needed to resolve these questions. Nevertheless, my results suggest that curlew populations are currently not strongly limited by food resources on the non-breeding grounds.
Chapter 7

General discussion

7.1 Foraging logic of deep-probing shorebirds

7.1.1 Substrate preference and bill morphology

Eastern Curlews achieved higher foraging success on less resistant substrates, and this explains a large part of their variation in density across Moreton Bay. Curlew density was highest on intertidal flats of low substrate resistance (Chapters 4 and 5), where biomass intake rate was highest (Chapter 6). Sand was the least resistant substrate and was preferred by feeding curlews at both large scales (between flats) and fine scales (within flats; Chapter 4). The curlew’s long bill provides the opportunity to reach prey deep below the substrate surface, which is a potential advantage. However, a deep prober needs a penetrable substrate free from solid objects buried within the sediment, and containing an adequate density of prey. Curlews feeding in areas where the substrate was highly resistant experienced lower foraging success, and these birds also risk damaging their bills while probing (Chapters 5 and 6). Even minor damage to a curlew’s sensitive bill may reduce its feeding efficiency, which may prevent it from laying down sufficient fat reserves for migration to the northern breeding grounds. Therefore, depending upon the nature of the substrate, a long bill can be either an advantage or a disadvantage for foraging.

In Moreton Bay, Eastern Curlews require deep, soft sediment to be able to use their extremely long bill to its full potential and achieve their greatest foraging
success. Intertidal flats with deep sand deposits are favoured and attract a higher curlew density (Chapters 2 and 4). In general, soft substrates free from solid objects allow deeper probing by shorebirds (Myers et al. 1980, Mouritsen and Jensen 1992) and lower foraging costs (Grant 1984, Gerritsen and van Heezik 1985, Kelsey and Hassall 1989). The results of the present study showed that there was a greater density and biomass of most types of benthic invertebrates in less resistant substrates but the curlews’ choice of feeding habitat was more strongly influenced by the physical nature of the substrate than by the composition or abundance of their prey (Chapter 5).

It seems highly likely that other deep-probing shorebirds also prefer soft substrates, however specific published information on this is lacking. Probing by curlews may be restricted by firm substrates because curved bills are anatomically weaker than equivalent straight bills (Burton 1974, Davidson et al. 1986). All three large curlews feed in a similar way on their respective non-breeding grounds (Goss-Custard and Jones 1976, Stenzel et al. 1976, Goss-Custard et al. 1977a, Piersma 1986, Tulp and de Goeij 1994, Perez-Hurtado et al. 1997, Rippe and Dierschke 1997, Colwell and Mathis 2001, Leeman et al. 2001, Zharikov and Skilleter 2003, 2004b, c), including occasionally feeding on pasture instead of intertidal flats, although the former occurs under particular environmental conditions that increase substrate penetrability and bring prey closer to the surface, making them more accessible (Townshend 1981, Minton 1995, Long and Ralph 2001, Leeman and Colwell 2005). Wet substrates are more penetrable than dry substrates (Myers et al. 1980, Mouritsen and Jensen 1992), and there is some evidence for Eurasian Curlews from the breeding grounds (Berg 1994) and both Eurasian and Eastern Curlews from the non-breeding
grounds (Piersma 1986, Rohweder and Baverstock 1996, Riak et al. 2003; see below) that their preferred feeding habitat consists of wet substrates.

A preference for more penetrable substrates does not necessarily mean that the finer the particle size the better. The softer, more penetrable, substrates are usually also those that are relatively free from hard obstructions that make them resistant to probing. Considering particle size alone, mud would be ‘softer’ than sand. However, in Moreton Bay, substrates consisting of mud frequently had higher proportions of resistant material such as rocks, coral or shells, just below the surface. Therefore, the substrates of some sandflats in Moreton Bay were less resistant than those of some mudflats. Substrates made up of very fine sediment, even if free from solid objects, may also reduce foraging success because wet sloppy mud may inhibit efficient walking by large shorebirds (Evans 1976) or burrowing by their prey (Esselink and Zwarts 1989).

It has been suggested that specialising on hammering open hard-shelled prey, as demonstrated by oystercatchers, is more risky in terms of bill damage than feeding on soft-shelled prey (Durell 2000). However, oystercatchers have relatively short, stout bills. Shorebirds feeding on soft-bodied prey using long, sensitive bills, whether they are probing into homogenous sediment or prey burrows, may be more likely to sustain bill damage by hard substrates or hard objects (Davidson et al. 1986). It is common for primarily probing shorebirds to switch between tactile hunting on soft substrates and visual hunting on hard substrates, even though tactile hunting may be used on hard substrates (e.g. Gerritsen and van Heezik 1985, Rompre and McNeil 1996).

There is some evidence to suggest that Eastern Curlews often feed in seagrass, for example on crabs (*Macrophthalmus crassipes*) in sandy areas of North Stradbroke
Island, Queensland (Zharikov and Skilleter 2004b), and that seagrass is possibly even preferred by males in Western Port Bay, Victoria (Dann 1987). The present study showed that percent seagrass cover was positively correlated with preferred feeding areas at a broad spatial scale \((r = 0.42, P < 0.05; \text{Table 4.1, Chapter 4})\). However, at the within-flat scale, the curlews showed no preference for foraging within stands of seagrass, and even a tendency to avoid them (Chapter 4). This tendency may occur because the dense mat of seagrass rhizomes and roots inhibits effective probing. Bare substrates would be less resistant than substrates of the same sediment composition which are covered with seagrass, and many shorebird species are known to avoid densely-vegetated substrates (Cabral et al. 1999, Raffaelli et al. 1999). For reasons discussed in the next section (7.1.2), male curlews may be more suited to feeding in seagrass, as Dann (1987) suggested.

Within intertidal flats, Eastern Curlews preferred to feed in the wettest areas (close to low water; Chapter 4) where the substrate would have been relatively less resistant than in adjacent dry areas. The curlews’ invertebrate prey may also have been more abundant near low water. Many shorebird species prefer to feed at the lowest levels of tidal exposure (Tulp and de Goeij 1994) and several species even follow the moving low water line down and back up the shore with the retreating and advancing tide (Granadeiro et al. 2006). It has been suggested that this might occur because of higher densities of benthic fauna in the lower sections of the flat, particularly the area exposed only at spring low tides, due to shorebirds gaining access relatively infrequently (Tulp and de Goeij 1994, Granadeiro et al. 2006). In the present study, the curlews’ foraging success rate was significantly greater during spring compared with neap tides, and feeding rate was significantly higher early compared with late in the tidal cycle (Chapter 6). This suggests that the curlews’ best
window of opportunity for feeding is early in the cycle of spring tides, following the
tide as it recedes to its lowest point. Other deep probers seem to behave in the same
way. Intake rate for Eurasian Curlews on the Dutch Wadden Sea was maximised
during the ebbing phase, and to a lesser degree the flooding phase, of the tide; and the
birds probed more often on a wet substrate and pecked more often on a dry substrate
(Zwarts and Esselink 1989). Also, Eurasian Curlews on non-breeding grounds in
Malaysia preferred to feed in wet mud and shallow water (≤4 cm) at the tide edge
(Riak et al. 2003).

7.1.2 Differences between the sexes

In the present study, there were statistically significant differences in feeding
techniques used by the different sexes: longer-billed females probed twice as often as
they pecked, whereas shorter-billed males pecked as often as they probed (Chapter 6).
Male curlews had significantly greater success rates at relatively resistant flats
compared with females (Chapter 6). Also, the proportion of male curlews utilising
sites made up predominantly of coral was much higher than that at sites made up of
sand, sandy-mud or mud (Chapter 6). Males may do better in habitats with relatively
resistant substrates because their shorter bills are better suited to avoiding physical
obstructions than the longer bills of females. Conversely, females may be
disadvantaged in these habitats because there may be fewer burrows to probe. In
addition, females showed a preference for wet micro-substrates (seagrass pools and
tidal water) whereas males preferred dry substrates (mud and sand; Chapter 6). Wet
substrates are more penetrable and this result may reflect the females’ higher
propensity to probe and/or the males’ greater ability in dealing with resistant
substrates. Longer-billed females obtained fewer food items per unit time than other
birds (shorter-billed males and young females) in this study. The average biomass
intake per prey item was nevertheless higher in females (Chapter 6), but this was not statistically significant, meaning that there was no clear evidence that the total biomass intake rate differed between males and females.

Previous research has found that in some situations, female curlews feed alone and defend territories within high quality sandflats containing large, deep-burrowing prey, while males feed in loose flocks, often within areas containing seagrass where prey may be closer to the surface (Dann 1986, 1987, Zharikov and Skilleter 2004a, b). This makes sense in terms of males and females using their different bill morphologies to their best advantage, as females have a longer bill and are therefore able to probe more deeply than males. However, in the present study there was very little evidence of territoriality recorded, with generally low rates of agonistic interaction and no greater incidence of these interactions at better quality flats (Chapter 6). Similarly, Piersma (1986) found no indication of territorial behaviour in Eastern Curlews feeding in South Korea early in the non-breeding period. The present study encompassed large spatial and temporal scales (i.e. the whole of Moreton Bay over the entire non-breeding period) where the quality of intertidal flats for feeding curlews varied widely (Chapters 4 and 5). Curlews are flexible foragers and appear to be territorial only in certain situations, for example at high quality flats and possibly only later in the non-breeding period (Dann 1986, 1987, Piersma 1986, Zharikov and Skilleter 2004a, b).

Male Eurasian Curlews overwintering on the Tees Estuary in north east England preferentially fed on earthworms in pasture irrespective of the tide height, while females fed on polychaete worms in intertidal flats (Townshend 1981), and this is also likely to be the case for Long-billed Curlews overwintering on Humboldt Bay, California (Leeman and Colwell 2005). In these studies, substrate resistance may
have been a factor in explaining the different behaviours of males and females, as pasture (similar to their breeding habitat) would be more resistant than most substrates on intertidal flats.

Owens (1984) argued that the curlews’ long, decurved bill is adapted for reaching and grasping insects among grassland on the breeding grounds. However, Davidson et al. (1986) disagreed on the basis that this explanation does not account for their sexual dimorphism or the fact that other shorebirds with long, straight bills also feed in this way on the breeding grounds. In a study comparing sexual dimorphism and parental role division among 57 shorebird species (all from the Family Scolopacidae and including Eurasian and Long-billed Curlews) during breeding, Jonsson and Alerstam (1990) argued that smaller body size and bill length in males are adaptations for greater parental duties, especially brood attendance. This argument is two-fold: firstly, higher parental efficiency should be achieved by smaller individuals because they need less energy to maintain themselves; and secondly, the shorter bills of males would be more versatile and better suited to foraging on terrestrial breeding grounds.

Although parental care in curlews is shared, males invest more time during the fledgling period (Jonsson and Alerstam 1990, Pampush and Anthony 1993, Gerasimov et al. 1997, Currie and Valkama 2000, Currie et al. 2001). In breeding Eurasian Curlews, males set up and defend a territory and both parents incubate equally but females desert halfway through the fledgling period (c. 16 days after hatching) while males remain with chicks until near independence (c. 35 days after hatching; Currie and Valkama 2000, Currie et al. 2001).

Jonsson and Alerstam (1990) also argued that the longer bills of females enable more efficient energy intake prior to egg formation, through being able to
capture larger, more profitable prey in soft-sediment intertidal zones. It has been suggested that most of the energy reserves required for egg production are gained on intertidal flats at migratory stopover sites several days before egg laying commences (Jonsson and Alerstam 1990, Mulder and Swaan 1992). Eastern Curlews concentrate their foraging efforts on deep burrowing prey which give the greatest energy intake rates (large thalassinid shrimps) immediately prior to northward migration (Zharikov and Skilleter 2004b). Longer-billed females are likely to be more successful in capturing these deep-burrowing shrimp (see Sections 1.1.2 and 1.1.3).

Berg (1993) found that shorter-billed male Eurasian Curlews on the breeding grounds caught significantly more surface-living invertebrates, whereas longer-billed females caught more earthworms and obtained more prey biomass, but concluded that it is difficult to determine whether sexual dimorphism evolved due to differences in foraging on breeding or non-breeding grounds. Breeding Eastern Curlews prefer to feed on sphagnum bogs (Ueta and Antonov 2000), but their sex-specific feeding patterns in this habitat have not been described. The adaptive significance of the longer bills of females cannot be explained with current information, complicated by the fact that the literature contains conflicting arguments.

7.1.3 Distance between feeding and roosting sites

The two main habitat requirements for curlews on non-breeding grounds are sites for feeding at low tide and roosting at high tide. The use of feeding grounds may be affected by their proximity to roost sites (Le Drean-Quenechdu et al. 1995) and vice versa, because minimising the flight distance between feeding and roosting sites conserves important energy reserves (Piersma et al. 1993b, Rogers 2003). In the present study, a very good correspondence between roosting and feeding numbers of Eastern Curlews occurred when sites within about a 5 km radius were grouped, and
this relationship weakened when a scale of 500 m was used (Chapter 3). Thus within Moreton Bay, the distance over which curlews typically travelled between feeding and roosting sites seemed to be in the order of 5–10 km, with high mobility between alternative roosts and/or feeding grounds occurring at or below this distance.

More accurate data on local movements between feeding and roosting sites can only be obtained through telemetry (radio- or satellite-tracking), which has not been conducted to date within the non-breeding period. However, this type of movement data has been obtained for knots, which are relatively large (body size about 155 g and bill length about 45 mm) and probing shorebirds (Higgins and Davies 1996), and as such broadly comparable to curlews. Radio tracking the movements of Great Knots (*Calidris tenuirostris*) in Roebuck Bay, Western Australia, revealed that they generally fly between 1 and 8 km from roosts to feeding grounds (Rogers 2003). This scale of movement is similar to that reported for Red Knots (*C. canutus*) in the Dutch Wadden Sea (Piersma *et al.* 1993b), Western Sandpipers (*C. mauri*) in the San Francisco Bay estuary (Warnock and Takekawa 1996), and various shorebirds in the Wash, east England (Rehfisch *et al.* 1996) and Moray Basin, Scotland (Rehfisch *et al.* 2003).

If feeding close to a good quality roost was limiting the curlews’ distance of operation then there would be some suitable feeding grounds far from roosts left under-utilised. This does not seem to be the case because high curlew densities were recorded at some feeding sites situated at relatively large distances from roosts, and some feeding flats in close proximity to roosts were often unoccupied (Chapters 2 and 3). Some roosts were clearly drawing birds from a relatively wide area of feeding habitat (Chapter 3). Arguably, if distance to roost was driving the choice of feeding area, it should have been a significant predictor in the broadscale analysis of factors
correlated with curlew density on feeding flats (Chapter 4), and the correlations between curlew density and prey density and substrate resistance (Chapter 5) would have been weaker. Therefore, the ultimate aim of feeding in a good quality area seemed to be driving the curlews’ distance of operation, as they appeared to be selecting roost sites in relatively close proximity to feeding grounds rather than feeding close to roost sites.

7.2 Population and habitat assessment

7.2.1 Counts of feeding and of roosting birds

Counts on feeding grounds compared with those on roost sites differ in their sources of error, amount of effort involved and ultimate utility. At roost sites, shorebirds are generally tightly packed into a relatively small area. In comparison, on feeding grounds they are usually loosely aggregated over a relatively large area. While birds on roost sites may be harder to count accurately due to their clumped distribution (Rappoldt et al. 1985, Zwarts et al. 1998), individual birds isolated from main flocks on feeding grounds may be overlooked (Dominguez 1986). The conspicuousness of large, deep-probing shorebirds means that count errors on both feeding grounds and roost sites may be significantly reduced, compared with counts of smaller species (Goss-Custard 1981, Barrett and Barrett 1984, Dominguez 1986, Yates and Goss-Custard 1991). High-tide roost counts may underestimate bird numbers for species that tend to roost in mangroves (Thompson 1993a, Houston and Mitchell 1997), and Eastern Curlews have occasionally been observed exhibiting this behaviour (Houston and Mitchell 1997).
Counting birds on feeding grounds compared with roosts requires a greater area to be surveyed due to their relatively sparse and wide distribution. In contrast, roost counts require a significant proportion of the total number of roosts within a system to be counted on the same day, due to potentially high mobility between alternative roosts (e.g. Peters and Otis 2007), thus requiring a considerable number of observers (Zwarts et al. 1998). Count error may accelerate as the number of observers increases (Goss-Custard 1981). Site fidelity to particular feeding flats may be higher than at roost sites, particularly with species that defend a feeding area (Zharikov and Skilleter 2004a, b), meaning that different feeding areas may be surveyed on different days.

In the present study, the survey of low-tide feeding grounds in Moreton Bay was of a scale and magnitude that is rare worldwide, and the relative numbers of curlews counted on consecutive days corresponded closely (Chapter 2). Due to the consistency of curlew numbers on feeding grounds across count days, one count per season may be sufficient to monitor their population. For shorebirds, accurate surveys of feeding grounds require coverage of whole sections of intertidal flat from high to low water as opposed to strips or plots within laterally divided sections of the flat (Burton et al. 2004, Dias et al. 2006). This is because shorebirds are highly mobile and may use different sections of intertidal flat under different tidal conditions (Burton et al. 2004, Dias et al. 2006). For example, counts of Eastern Curlews, which tend to follow the moving low water line (Chapter 4), that do not include the section close (0–50 m) to the waters edge would underestimate their numbers.

Roost counts may be preferable for population monitoring across different years because less time and effort is involved to survey a significant proportion of the population, even if a large number of observers is required. Furthermore, in discrete
estuaries where mobility is localised there is generally good correspondence between feeding and roosting numbers of birds (e.g. Goss-Custard 1981, Barrett and Barrett 1984, Dominguez 1986, Yates and Goss-Custard 1991) and counts at roost sites are therefore more likely to provide a good indication of the numbers on adjacent feeding grounds (Dominguez 1986, Kirby et al. 1988). At a scale of around 5 km, the present study found a very close correspondence between roosting and feeding numbers of Eastern Curlews in Moreton Bay (Chapter 3). Similarly, good correspondence between roosting and feeding numbers of Eurasian Curlews has been recorded in Burntisland Bay, Scotland (Barrett and Barrett 1984), in the Ortigueira estuary, north west Spain (Dominguez 1986), and on the Wash, east England (Goss-Custard 1981, Yates and Goss-Custard 1991). These findings support the use of counts at roosts for tracking changes in numbers over time, provided that all roosts are known and included in surveys.

7.2.2 Indicators of good feeding habitat

Surveys of roost sites are of limited usefulness in identifying important intertidal feeding habitat (Barrett and Barrett 1984). Shorebird numbers and distribution patterns at intertidal flats are needed to provide information on feeding habitat. However, monitoring bird numbers may not be a reliable way to assess the quality of a site (Winker et al. 1995, Gill and Crawford 1999, West et al. 2005, 2007, Johnson 2007). West et al. (2005) suggested measuring the prey biomass available per bird as a way of monitoring estuary quality for shorebirds. However, it is difficult and time consuming to measure the abundance and distribution of the invertebrate prey of shorebirds (Durell et al. 2005, Stillman et al. 2005).

Ultimately, the best measure of habitat quality is the success of the individuals utilising it (Winker et al. 1995). Biomass or energy intake rates take into account the
size, type and quality of the prey consumed and therefore are arguably the most accurate way of assessing the relative importance of feeding habitats to shorebirds (Zwarts et al. 1996, Wong et al. 2000, Goss-Custard et al. 2006). Biomass intake rate proved to be the best measure of the actual importance of different sites and substrates to curlews in the present study (Chapter 6), as feeding and success rates varied in contradictory ways. However, in terms of assessing and monitoring the quality of feeding grounds for deep-probing shorebirds, measuring the physical properties of the substrate (e.g. penetrability or substrate resistance; see Chapter 4) may be better than measuring biomass intake rate for several reasons (Table 7.1). Particularly because substrate resistance is about twice as time-efficient to measure compared with biomass intake rate and could be simplified even further. When measuring habitat quality directly, the measure must be closely related to a critical resource of the species in question, such as food (Johnson 2007). Substrate resistance was an important predictor of curlew density and their invertebrate prey in the present study (Chapter 5). Knowledge of what habitat characteristics are most important to deep-probing shorebirds (i.e. substrates of low resistance) could be used to map their probability of use across landscapes (see Boyce and McDonald 1999).
Table 7.1. Pros and cons of biomass intake rate versus substrate resistance as measures of habitat quality for deep-probing shorebirds.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Pros</th>
<th>Cons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass intake rate</td>
<td>More closely correlated with curlew density than substrate resistance (Chapter 6).</td>
<td>1More time consuming compared with obtaining a measure substrate resistance, and more than one visit per site is required.</td>
</tr>
<tr>
<td></td>
<td>Provides more information about the birds’ feeding ecology than a measure of substrate resistance.</td>
<td>AFFECTED BY SHORT TERM AND SEASONAL EVENTS (E.G. ADVERSE WEATHER OR HUMAN DISTURBANCE) OR RECENT CHANGES IN HABITAT QUALITY.</td>
</tr>
<tr>
<td></td>
<td>Causes less impact via disturbance to the birds and the sediment than a measure of substrate resistance.</td>
<td>Requires a considerable level of skill to measure.</td>
</tr>
<tr>
<td>Substrate resistance</td>
<td>Closely correlated with curlew density (Chapter 4), prey density (Chapter 5) and biomass intake rate (Chapter 6).</td>
<td>Less closely correlated with curlew density than biomass intake rate (Chapter 6).</td>
</tr>
<tr>
<td></td>
<td>1Less time consuming compared with obtaining a measure of biomass intake rate, and only one visit per site is required.</td>
<td>Causes some disturbance to the birds, their prey and the sediment.</td>
</tr>
<tr>
<td></td>
<td>Not affected by season.</td>
<td>Hauling out large cores is arduous but the method could be refined and simplified to be more efficient in regard to time and effort.</td>
</tr>
<tr>
<td></td>
<td>Minimal skill required for measurement.</td>
<td></td>
</tr>
</tbody>
</table>

1Measuring substrate resistance as performed in the present study required about 7 hours per flat and only one visit (Chapter 4), including travel (1 hour), taking 20 cores (3 hours) and sieving (3 hours). On the other hand, measuring biomass intake rate required about 14 hours per flat and multiple visits (Chapter 6), including the 3-minute focal observations of about 80 birds (6 hours) and travel for eight separate visits (8 hours), as well eight times as much vehicular mileage compared with measuring substrate resistance.

7.3 Habitat change and shorebird response

7.3.1 Substrate structural change

The loss or alteration of foraging habitat is considered to be a major threat to shorebird conservation worldwide (Lane and Sagar 1987, Smit et al. 1987, Durell et al. 1997, Kennish 2002, Straw 2006). Eastern Curlews require deep deposits of soft, penetrable sediment to realise their greatest foraging potential. Like other migratory shorebirds, both their survival during the overwintering period and their subsequent journey to northern breeding grounds depends on obtaining sufficient fat reserves.
Any structural modification of the curlews’ soft-sediment feeding flats that reduces the substrate penetrability may inhibit successful foraging and be detrimental to them. There are several causes of structural modification that may reduce the substrate penetrability of intertidal flats (Table 7.2). Direct effects include activities such as intertidal oyster farming, the compaction of sediments by vehicles, the dumping of rubbish or debris and the artificial building up of beaches by adding foreign sediment to the intertidal zone (i.e. beach filling or nourishment; Peterson et al. 2006). Indirect effects on the structure of soft-sediment intertidal zones can come from processes such as nutrient enrichment.

**Table 7.2.** Potential causes and effects of structural modification that may reduce the substrate penetrability of soft-sediment intertidal zones.

<table>
<thead>
<tr>
<th>Cause</th>
<th>Effect</th>
<th>Action</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intertidal oyster farming</td>
<td>Adds hard material to the substrate in the form of bivalves and the structures they are attached to.</td>
<td>Direct</td>
</tr>
<tr>
<td>The compaction of sediments by vehicles</td>
<td>Reduces interstitial spaces that aid effective probing by shorebirds and burrowing by their prey.</td>
<td>Direct</td>
</tr>
<tr>
<td>The dumping of rubbish or debris</td>
<td>Adds hard material to the substrate.</td>
<td>Direct</td>
</tr>
<tr>
<td>Beach nourishment</td>
<td>May introduce coarser sediment than that naturally occurring.</td>
<td>Direct</td>
</tr>
<tr>
<td>Nutrient enrichment</td>
<td>Resulting macroalgal blooms reduce the penetrability of the substrate surface.</td>
<td>Indirect</td>
</tr>
</tbody>
</table>

Intertidal oyster or mussel farming, whether bottom or suspended culture, may degrade the foraging habitat of shorebirds (Hilgerloh *et al.* 2001, Caldow *et al.* 2003, Connolly and Colwell 2005). The sediment structure may be rendered less penetrable
by the presence of hard-shelled bivalves in abnormally high densities, the structures
used for attaching bivalves (such as trestles) and/or the use of mechanical devices
during harvest (such as dredges; Piersma et al. 2001, Connolly and Colwell 2005).
However, those studies aiming to quantify the affects of these aquaculture techniques
on shorebirds have found mixed results among different species and locations
(Hilgerloh et al. 2001, Caldow et al. 2003, Connolly and Colwell 2005). The fine
organic waste produced by the feeding bivalves themselves and wet depressions
created around poles and along cultivated rows can increase the prey density and
availability to some probing shorebirds (Hilgerloh et al. 2001, Caldow et al. 2003,
Connolly and Colwell 2005). Hilgerloh et al. (2001) found that Eurasian Curlews
occurred at significantly lower densities in tidal flats with oyster-culture plots
compared with control plots in the Saleen Estuary, south west Ireland. Conversely,
Caldow et al. (2003) found that Eurasian Curlews occurred at significantly higher
densities in tidal flats with mussel-culture plots compared with control plots in the
Menai Strait, North Wales. Consequently, the affects of intertidal oyster or mussel
farming on deep-probing shorebirds need to be assessed on a case-by-case basis.

The compaction of sediments by vehicles may reduce the penetrability of the
substrate and thereby inhibit burying by invertebrates and probing by shorebirds.
Evans et al. (1998) noted undesirable effects from the compaction of sediments by
heavy earth-moving vehicles following the restoration of intertidal areas for
shorebirds. Sediment compaction slowed the re-colonisation process of benthic
infaunal species by inhibiting their ability to bury (Evans et al. 1998). In the present
study, the density and biomass of benthic invertebrates was much higher within
substrates of low resistance than within substrates of high resistance (Chapter 5). The
driving of off-road vehicles along sandy intertidal zones is a popular recreational
activity in many coastal areas utilised by shorebirds (Priskin 2003, Moss and McPhee 2006, Schlacher et al. 2008, Schlacher and Thompson 2008). Locally (i.e. around Moreton, North Stradbroke and Fraser Islands; Moss and McPhee 2006, Schlacher et al. 2008, Schlacher and Thompson 2008), off-road vehicles have mainly travelled along eastern surf beaches, however some traffic has occurred along the tidal sandflats of the western side of Moreton Island which the present study found to be good quality feeding habitat for curlews (Chapters 2 and 4). Although these off-road vehicles are not as heavy as earth moving equipment, the intensity of their use in some soft-sediment areas is much greater, and they have been found to cause sediment compaction (Priskin 2003, Schlacher and Thompson 2008) and declines in the diversity and abundance of benthic invertebrates (Moss and McPhee 2006, Schlacher et al. 2008).

Physical modifications of soft sediments that increase their coarseness or hardness such as that caused by the dumping of rubbish or debris (including dredge spoil) and even beach filling (nourishment) are highly likely to degrade feeding habitats for deep-probing shorebirds. Peterson et al. (2006) noted that the filling of beaches with sediment much coarser than that which was naturally-occurring degraded the habitat for foraging shorebirds. The coarse sediment reduced the abundance of benthic invertebrates and the penetrability of the substrate (Peterson et al. 2006). The dumping of dredge spoil may however be important in some areas above highest astronomical tide for providing suitable roosting habitat for shorebirds (Yozzo et al. 2004).

Processes that increase the available nutrients in the intertidal zone (such as sewage discharge and runoff from terrestrial soils) may lead to eutrophication and the proliferation of algal mats (Raffaelli 1999, Lopes et al. 2006). These algal mats may
reduce substrate penetrability and are therefore likely to be avoided by deep-probing shorebirds, unless there is an associated increase in suitable prey at the substrate surface. Lewis and Kelly (2001) reported that Black-tailed Godwits (*Limosa limosa*) avoided areas covered with dense algal mats in Clonakilty Bay, Ireland, because the algae appeared to physically interfere with their probing action. Algal mats initially increase the availability of invertebrate prey to shorebirds, as the prey beneath them move upwards to escape the anoxic sediment forming underneath. However, in time the prey in the algae above the sediment are diminished and if the algal mats persist they become unattractive to foraging shorebirds (Metzmacher and Reise 1994, Cabral *et al.* 1999, Raffaelli 1999, *et al.* 1999, Lopes *et al.* 2006).

Algal mats change the invertebrate assemblages within and underneath them, reducing the density of some species and increasing the density of others (Raffaelli 1999, 2000, Lopes *et al.* 2000, Lewis *et al.* 2003). Algae have an associated range of invertebrate consumers (Raffaelli 2000) and therefore added nutrients may lead to greater densities of certain species. In this way nutrient enrichment could be beneficial for those shorebirds able to feed on the particular types of prey associated with macroalgal blooms (Essink 2003, Morris and Keough 2003). Curlews in the present study consumed a wide range of invertebrates (Chapter 5) and it is possible that they may be initially able to switch to alternative prey and feeding techniques in areas heavily impacted by eutrophication, even if this is not their preferred feeding habitat. However, curlews experience greatest foraging success within bare, soft substrates that allow deeper probing, and it is likely that persistent macroalgal blooms would be relatively poor feeding habitat for them.
7.3.2 Deep-probing shorebirds as habitat generalists

In general, shorebirds with longer bills are able to use a greater number of habitats for feeding than those with shorter bills (Baker 1979). In the present study, curlews foraged in a broad variety of habitats (Chapter 2) and consumed a variety of different types and sizes of prey (Chapter 5). Even flats of high substrate resistance, delivering low biomass intake rates (i.e. marginal or less preferred habitat), were used for feeding by some curlews, these may possibly have been less fit or younger individuals (Chapter 6).


Within intertidal flats of Moreton Bay, Eastern Curlews used most substrates for feeding in roughly the same proportions as they occurred (Chapter 4). Summers et al. (2002) recorded a similar result for Eurasian Curlews, although the study area was predominantly rocky shorelines, the birds exhibited only weak preferences for certain substrates and even foraged for crabs under rocks. During the non-breeding season, Eurasian and Long-billed Curlews are often observed opportunistically feeding on pasture at high tide when intertidal flats are unavailable (Long and Ralph 2001) or
when rain brings earthworms closer to the substrate surface and softens the soil (Townshend 1981, Leeman and Colwell 2005). Thus, deep-probing shorebirds are omnivorous, habitat generalists or opportunists. Their ability to use their long bills to obtain many different types of prey in widely-differing habitats may aid them in coping with future habitat changes. Generalist foraging strategies are theoretically optimal when animals use a wide range of variable habitats, and should equip the species with a better chance of survival in the event of habitat degradation or loss (Kober and Bairlein 2006, Ryall and Fahrig 2006). However, it is also possible that deep-probing shorebirds need to feed on the high quality prey buried within soft sediment on non-breeding grounds, at least during the pre-migratory period, to reach the condition required to make the arduous journey to their breeding grounds (Zharikov and Skilleter 2004b). This may also be the case during migratory stop-overs (particularly the last) to recover from migration and lay down reserves for egg production (Jonsson and Alerstam 1990, Mulder and Swaan 1992).

Therefore it would be prudent to confer the highest protection possible on the curlews’ remaining soft-sediment intertidal habitat at non-breeding grounds and along migration routes, and conduct further research to address the major knowledge gaps revealed by the present study. These crucial priority areas for further research include: comparable studies of Eurasian and Long-billed Curlews to determine if other deep probers also show strong preferences for penetrable substrates; assessing the behaviours and roles of male and female Eastern Curlews on the breeding grounds to determine if either sex has a foraging advantage; and detailed studies into the foraging ecology of Eastern Curlews on their breeding grounds, and at migratory stop-over sites close to their breeding grounds, to determine if the availability of food
resources may be limiting their population in these habitats and further elucidate the adaptive significance of deep probing.
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