Estuarine, Coastal and Shelf Science 80 (2008) 381–390

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Prey versus substrate as determinants of habitat choice in a feeding shorebird

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A R T I C L E I N F O

Article history:
Received 3 April 2008
Accepted 5 September 2008
Available online 13 September 2008

Keywords:
habitat selection
foraging behaviour
Charadrii
wintering grounds
substrate penetrability
macrobenthos
Australia, Moreton Bay

A B S T R A C T

Many shorebirds on their non-breeding grounds feed on macrobenthic fauna which become available at low tide in coastal intertidal flats. The Eastern Curlew *Numenius madagascariensis* in Moreton Bay Australia, varies greatly in density among different tidal flats. This study asks: how important is the abundance of intertidal prey as a predictor of this variation? We quantified feeding curlews' diet across 12 sites (different tidal flats, each re-visited at least eight times), through 970 focal observations. We also estimated the abundance of total macrobenthic fauna, potential prey taxa and crustacean prey on each tidal flat; measured as the number of individuals and a relative biomass index per unit substrate surface area obtained from substrate core samples. We estimated curlew density at each site using low-tide surveys from every site visit.

Curlew density showed a strong positive association with both the density and biomass of fauna and of potential prey (r values all around 0.70) across the 12 flats. Associations with crustacean density and biomass were also statistically significant (r values both 0.60). However, these variables also showed a strong negative correlation with a measure of substrate resistance (based on the amount of hard material in the substrate core), which was the best predictor of curlew density ($r = -0.82$). Curlews were most abundant at sites with the least resistant substrate, and these sites also generally had the highest faunal density and biomass. When the effect of substrate resistance was statistically removed, curlew density was no longer significantly correlated with fauna density and biomass. This suggests that macro-scale habitat choice by Eastern Curlew 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.

1. Introduction

Migratory shorebirds generally utilise very different habitats, great distances apart, during breeding and non-breeding (wintering) seasons (Hale, 1980; Lane, 1987; Piersma, 1997). On the wintering grounds their primary concern is fuelling up in recovery from, and preparation for, long distance migration (Dann, 1987; Piersma, 1997; Battley et al., 2003, 2004; Kvist and Lindstrom, 2003). 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; Goss-Custard et al., 1977; 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, 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., 1993), 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 (Grant, 1984; Gerritsen and van Heezik, 1985; Kelsey and Hassall, 1989).

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doi:10.1016/j.ecss.2008.09.001

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). Finn et al. (2007) 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. However, that study did not measure prey density. 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.

2. Study site and methods

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 (Fig. 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 5000 of the global population of 31 000 Eastern Curlew (hereafter ‘curlew’) during the austral summer months (Thompson, 1993; Watkins, 1993; Driscoll, 1997; Finn et al., 2001). 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) (Finn et al., 2001). 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, 1995) 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; personal observation), reaching a depth of over 20 cm (Barter, 1990; Rogers, 1995).

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 9500 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 Finn et al. (2001, 2002, 2007). Ancillary curlew density estimates were also made, as part of the feeding observations and benthic fauna assessments, as noted below.

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

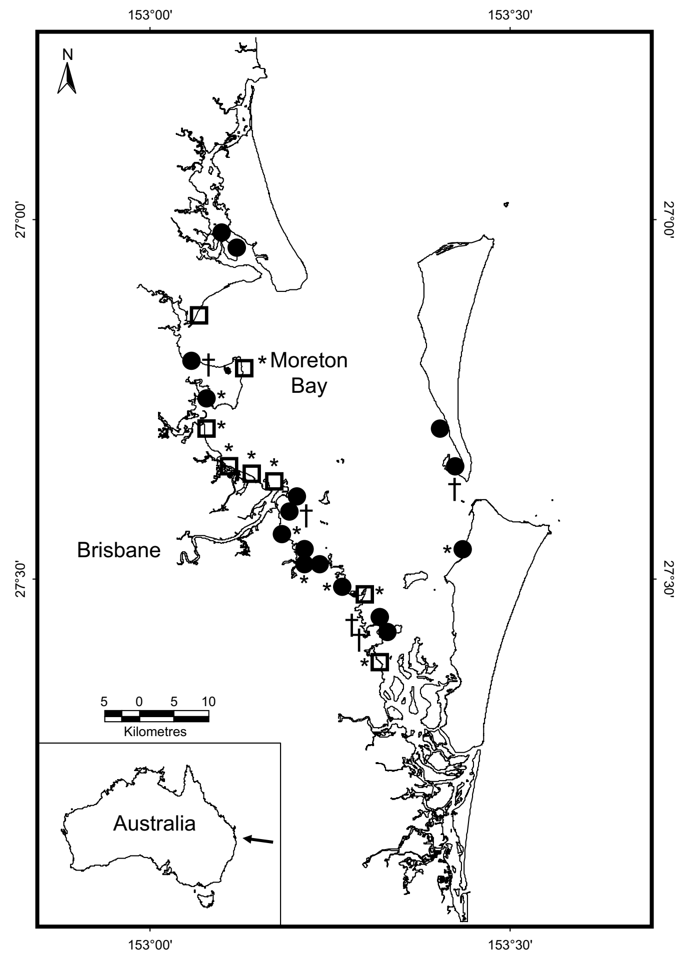

Fig. 1. Sites in Moreton Bay used for observations of curlew feeding and for substrate coring to sample their prey (sites marked with ‘*’ or ‘†’ were only used for coring or feeding observations respectively). Symbols represent: □, low curlew density (<7 birds/100 ha); •, high curlew density (>12 birds/100 ha).

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 (Finn et al., 2001) 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 (Fig. 1). Focal flats ranged in length from 500 to 1500 m, in width from 200 to 1000 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 min 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