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Distribution and prey of migratory shorebirds on the northern coastline of Singapore

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Abstract. Singapore is a part of the East Asian-Australasian Flyway. The identification and continued protection of breeding, wintering and stopover sites within the flyway are essential for the survival of the flyway's migratory shorebirds. Here, we conducted 11 monthly (March 2003 to January 2004) high tide and low tide surveys of shorebirds in eight wetland sites (comprising mainly mangroves and intertidal mudflats) along the northern coast of Singapore. Internationally important numbers of common redshank, common greenshank and Pacific golden plover were found during the southward migration period in two sites. Other common shorebird species in our sites were: whimbrel, marsh sandpiper, common sandpiper, curlew sandpiper and lesser sand plover. Our data suggest that at least common redshank and Pacific golden plover used Singapore's wetlands for staging during southward migration. Two species, curlew sandpiper and lesser sand plover, did not use our sites for wintering, although the latter were found in other, sandier intertidal habitats in Singapore during countrywide winter counts. Mud coring and diet analysis revealed that polychaetes (in particular Family Nereididae) were dominant members of the benthic infauna, and were commonly depredated by shorebirds. The benthic infauna communities of the study sites were rich, with sites containing polychaetes belonging to 8–15 families. At the level of ponds or mudflat patches, we found a weak positive influence of nereidid polychaete density on shorebird abundance during low tides. Given the recent loss of natural habitats from Singapore's shores, we suggest that some of these sites be protected to serve conservation and educational purposes.

Key words. East Asian-Australasian Flyway, intertidal ponds, mudflats, plovers, polychaetes, sandpipers

INTRODUCTION

Human activities in the past century have rapidly altered ecosystems throughout the planet and continue to threaten an increasing number of species with extinction (Barnosky et al., 2011). Habitat change is the greatest driver of biodiversity loss, with natural systems being degraded or converted into other land uses, often permanently (Millenium Ecosystem Assessment, 2005). Nevertheless, even human-dominated and -altered landscapes can contribute to protecting species at risk, especially if their conservation values are accounted for during land-use planning (e.g., Gordon et al., 2009). The conservation of migratory species is especially challenging because they often travel across international boundaries, making concerted conservation efforts hard to implement (Martin et al., 2007; Kirby et al., 2008). To complete their annual journeys, migratory shorebirds stopover in coastal areas and wetlands along their migration routes for resting and refueling. However, vital intertidal habitats have often been converted into other land uses such as aquaculture, salt extraction, and urban development. It is estimated that worldwide, 48% of migratory shorebird populations for which there are sufficient data are declining (International Wader Study Group, 2003). In this respect, routes along the East Asian-Australasian Flyway (EAAF) are of particular concern, as this region is used by more shorebirds (in total numbers) and support more threatened waterbird species than any of the other major flyways (Milton, 2003; MacKinnon et al., 2012). The sharp declines observed in shorebird numbers are in large part attributed to habitat loss and degradation of wetlands and coastal areas used as stopover sites (Barter, 2002; Kirby et al., 2008; Nebel et al., 2008; MacKinnon et al., 2012). Thus, if Asian migratory shorebirds are to be safeguarded from further declines, it is vital to maintain habitat connectivity by preserving stopover sites along the flyway.

Singapore (1°17′N, 103°50′E), is a densely populated (c. 7,400 persons km^{-2}) island city-state that lies at the southern tip of the Malay Peninsula. As an extension of continental Asia, the Malay Peninsula funnels a portion of the migratory shorebirds of the EAAF (especially those that use short-flight hopping strategy) along its coasts down to Singapore, where some remain, but many disperse to other winter grounds (Parish & Wells, 1984; Bamford et al., 2008; Gan et al., 2012; Note: All references to winter in this paper refers to boreal winter). Despite its geographic importance, large-scale coastal land reclamation and damming of rivers, driven by rapid population growth and urbanisation, has led to severe loss of Singapore's wetlands and its ability support shorebirds (Hilton & Manning, 1995; Liow, 2000; Lim,

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Table 1. List of study sites with their descriptions. Asterisks indicate that the site was used by shorebirds as a high tide roost; crosses indicate that site was sampled for benthic infauna.

Site Name (Abbreviation)	Latitude (°N)	Longitude (°E)	Area of mud-flat (km^2)	Area of mangrove abutting mudflats (km^2)	Land use
Khatib Bongsu (KB)*†	1.437	103.854	0.06	0.07	Disused mariculture/ aquaculture ponds
Pulau Seletar (PS)	1.444	103.862	0.005	0.05	Uninhabited; currently part of a water sports zone
Seletar Dam North (SDN)†	1.431	103.86	0.07	0.015	Previously mouth of the Seletar River
Seletar Dam South (SDS)†	1.424	103.865	0.185	0.03	Previously mouth of the Seletar River
Simpang Central (SC)	1.447	103.855	0.03	0.005	Most mangrove drained and filled in; untended land
Simpang North (SN)*†	1.450	103.85	0.04	0.02	Disused mariculture/ aquaculture ponds
Sungei Buloh Wetland Reserve (SBWR)*†	1.447	103.725	0.19	0.365	Protected wetlands
Sungei Mandai (MD)†	1.441	103.765	0.29	0.16	Unprotected mangrove; previously occupied by a village

2009). As an indication of the severity of human disturbance, approximately 90% of mangrove forests have been lost since human settlement (Yee et al., 2010). Despite these threats, there have been some efforts to preserve coastal habitats, such as gazetting a 1.3 km^2 wetland reserve (Sungei Buloh Wetland Reserve [SBWR]) (Gan et al., 2012). Preserved (but unprotected) alongside this wetland reserve are a series of small, isolated patches of mangroves and mudflats that provide a moderate amount of habitat for shorebirds and resident waterbirds.

Here, we describe how migratory shorebirds use these wetland habitat patches along the sheltered north coast of Singapore. Understanding how shorebirds use disturbed wetlands along the fringes of dense urban centers helps to evaluate their importance as wintering and stopover sites. Principally, we investigated changes in abundance of common shorebird species across the non-breeding periods. We also evaluated the importance of each site with respect to Singapore and the entire EAAF based on the number of birds they supported during high and low tides. As Asia's coast becomes more developed, small fragmented coastal wetlands like those of Singapore may play an increasingly important role in sustaining shorebirds during the migratory and wintering periods. Because shorebird distributions can be strongly influenced by the availability of food (Colwell & Landrum, 1993), we also studied the diversity and biomass of benthic infauna, and examined the influence of dominant prey items on shorebird abundance at the pond/mudflat level. By studying shorebird use of these sites, we show that small isolated wetland sites, even when heavily disturbed, can support rich benthic infauna and important numbers of shorebirds when they are migrating or wintering.

MATERIAL AND METHODS

Site descriptions. Singapore is a small city-state with an approximate size of 710 km^2. Its climate is characteristically tropical perhumid, with annual temperatures ranging from 23°C to 32°C, and an annual precipitation of around 2300 mm. Because of the narrowness (<5 km wide) of the Johor Straits that separates Singapore from the mainland (Peninsular Malaysia), wave and tidal energy on the north coastline is low, creating conditions ideal for the growth of mangroves and mudflat formation (Chia et al., 1998). However, because of intense coastal land conversion, the area of mangroves in Singapore has declined dramatically from c. 11% of the land area in the 1820s to about 0.95% presently (Yee et al., 2010).

This study was conducted at eight sites along the northern coast of Singapore that contain remnant coastal mudflats and mangrove habitats. The sites chosen constitute the majority of the larger, relatively intact stands of mangrove remaining in mainland Singapore. These sites were: Khatib Bongsu (KB), Pulau Seletar (PS), Seletar Dam North (SDN), Seletar Dam South (SDS), Simpang Central (SC), Simpang North (SN), Sungei Mandai (MD) and Sungei Buloh Wetland Reserve (SBWR) (Fig. 1). Our study sites vary in the extent of mangrove cover, mudflat area and land use history (Table 1). All of the sites have experienced various forms of disturbance in the past, including human settlement, cultivation, and prawn pond construction (Hilton & Manning, 1995; Friess et al., 2012; Gan et al., 2012). For instance, KB, SN and SBWR contain disused mariculture ponds. Only SBWR is currently protected under Singapore's National Parks Act, and is managed for conservation, educational, recreational and scientific purposes.

Shorebird surveys. At each site, shorebirds belonging to the families Charadriidae and Scolopacidae were counted once (at low tide only) or twice a month (at low and high tides) from March 2003 to January 2004 by the same observers (HCL and Subaraj Rajathurai). Before formal surveys, multiple reconnaissance trips were first carried out to identify all possible shorebird habitats (including potential high tide roosts) within each site. We did not visit a site for subsequent formal high tide counts if no shorebirds were detected during the reconnaissance trips at high tide. The decision of not treating a site as a high tide habitat (i.e., roosting ground) was also based on the physical characteristics of a site (e.g., high grounds within a site were subjected to high levels of human disturbance) and general knowledge of the sites based on past experiences. Despite these precautions, it was possible that birds in inconspicuous or small roosting sites were missed. Further, it was possible that birds roosted outside of our study sites, and in areas not associated with intertidal wetlands (e.g., grass fields). Counts were carried out in good weather, within $\pm$ 1.5 h of the lowest or highest tide of the day. Each site was comprehensively surveyed by walking on embankments, shorelines or other firm surfaces. To ensure that the same counting effort was maintained, we named ponds or sections of the mudflats and used the same look-out points during each visit. We counted and identified shorebird species using 10× 30 binoculars and 40× spotting scopes. Counting at a site was conducted by only one person, who systematically and unidirectionally scanned flocks on the ground to identify and count birds. If birds were disturbed or took flight during a count, the count for that particular pond or mudflat section was restarted after the birds had settled. Both observers had several years of experience identifying and counting shorebirds in Singapore, either as a member of a scientific team or as a professional birding guide. We consulted appropriate local and regional bird guides to aid bird identification and followed nomenclature in Wang & Hails (2007).

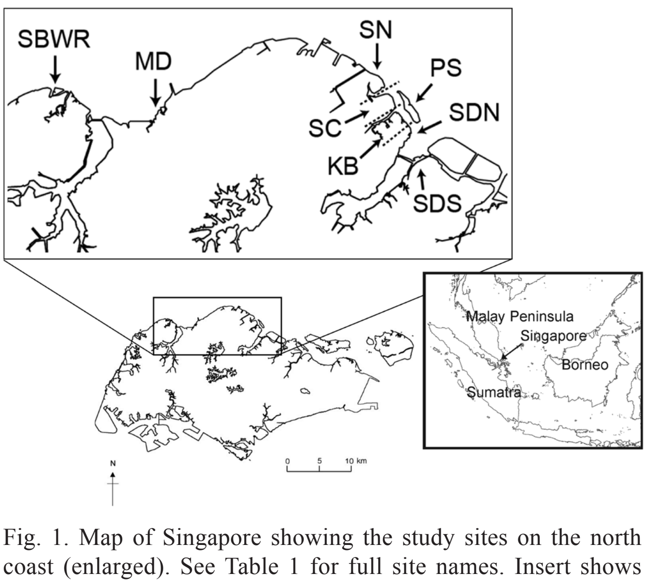

Fig. 1. Map of Singapore showing the study sites on the north coast (enlarged). See Table 1 for full site names. Insert shows position of Singapore in relation the Malay Peninsula and other Southeast Asian islands.

Shorebird diet. To determine dietary preferences of shorebirds, we mist-netted birds during the night using five to six 18 × 2.6 m nets that were set-up along mudflats or embankments. Since nets were placed in open areas, night time netting ensured that the nets were less visible. Trapped birds were fed an emetic (1.5% [weight:volume] potassium antimony tartrate solution); the amount of emetic used was proportional to the weight of the bird (0.8 ml per 100g body mass; Poulin et al., 1994). Regurgitated stomach contents were collected, stored in 70% ethanol and identified. A total of 16 mist-netting sessions were carried out between April and December 2003.

Benthic infauna sampling. Benthic infauna was sampled at all but two sites. Sampling was not carried out in PS because its intertidal shore was primarily sandy. In addition, the extent of mudflat in SC was very small (width $\leq$ 10 m) and therefore it could not be sampled effectively. Each site was sampled over two 11-week periods: once before most migratory birds arrive in Singapore (May–July 2003) and once during the first half of the migratory season (September–December 2003). We collected benthic infauna by inserting a coring device constructed from PVC pipes (diameter 110 mm) during low tide into the mud to a depth of 15 cm (volume of core sample =1249.9 cm^3). Cores were taken 20 m apart along linear transects, which typically extended from the lowest part of the pond/mudflat (seaward edge) to the highest part (landward edge) to sample the greatest variation of benthic communities. In KB, SN and SBWR, transects were located in disused intertidal ponds while at the other sites, transects were located along coastal mudflats. The number of transects at each site ranged from one to five, and the number was roughly proportional to the size of the intertidal area a site contained. Within each site, the ponds or mudflat sections selected for coring were randomly chosen from the available ones. Only one transect was placed within a pond or mudflat section. The number of cores per transect ranged from a minimum of three to a maximum of 10, depending on the length of the transect. This sampling scheme ensured that the number of cores taken from each site was roughly proportional to the area of accessible mudflat. The cored samples were stored in saline formaldehyde solution and then washed through a 2 mm sieve, followed by a 1 mm sieve. Polychaete worms (Class Polychaeta), which were the dominant prey item in the diet analysis, were then picked out using fine forceps, kept in 4% formaldehyde and later identified to family by an expert taxonomist (Christopher J. Glasby, Museum and Art Gallery of the Northern Territory, Australia). Abundance data was collected by counting the number of specimens found, and if the specimens had broken apart, only the heads were counted. The total weight of all polychaete specimens (intact worms and worm fragments) was measured after drying the specimens on absorbent paper towels to remove as much water as possible. Other invertebrates were identified to the levels of Class or Order and counted. Over the two sampling periods, a total 254 core samples were collected and processed.

Data analysis. To determine the importance of sites, we compared the average per-month number of birds of each site during the different periods in the migratory cycle (southward migration, wintering and northward migration) against other sites. We follow Wetlands International's description (Bamford et al., 2008) to define the various periods of a shorebird's annual cycle as: (1) summer (June to July); (2) southward migration (August to November), (3) wintering (December to February) and (4) northward migration (March to May). Using published Wetlands International data and criteria set by the Ramsar Convention on Wetlands and the EAAF Partnership (Bamford et al., 2008), we also determined if individual sites contained internationally important numbers of each shorebird species. A site is considered important if it supports: (1) 1% of the flyway population during the wintering period; or (2) 0.25% of the flyway population during southward or northward migration periods (staging criterion). To generate a general picture of how the eight most common shorebird species (based on this study) utilised Singapore's wetlands as stopover and wintering sites, we pooled, across all sites, the number of birds counted each month and obtained temporal patterns.

To visualise benthic community differences at the transect level, we took average per-core abundance of polychaete worms belonging to different families and analysed them using non-metric multidimensional scaling (NMDS) implemented in the vegan package of R (R Core Team, 2013). Ordination results based on average per-core wet weight of worms (highly correlated to abundance; Pearson's $r > 0.93$) were similar to those based on abundance and are not shown. Given that nereidid worms (Family Nereididae) were the dominant prey item identified in shorebirds stomach contents from the results of the dietary analysis, we used linear least square regression to determine the influence of nereidid abundance on shorebird density at the pond/mudflat level. Specifically, we took the density of shorebirds present during low tides throughout the entire study period for a particular pond or mudflat section and compared them against the average per-core abundance of nereidids (combining data from the two sampling cycles). For this analysis, we only used ponds or mudflats with associated benthic infauna data (i.e., the ponds or mudflats that contained a benthic infauna sampling transect) ($n = 20$).

RESULTS

Shorebird occurrence across the seasons and in different sites. We visited three sites twice a month (once during high tide and once during low tide) and the remaining sites once a month (low tides only) during the 11-month study period. The three sites that were visited twice a month (KB, SN and SBWR) were determined during initial surveys to contain high tide shorebird roosts or suitable habitats. In all, we counted a total of 17,955 shorebirds of 15 species (Table S1). With the exception of the red-wattled lapwing (*Vanellus indicus*), all the shorebird species observed in this study are non-breeding visitors in Singapore (Lim, 2009; Lok & Subaraj, 2009). The total number of birds observed per species ranged from one (broad-billed sandpiper, *Limicola falcinellus*) to 6,960 (Pacific golden plover, *Pluvialis fulva*). The shorebird community visiting our study sites was dominated by eight species, which accounted for 98.3% of the total number of shorebirds counted. These eight species were: whimbrel (*Numenius phaeopus*), common redshank (*Tringa totanus*), marsh sandpiper (*T. stagnatilis*), common greenshank (*T. nebularia*), common sandpiper (*Actitis hypoleucos*), curlew sandpiper (*Calidris ferruginea*), Pacific golden plover and lesser sand plover (*Charadrius mongolus*). Species of non-shorebird waterbirds detected in this study are listed in Table S2.

Our monthly counts reveal different migration patterns of the various shorebird species in Singapore. Of the common species, two (curlew sandpiper and lesser sand plover) visited our study sites almost exclusively during the southward migration period (Fig. 2; Table S1). Two other species (common redshank and Pacific golden plover) also utilised Singapore mudflats relatively more during the southward migration period. The average monthly counts (summed across all sites) during the southward migration period for each of these two species were at least 21.5 % more than the average monthly counts in the northward migration and wintering periods (Table S1). Three species (marsh sandpiper, common greenshank and common sandpiper) occurred in greater numbers during the wintering period than the other periods. Among all the species, only whimbrels were observed to remain in Singapore over the summer period (June–July), albeit in small numbers (average monthly count = 12.5), and most likely as juveniles or subadults (Table S1).

We found significant variation across the study sites in the number of shorebirds they supported during the two periods of passage migration and the wintering period (Fig. 3; Table S1). SBWR was consistently the most important high tide site across all three seasons (seasonal monthly $\bar{x}$: 275.0–1061.75). MD on the other hand, was a highly important low tide site (seasonal monthly $\bar{x}$: 499.0–598.3). Collectively, these two sites accounted for 61.7 % (northward migration period) to 83.3% (wintering period) of all the shorebirds counted during low tides in our sites. During high tides, shorebirds encountered in SBWR were 60.2% (wintering period) to 88.0% (south migration period) of the total in each season (Table S1). To ascertain the importance of each site for specific shorebird species, we compared the maximum number of individuals of each species encountered in one survey during the migration periods and the wintering period against the criteria set by the Ramsar Convention and the EAAF Partnership (Bamford et al., 2008) for each species (Table 2). In SBWR, three species (Pacific golden plover, common redshank and common greenshank) met the staging criterion during high tide counts. MD contained a significant number (>250) of Pacific golden plover in September and November (southward migration) and March and April (northward migration). No site contained internationally important numbers for any species during the wintering period (Table 2).

Shorebird diet. Nineteen shorebirds from five different species were caught in mistnets for the diet analysis, out of which, seven individuals did not regurgitate any undigested prey. For the 12 remaining individuals (of Pacific golden

Table 2. Maximum number of birds counted in one survey during the migratory or wintering periods. SM = southward migration period; NM = northward migration periods; W = wintering period. Numbers exceeding flyway criteria are in bold and italics. In parenthesis are number of monthly counts when a flyway criterion was exceeded.

Migratory period	Site	Tide	Black-tailed Godwit	Broad-billed Sandpiper	Common Redshank	Common Sandpiper	Curlew Sandpiper	Green shank	Lesser Sand Plover	Little Ringed Plover	Marsh Sandpiper	Pacific Golden Plover	Red-necked Stint	Red-wattled Lapwing	Ruddy Turnstone	Terek Sandpiper	Whimbrel
1% of flyway population			1600	250	759	250	1800	600	1400	250	1000	1000	3250	None available	350	600	1000
0.25% of flyway population			400	63	188	63	450	150	350	63	250	250	813	None available	88	150	250
SM/NM	KB	H	0	0	125	10	0	13	0	0	123	48	0	0	0	15	40
SM/NM	SN	H	0	0	28	30	0	4	0	0	31	14	0	0	0	1	0
SM/NM	SBWR	H	4	0	***270 (2)***	18	73	***192 (1)***	0	1	217	***1111 (2)***	0	0	9	19	220
SM/NM	KB	L	0	1	112	11	0	31	4	0	170	103	0	0	0	3	26
SM/NM	PS	L	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
SM/NM	SDN	L	0	0	3	50	10	0	53	0	44	14	58	0	0	2	25
SM/NM	SDS	L	0	0	0	14	1	1	49	0	0	56	15	0	0	0	17
SM/NM	SC	L	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
SM/NM	SN	L	0	0	66	34	0	23	7	1	27	143	0	0	0	2	1
SM/NM	SBWR	L	0	0	81	49	0	9	0	0	163	248	0	1	4	13	4
SM/NM	MD	L	8	0	35	22	335	126	56	0	114	***785 (4)***	0	0	0	7	242
W	KB	H	0	0	15	0	0	40	0	0	80	30	0	0	0	15	14
W	SN	H	0	0	34	24	0	12	0	0	35	83	0	0	0	0	0
W	SBWR	H	0	0	170	11	2	94	1	0	206	162	0	0	0	0	49
W	KB	L	0	0	72	5	0	26	0	0	8	94	0	0	0	8	12
W	PS	L	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
W	SDN	L	0	0	0	30	0	2	0	0	0	0	0	0	0	0	0
W	SDS	L	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
W	SC	L	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
W	SN	L	0	0	19	47	0	9	0	0	38	0	0	0	0	0	0
W	SBWR	L	0	0	169	29	32	32	0	0	173	259	0	1	4	10	4
W	MD	L	6	0	0	6	0	100	0	0	8	365	0	0	0	0	252

plover, common redshank, common sandpiper and lesser sand plover) from which stomach contents were obtained, the majority contained partially digested polychaetes of the genus *Neanthes* (75%). Other prey items found consisted of insects (16.7%), fish (16.7%), and crustaceans (25%) (Table 3).

Benthic infauna communities. A total of 254 benthic cores were collected from six of the study sites (KB, SS, SD, MD, SN, SBWR) in the two sampling cycles. Polychaetes were the most abundant invertebrates in all study sites (Table 4). Our sampling yielded 3,487 polychaete specimens which were

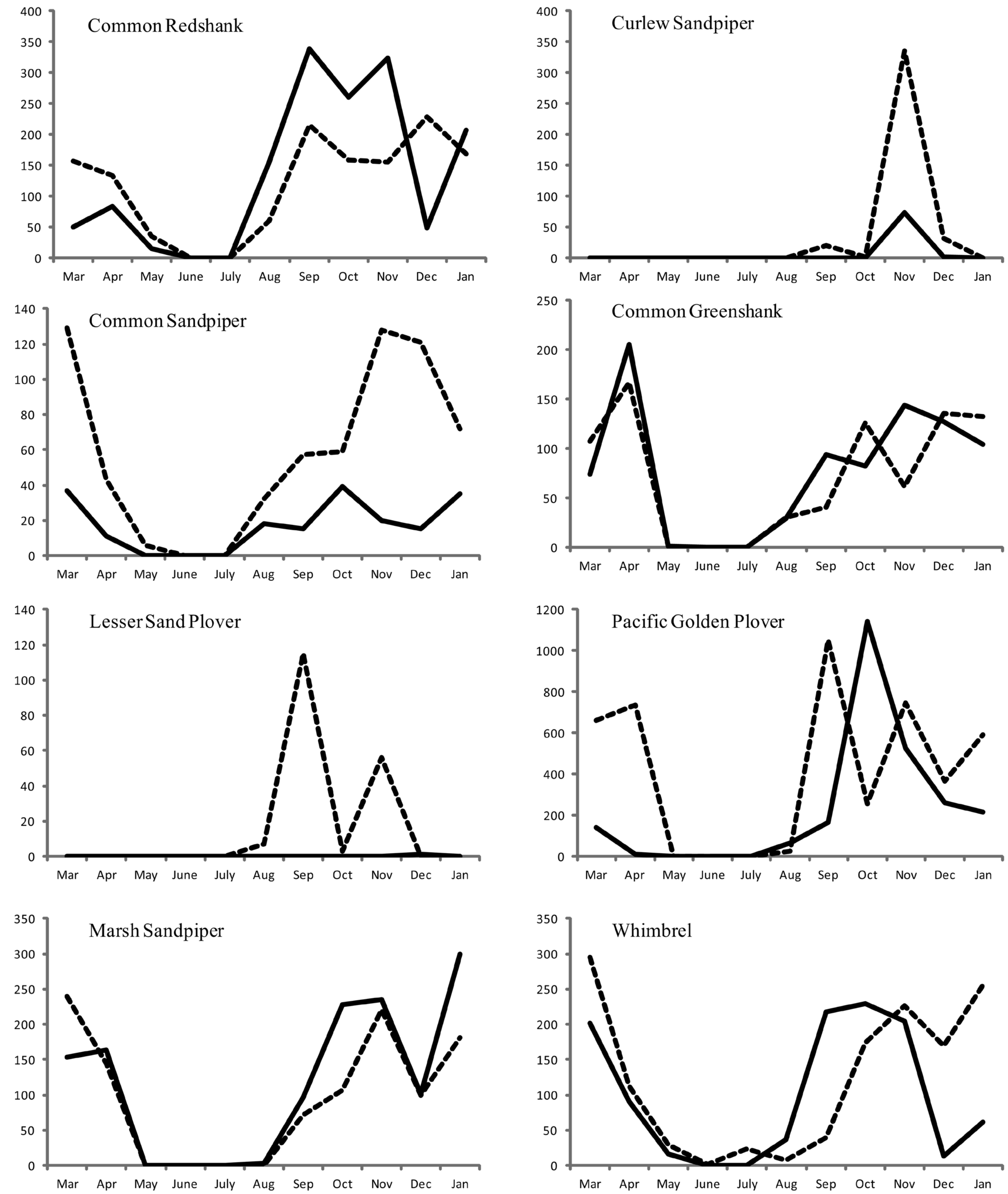

Fig. 2. Monthly counts of the eight most common shorebird species, summed across all study sites. Solid lines represent high tide counts and dashed lines low tide counts.

Table 3. Types of prey consumed by shorebirds caught in mistnets (based on regurgitated stomach contents).

Species	Number of individuals	Stomach contents
Common Redshank	6	Empty
	1	*Neanthes* sp. and crustacean
	1	Fish
Common Sandpiper	2	*Neanthes* sp.
	1	Fish
Lesser Sand Plover	1	*Neanthes* sp.
	1	*Neanthes* sp. and crustacean
	1	*Neanthes* sp. and insect
	1	Insect
Marsh Sandpiper	1	Empty
Pacific Golden Plover	2	*Neanthes* sp.
	1	*Neanthes* sp. and crustacean

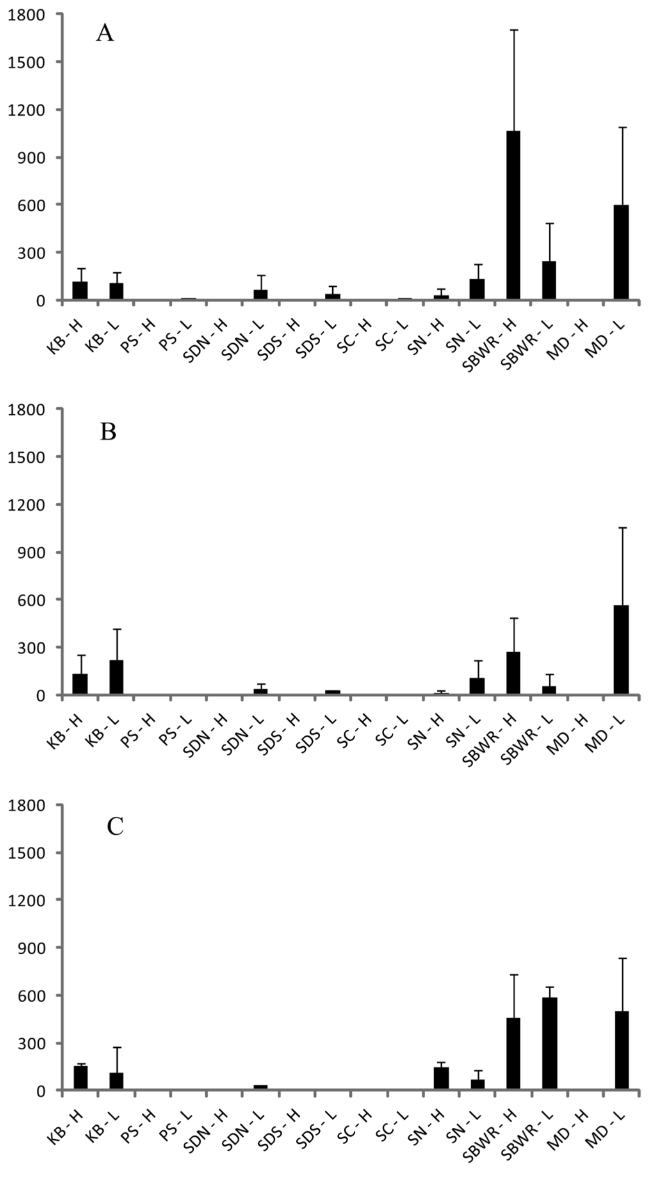

Fig. 3. Average number of birds per month at different tide levels at the study sites during: A, southward migration; B, northward migration; and C, the wintering period. See Table 1 for full site names.

identifiable into 18 families (Table 4). Nereidid worms were the most common and abundant, occurring in 39 out of the 40 sampling transects with an average of 10.98 specimens in each core. Families Chrysopetalidae, Lumberineridae, Nereididae, Orbiniidae, Serpulidae and Syliidae were rare, each being recorded from only one transect throughout the sampling periods. Among the sites, SBWR had the highest polychaete richness at the family-level, as well as the highest average density and biomass per core (Table 4).

Two-dimensional Non-metric Multidimensional Scaling (NMDS) ordination based on Bray-Curtis distances and mean number of worms (per core) in each polychaete family reached an optimal solution with 17 randomised starts (stress = 0.250). The analysis showed that transects from different sites were not highly differentiated in terms of their polychaete communities, as indicated by overlapping minimum convex polygons that link transects of each site in the 2-D NMDS space (Fig. 4). Linear least square regression showed that shorebird density at a pond/mudflat was significantly influenced by nereidid abundance (Fig. 5; Table 5). However, three ponds/mudflats had high standardised residuals (> 2.0) in the regression. Upon their removal, a new regression analysis again showed a positive impact of nereidid abundance on shorebird density, albeit with a lower statistical significance.

DISCUSSION

Shorebird feeding. Our benthic infauna sampling and stomach content analysis suggest that the most common benthic invertebrates (i.e., nereidid polychaetes) were also most frequently depredated by shorebirds. Other studies, conducted either within EAAF or elsewhere, also indicate that shorebirds feed opportunistically and target prey in proportion to their availability (Recher, 1966; Nuka et al., 2005; Iwamatsu et al., 2007; Jing et al., 2007; Zhang et al., 2011), a strategy that likely allows the birds to rapidly accumulate energy reserves during short stopover windows.

At the scale of individual ponds/mudflats, we found that the influence of nereidid abundance on shorebird density was

Table 4. Summary of sampling and results of benthic infaunal density (average number per core with SD in parentheses) in the different sampling sites. See Table 1 for full site names.

Site	KB	SDN	SDS	MD	SN	SBWR
Cycle 1 Dates	May 13	June 21	June 21	May 16 and July 25	June 19	May 27–28
Cycle 2 Dates	Sept 25–26	Sept 26 and Oct 10	Oct 11	Nov 7	Sept 26	Dec 4 and Oct 29
No. of transects (per cycle)	5	3	1	3	4	4
No. of cores (per cycle)	29	20	6	27	21	24
Gastropods	0.28 (0.83)	–	0.08 (0.29)	0.69 (1.27)	0.05 (0.22)	–
Bivalves	0.45 (0.70)	0.45 (1.13)	1.58 (1.31)	0.87 (1.51)	1.0 (1.86)	0.35 (1.02)
Amphipods	1.59 (3.19)	1.63 (3.78)	2.67 (7.44)	0.02 (0.14)	0.60 (2.69)	0.67 (1.96)
Decapods	0.03 (0.18)	–	–	–	0.05 (0.31)	0.69 (1.02
Polychaetes by Family						
Amphretidae	0.12 (0.79)	–	–	–	–	0.04 (0.29)
Capitellidae	0.07 (0.25)	0.18 (0.71)	–	0.2 (0.76)	0.26 (0.80)	1.17 (2.18)
Chrysopetalidae	–	–	–	–	–	0.02 (0.14)
Eunicidae	0.03 (0.26)	0.6 (1.13)	–	0.13 (0.55)	0.33 (0.69)	0.15 (0.55)
Glyceridae	0.02 (0.13)	0.18 (0.55)	0.5 (0.67)	0.04 (0.19)	0.05 (0.31)	–
Hesionidae	–	–	–	0.09 (0.35)	–	0.10 (0.37)
Lumberineridae	–	–	–	–	–	0.02 (0.14)
Maldanidae	0.22 (0.97)	0.10 (0.30)	0.08 (0.29)	–	0.74 (1.13)	0.15 (0.41)
Nereididae	4.60 (5.44)	9.55 (11.53)	8.42 (9.76)	17.74 (22.07)	9.19 (8.26)	18.58 (25.71)
Onuphidae	–	0.23 (0.58)	1.00 (1.26)	–	–	0.08 (0.28)
Orbiniidae	–	–	–	–	0.02 (0.15)	–
Pectinariidae	0.03 (0.18)	–	0.08 (0.29)	0.2 (0.49)	–	0.02 (0.14)
Pilargidae	0.79 (1.50)	0.63 (1.31)	0.58 (1.44)	0.80 (1.38)	0.57 (1.93)	0.13 (0.33)
Poecilochaetidae	0.07 (0.41)	0.23 (0.77)	0.42 (0.90)	–	–	0.15 (0.55)
Sabellidae	0.09 (0.28)	0.05 (0.22)	–	0.09 (0.40)	0.10 (0.30)	0.23 (0.59)
Serpulidae	–	–	–	0.02 (0.14)	–	–
Spionidae	0.03 (0.18)	0.08 (0.27)	0.08 (0.29)	0.09 (0.35)	0.07 (0.26)	0.13 (0.49)
Syliidae	–	–	–	–	–	0.02 (0.14)
$\bar{x}$ polychaete abundance per core	6.09	11.8	11.17	19.35	11.33	20.97
$\bar{x}$ polychaete wet weight per core (g)	0.23	0.51	0.41	0.85	0.56	1.54

weakly positive. Many other studies show that shorebird distribution is strongly affected by the distribution of their invertebrate prey, but these studies were often conducted at larger spatial-scales, such as bays or estuaries (Evans & Dugan, 1984; Hicklin & Smith, 1984). At smaller spatial scales (with sampling sites separated by 10–100 m), this strong relationship tends to diminish or disappear (Wilson, 1990; Colwell & Landrum, 1993), suggesting that different mechanisms dictate shorebird distribution at different spatial scales. Greenberg and Marra (2005) hypothesised that given the short time migrants spend at individual stopover sites, choice of sites are often not based on habitat exploration, but through site fidelity that is transmitted from generation to generation. This strategy is advantageous at larger spatial scales since productivity of sites at these levels tend to be relative stable through time. However, at smaller spatial scales (e.g., individual inlets, ponds, mudflat patches), the attractiveness of a site is often additionally influenced by more ephemeral factors such as substrate resistance (Finn et al., 2008), the extent of sheltering from waves (Placyk & Harrington, 2004), risk of predation (Lank et al., 2003) and water depth (Safran et al., 1997).

Migration pattern in Singapore. Based on the substantial numbers detected during the wintering period (December–February), our study shows that at least six of the eight common shorebird species winter here in Singapore, supporting observations reported by others (Wang & Hails 2007; Gan et al., 2012). Additionally, common redshank and Pacific golden plover appear to use Singapore as a southward migration staging site, based on their higher numbers in August to November. This conclusion is supported by multi-year (2000–2006) high-tide count data from SBWR (Gan, 2007). Average monthly peak counts from SBWR show that common redshank and Pacific golden plover numbers reached maximum in the months of September and November, respectively (Fig. S1). To more accurately determine if shorebird populations in different months comprise transient individuals, turnover studies using individuals with visual marks (e.g., flags) or tracking devices (e.g., geolocators transmitting via cell phone towers) need to be carried out (Straw et al., 2006). The curlew sandpiper, which occurred in large numbers in our study sites only in the month of November, were not common throughout Singapore in January either (AWC, 2000–2006, Table S1). Interestingly, this species once wintered in Singapore in substantial numbers (average = 605.0; AWC, 1992–1993, Table S1), suggesting that the species' winter use of Singapore has declined in recent years. Through long-term flag-sighting and band-recovery studies, individuals of this species have been shown to continue their journeys to Australia, and may return to their breeding sites in spring via a direct overwater Australia-East Asia route (Minton et al., 2011). Another species that was not found in big numbers outside of the southward migration period in our study site was the lesser sand plover. However, this is not a good indicator that the species does not overwinter in Singapore as large numbers (hundreds) have been found in sandier Singapore sites (Crossland, 2002; AWC counts, Table S1), and also, on one occasion, on pontoon structures of off-shore fish farms (Gan, 2004). Overwintering of lesser sand plover away from Singapore sites with muddy substrate (like our study sites) to those with sandy substrate may be a recent phenomenon, as suggested by their declining numbers in SBWR since 2000 (Gan, 2007).

Conservation importance. The conservation of migratory shorebirds, which face increased threats along their entire flyways, requires careful planning and maximising the use of scarce inland and coastal wetland resources. Threats to shorebird populations vary widely; they range from extensive reclamation and intensification of agriculture at stopover sites (Barter, 2002; Amano et al., 2010; MacKinnon et al., 2012), degradation of tundra and boreal breeding areas as a result of changing fire regimes, soil desiccation and tree-line incursion (Sutherland et al., 2012), and disturbance/destruction of wintering areas (Burton et al., 2006). As a staging and wintering site for many shorebirds, Singapore faces the challenge of maintaining viable habitats (mainly coastal wetlands) in the face of competing land uses, a scenario that is playing out in many other places in the flyway (Barter, 2002). Given that many of Asia's cities are found along the coast and human populations are expected to continue increasing (Jones, 2013), the loss and degradation of stopover sites will be one of the key challenges faced by migratory shorebirds of the EAAF in the coming decades.

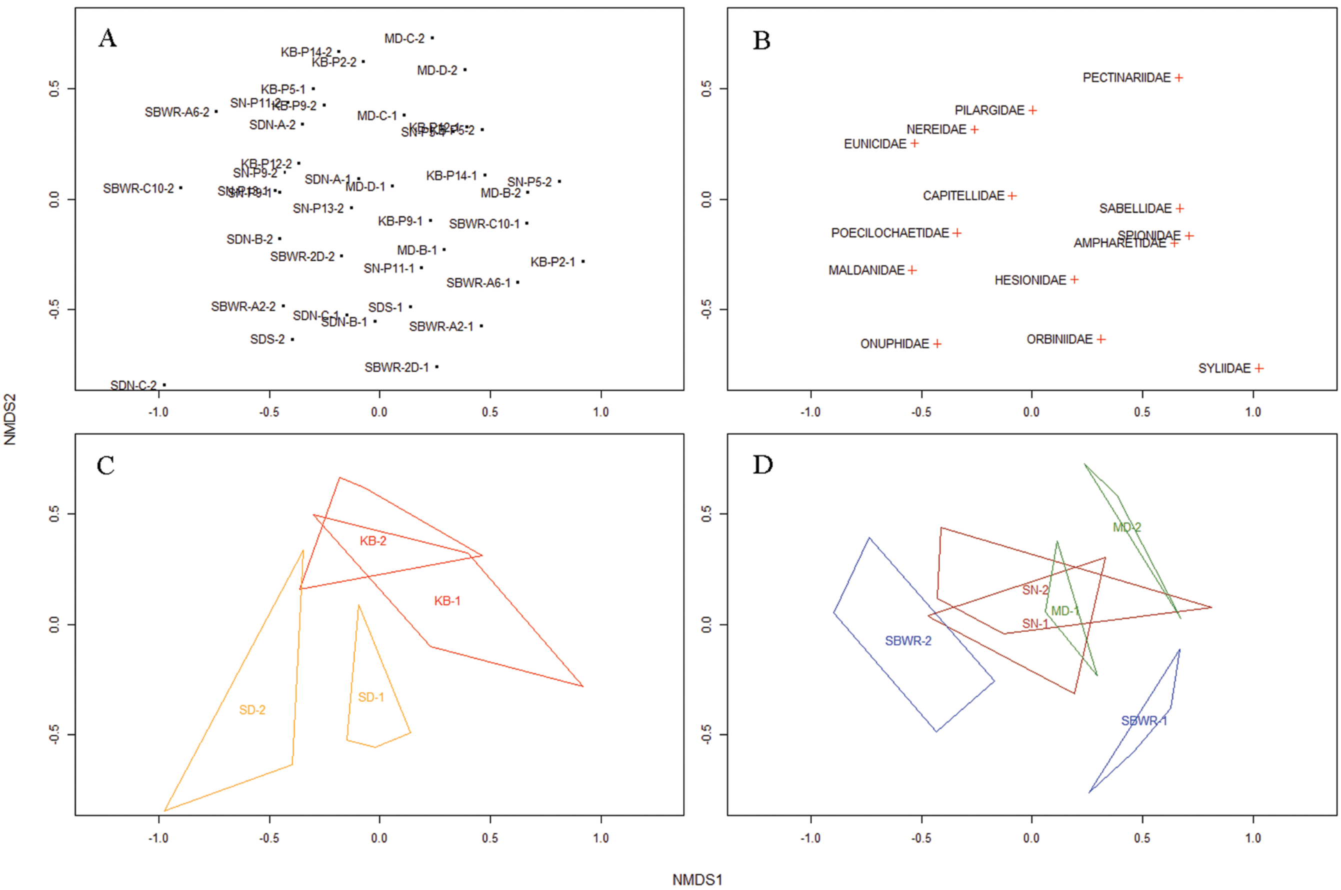

Fig. 4. A, Plot of transects; and B, polychaete families along NMDS axes one and two. A, transects are labeled as "site name", followed by "transect name" (if there were more than one transect in that site) and sampling cycle (one or two). C, D, Transects belonging to different sites and sampling cycles are connected by lines to form minimum convex polygons (e.g., polygon labeled as MD-1 encompasses all transects from Sungei Mandai sampled during cycle one). In the plotting of polygons, transects from SDN and SDS are combined, and collectively labeled as SD. See Table 1 for full site names.

Table 5. Results of linear least square regressions of pond/mudflat shorebird density (per 0.01 km^2) versus average (per core) nereidid (Family Nereididae) worm abundance. Results of two analyses (one with outlier ponds/mudflats removed) are shown.

All ponds/mudflats included (n = 20)				
Predictor	Coefficient	SE Coefficient	*t*-statistic	*P*
Constant	10.93	72.59	0.15	0.882
Average nereidid abundance (per core)	13.00	4.612	2.82	0.011
S = 226.558 R^2= 30.6% adjusted R^2 = 26.8%				
Three outlier ponds/mudflats excluded (n = 17)				
Predictor	Coefficient	SE Coefficient	*t*-statistic	*P*
Constant	22.50	35.74	0.63	0.538
Average nereidid abundance (per core)	6.653	3.460	1.92	0.074
S = 83.9188 R^2 = 19.8% adjusted R^2 = 14.4%				

Our study shows that it is possible to have a small area (less than 1 square kilometer) and provide suitable and regionally important stopover habitats for migratory shorebirds. Among the sites that support birds during high tides, SBWR consistently had the highest numbers. This is attributable to the protected status and management strategies for this site, whereby mudflats are artificially kept dry during high tides (using water control structures) to provide roosting and additional feeding opportunities for birds (Gan & Ang, 2007). This shows that creation of additional roosting sites through intervention measures can be highly effective, especially in situations where much of the landward habitats (high grounds) have been lost to development. During low tides, MD was the most important site overall, followed by SBWR, which was more important than MD as a low tide site for some species (common redshank and marsh sandpiper) (Table S1). These two sites also have the highest polychaete density and biomass, probably a result of the large extent of abutting mangrove forests that generate plant detritus and organic materials (Alongi & Christoffersen, 1992).

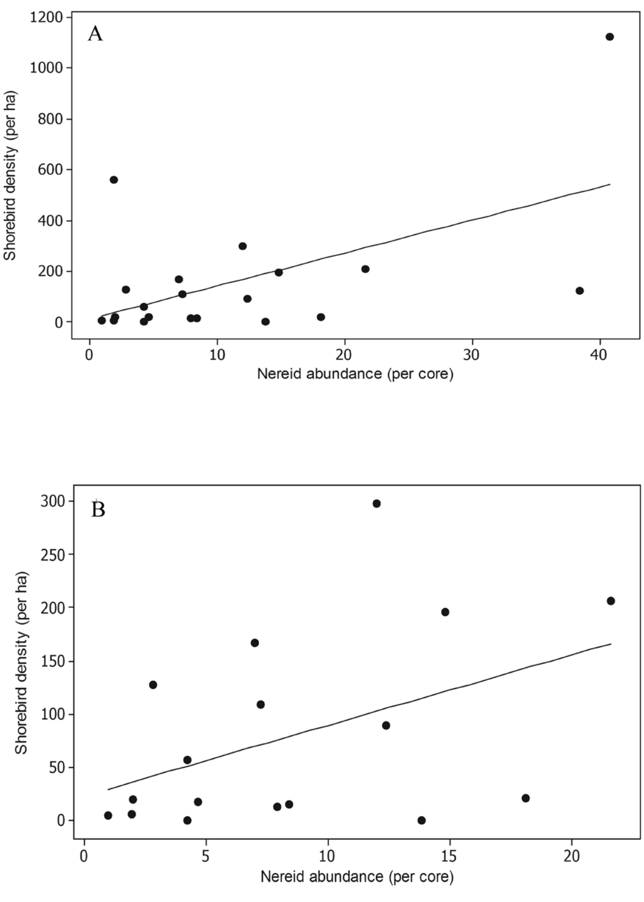

Fig. 5. Plots of linear least square regression showing relationship between nereidid (Family Nereididae) worm abundance and shorebird density at the pond/mudflat level. A, regression with all 20 ponds/mudflats with benthic infauna data; B, regression with three outlier ponds/mudflats removed.

Collectively, our study sites, which were all located in the sheltered north coast of Singapore, provide habitats and feeding grounds for significant numbers of migratory shorebirds that visit Singapore yearly in winter. Their importance is evident when their shorebird numbers are compared to those obtained through the Asian Waterbird Census (AWC), where counts are conducted annually in January (during the wintering period) at various locations in Singapore (Li et al., 2009). For many of the common shorebird species detected, our study sites contained, during the comparable period and at low tide, > 40% of the total number of birds counted throughout Singapore (AWC, 2000–2006; Table S1). However, for other species (e.g., red-necked stint, *Calidris ruficollis* and lesser sand plover), wintering birds tend to be found elsewhere. Not surprisingly, shorebird species found in greater numbers elsewhere in Singapore prefer sandy shores, the other major intertidal habitat generally lacking in our study sites (Crossland, 2002). Considering that Singapore has already lost important wetlands associated with muddy substrates (e.g., Sungei [=River] Serangoon, Sungei Punggol, Sungei Sembawang [Senoko prawn ponds] and Sungei Poyan) to land reclamation or reservoir impoundment (Hilton & Manning, 1995; Wang & Hails, 2007; Lim, 2009), it is critical to consider the conservation values of these remaining wetlands in the sheltered north coast of Singapore. Given its importance as a low tide site and the fact that it probably provides feeding grounds for many of the birds that roost in the nearby SBWR during high tides, MD in particular deserves special attention (Friess et al,. 2012).

While shorebirds numbers in Singapore may not be spectacular when compared to larger sites in the flyway

(Bamford et al. 2008), the island supports wader assemblages similar to that in the nearby Riau archipelago, whose many small coastal or estuarial mudflats may collectively support shorebird numbers rivaling those of nearby large deltaic and coastal mudflats, such as those found in eastern Sumatra (Crossland et al., 2006) and southwestern Borneo (Edwards & Parish, 1998), where tens of thousands of birds were routinely found during the migratory or wintering seasons. More studies in the Riau islands (e.g., conducted in Batam; Crossland & Sinambela, 2005) will also bring into better focus how staging and wintering communities here differ from those found other parts of Southeast Asia. For example, while eastern Sumatra supports large numbers of shorebirds of species that are not common in Singapore (e.g., Asian dowitcher (*Limnodromus semipalmatus*), Eurasian curlew (*Numenius arquata*) and Black-tailed godwit (*Limosa limosa*), the numbers of marsh sandpiper and common greenshank found there have been lower (in tens or hundreds; Crossland et al., 2006).

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APPENDICES

Table S1. Total number of each shorebird species counted during each migratory period of the annual cycle (B = breeding; SM = southward migration; W = wintering; NM = northward migration). Counts are broken down by sites and tides (H = high tide; L = low tide). High tide counts were conducted in only a portion of the sites. Total number of birds counted in Singapore during the Asian Waterbird Census (AWC, two periods: 1992–1993 and 2000–2006; Li et al., 2009) are provided for comparison. Here, we show the total number of birds for each species, averaged across census years. AWC counts were conducted in January during low tides.

Species	Migratory Period	No. of monthly counts in each period	KB		PS	SDN	SDS	SC	SN		SBWR		SM	Grand Total	Average monthly count (all sites combined)		x̄ (SD) number of birds counted in Singapore during AWC (2000-06); 8–10 locations	x̄ (SD) number of birds counted in Singapore during AWC (1992-93); 15 & 17 locations
			H	L	L	L	L	L	H	L	H	L	L		H	L		
Black-tailed Godwit	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	0	0	0	0	0	0	0	0	4	0	9	13	1.0	2.3		
(*Limosa limosa*)	W	2	0	0	0	0	0	0	0	0	0	0	9	9	0.0	4.5	0.1 (0.4)	1.0 (0.0)
	NM	3	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
Whimbrel	B	2	0	0	0	0	0	0	0	0	0	0	25	25	0.0	12.5		
	SM	4	51	22	0	34	0	0	0	1	638	11	380	1137	172.3	112.0		
(*Numenius phaeopus*)	W	2	27	12	0	0	0	0	0	0	49	4	409	501	38.0	212.5	219.7 (140.5)	281.0 (48.1)
	NM	3	56	26	0	37	34	0	0	0	253	4	335	745	103.0	145.3		
Common Redshank	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.		
	SM	4	280	240	0	6	0	0	50	93	746	198	51	1664	269.0	147.0		
(*Tringa totanus*)	W	2	18	72	0	0	0	0	65	19	173	306	0	653	128.0	198.5	308.4 (146.3)	363.0 (135.8)
	NM	3	101	206	0	0	0	0	0	51	50	44	24	476	50.3	108.3		
Marsh Sandpiper	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	41	68	0	44	0	0	31	35	491	230	22	962	140.8	99.8		
(*Tringa stagnatilis*)	W	2	131	8	0	0	0	0	48	38	221	226	8	680	200.0	140.0	312.0 (192.8)	1141.5 (215.7)
	NM	3	151	189	0	0	0	0	0	31	166	32	132	701	105.7	128.0		
Common Greenshank	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	4	9	0	0	1	0	6	32	339	12	205	608	87.3	64.8		
(*Tringa nebularia*)	W	2	66	26	0	2	0	0	19	9	146	46	185	499	115.5	134.0	206.0 (58.7)	368.5 (146.4)
	NM	3	26	57	0	0	0	0	0	39	254	7	172	555	93.3	91.7		
Terek Sandpiper	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	25	3	0	2	0	0	1	2	45	19	7	104	17.8	8.3		

Table S1. Cont'd.

Species	Migratory Period	No. of monthly counts in each period	KB		PS	SDN	SDS	SC	SN		SBWR		SM	Grand Total	Average monthly count (all sites combined)		$\bar{x}$ (SD) number of birds counted in Singapore during AWC (2000-06); 8–10 locations	$\bar{x}$ (SD) number of birds counted in Singapore during AWC (1992-93); 15 & 17 locations
			H	L	L	L	L	L	H	L	H	L	L		H	L		
(*Xenus cinereus*)	W	2	23	8	0	0	0	0	0	0	0	14	0	45	11.5	11.0	21.0 (22.9)	57.5 (58.7)
	NM	3	10	1	0	0	0	0	0	0	0	3	0	14	3.3	1.3		
Common Sandpiper	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	10	26	4	36	22	9	16	60	66	80	39	368	23.0	69.0		
(*Actitis hypoleucos*)	W	2	0	5	4	60	0	2	39	66	11	45	11	243	25.0	96.5	121.6 (54.1)	208.0 (56.6)
	NM	3	5	11	0	65	26	0	41	36	2	6	34	226	16.0	59.3		
Ruddy Turnstone	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	0	0	0	0	0	0	0	0	16	7	0	23	4.0	1.8		
(*Arenaria interpres*)	W	2	0	0	0	0	0	0	0	0	0	5	0	5	0.0	2.5	3.6 (2.1)	8.5 (12.0)
	NM	3	0	0	0	0	0	0	0	0	0	1	0	1	0.0	0.3		
Red-necked Stint	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	0	0	0	58	15	0	0	0	0	0	0	73	0.0	18.3		
(*Calidris ruficollis*)	W	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0	111.1 (169.2)	33.5 (24.7)
	NM	3	0	0	0	0	15	0	0	0	0	0	0	15	0.0	5.0		
Curlew Sandpiper	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	0	0	0	10	1	0	0	0	73	0	345	429	18.3	89.0		
(*Calidris ferruginea*)	W	2	0	0	0	0	0	0	0	0	2	32	0	34	1.0	16.0	11.0 (19.5)	605.0 (248.9)
	NM	3	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
Broad-billed Sandpiper	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	0	1	0	0	0	0	0	0	0	0	0	1	0.0	0.3		
(*Limicola falcinellus*)	W	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.0 (0.0)	0.0 (0.0)
	NM	3	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		

Table S1. Cont'd.

Species	Migratory Period	No. of monthly counts in each period	KB		PS	SDN	SDS	SC	SN		SBWR		SM	Grand Total	Average monthly count (all sites combined)		x̄ (SD) number of birds counted in Singapore during AWC (2000-06); 8–10 locations	x̄ (SD) number of birds counted in Singapore during AWC (1992-93); 15 & 17 locations
			H	L	L	L	L	L	H	L	H	L	L		H	L		
Pacific Golden Plover	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	40	46	0	14	56	0	25	286	1828	410	1271	3976	473.3	520.8		
(*Pluvialis fulva*)	W	2	46	94	0	0	0	0	120	0	309	487	376	1432	237.5	478.5	1133.9 (229.5)	2053.0 (142.8)
	NM	3	54	179	0	0	0	0	0	153	100	77	989	1552	51.3	466.0		
Little Ringed Plover	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	0	0	0	0	0	0	0	1	1	0	0	2	0.3	0.3		
(*Charadrius dubius*)	W	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0	32.9 (54.6)	69.5 (13.4)
	NM	3	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
Lesser Sand Plover	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	0	4	0	53	50	0	0	10	0	0	64	181	0.0	45.3		
(*Charadrius mongolus*)	W	2	0	0	0	0	0	0	0	0	1	0	0	1	0.5	0.0	315.9 (336.2)	475.5 (420.7)
	NM	3	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
Red-wattled Lapwing	B	2	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		
	SM	4	0	0	0	0	0	0	0	0	0	1	0	1	0.0	0.3		
(*Vanellus indicus*)	W	2	0	0	0	0	0	0	0	0	0	1	0	1	0.0	0.5	0.3 (0.8)	1.0 (1.4)
	NM	3	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0		

Table S2. Non-shorebird species counted during the surveys across all migratory periods, broken down by sites and tides (H = high tide; L = low tide). High tide counts were conducted in only a portion of the sites.

Species	KB		PS	SDN	SDS	SC	SN		SBWR		MD	Grand Total	Average monthly count (all sites combined)	
	H	L	L	L	L	L	H	L	H	L	L		H	L
Lesser crested tern (*Sterna bengalensis*)	0	0	0	0	20	0	0	0	0	0	1	21	0.0	1.9
Great crested tern (*Sterna bergii*)	0	0	0	10	16	0	0	0	0	0	0	26	0.0	2.4
Little tern (*Sterna albifrons*)	0	0	0	0	8	0	0	0	0	0	57	65	0.0	5.9
White-winged tern (*Chlidonias leucopterus*)	0	0	0	0	0	0	0	0	0	0	6	6	0.0	0.5
Little egret (*Egretta garzetta*)	0	24	0	203	13	0	39	68	288	410	300	1345	29.7	92.5
Chinese egret (*Egretta eulophotes*)	0	0	0	5	2	0	0	0	0	0	0	7	0.0	0.6
Pacific reef egret (*Egretta sacra*)	0	0	0	8	0	0	0	0	0	1	0	9	0.0	0.8
Grey heron (*Ardea cinerea*)	0	16	14	240	179	6	6	22	20	16	87	606	2.4	52.7
Purple heron (*Ardea purpurea*)	0	0	0	0	0	0	1	0	3	3	1	8	0.4	0.4
Great egret (*Casmerodius albus*)	0	1	0	7	0	0	4	4	17	12	47	92	1.9	6.5
Intermediate egret (*Mesophoyx intermedia*)	0	0	0	0	1	0	0	1	2	17	0	21	0.2	1.7
Chinese pond heron (*Ardeola bacchus*)	0	3	0	0	0	0	0	0	4	13	3	23	0.4	1.7
Striated heron (*Butorides striatus*)	1	131	2	72	39	10	1	31	19	42	85	433	1.9	37.5
Black-crowned night heron (*Nycticorax nycticorax*)	0	1	0	0	0	0	0	1	2	1	6	11	0.2	0.8
Yellow bittern (*Ixobrychus sinensis*)	0	4	0	0	0	0	0	0	0	4	0	8	0.0	0.7
Black bittern (*Dupetor flavicollis*)	0	0	0	0	0	0	0	0	0	0	1	1	0.0	0.1
Milky stork (*Mycteria cinerea*), Painted stork (*Mycteria leucocephala*) or hybrid between the two	0	0	0	0	0	0	0	5	16	12	0	33	1.5	1.5

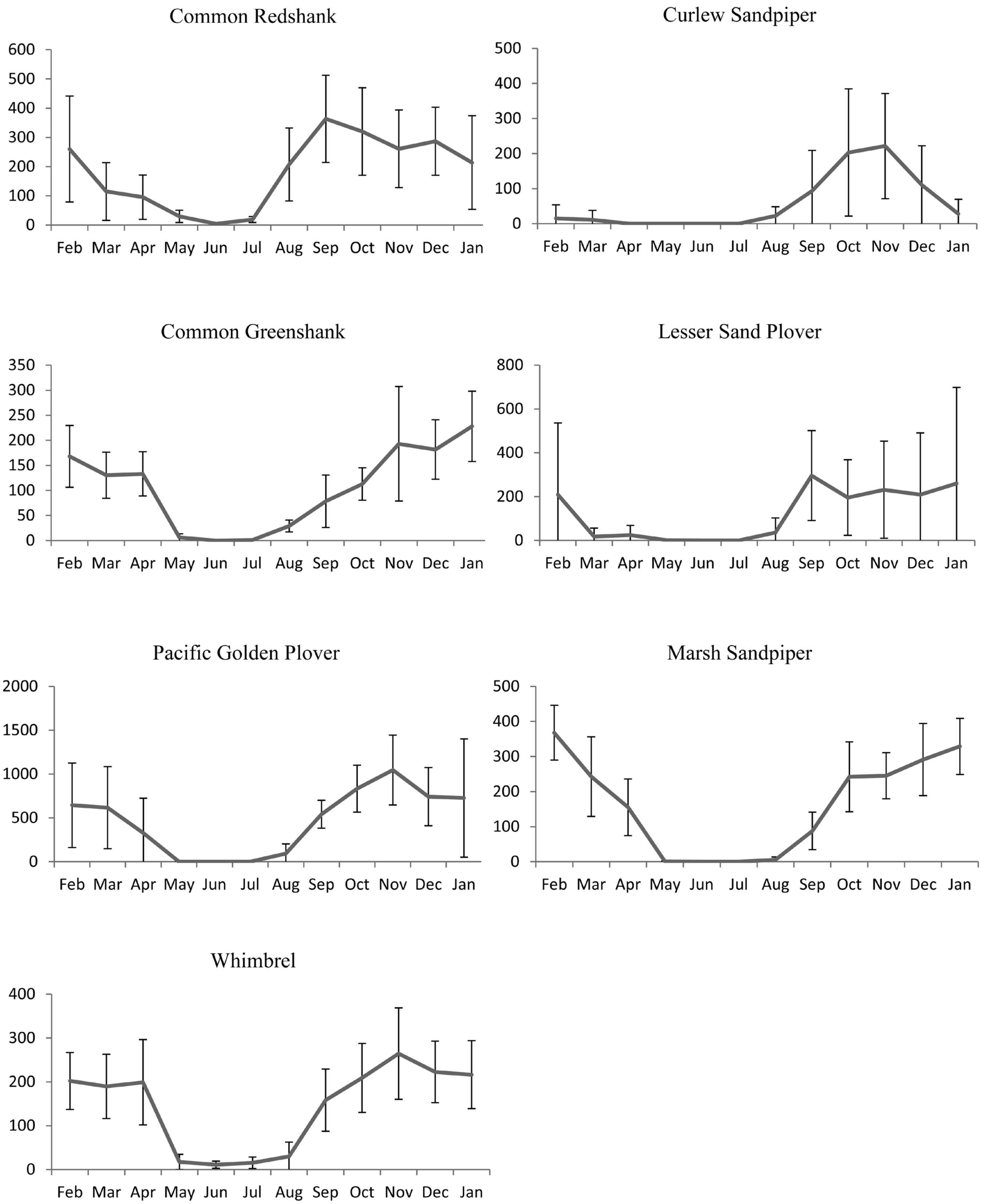

Fig. S1. Average monthly high tide peak counts of seven shorebird species from Sungei Buloh Wetland Reserve. Counts were conducted from 2000 to 2006. Error bars indicate standard deviation. Raw data from Gan (2007).