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Effect of Food Supply on Foraging Patterns and Body Weights of Long-toed Stints (*Calidris subminuta*)

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Abstract.—Multiple species of shorebirds are now globally threatened, particularly across tropical Asia, yet we know relatively little of the detailed habitat usage and resource characteristics of sites in the region. The objective of this study was to determine how seasonal variation in food density affected foraging patterns and body weights of Long-toed Stint (*Calidris subminuta*), a relatively common winter visitor. Research was conducted during the passage and overwintering seasons in wastewater treatment ponds and salt-pans on the Inner Gulf of Thailand. Predictions were that during periods of higher food density, shorebirds should be relatively more abundant and heavier, and have increased foraging attempts, reduced step rates and reduced chase rates. Furthermore, adults were expected to have higher weights than juveniles. Overall, shorebird abundance was significantly positively correlated with invertebrate abundance during the 2-year study period. Long-toed Stints had greater body mass following their arrival in July-September, compared with later periods during the winter. Although food density and Long-toed Stint step rate were not significantly correlated, the data were consistent with previous studies suggesting a negative relationship. Step rates in salt-pans were significantly higher than in the wastewater treatment ponds, probably reflecting lower food densities in the salt-pans. There was no clear relationship between food density and Long-toed Stint peck rate, perhaps reflecting the weak correlation between number of pecks and the number of successful foraging bouts as well as limited sample sizes for prey estimates. There was no significant relationship between food density and chase rates. There was no significant difference in median body mass between adults and juveniles/first-year birds, implying young birds learn to forage as efficiently as adults relatively rapidly. This study suggests that further work on invertebrate dynamics and shorebird diets in the region is needed in order to build more predictive models of shorebird site usage and population dynamics. Received 1 March 2013, accepted 12 July 2013.

Key words.—*Calidris subminuta*, foraging patterns, invertebrates, Long-toed Stint, Thailand.

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Food supplies on staging and wintering grounds are of critical importance to migratory shorebirds (Howes and Bakewell 1989), many of which are now globally threatened (Barter 2002; International Wader Study Group 2003; BirdLife International 2004; MacKinnon *et al.* 2012). Specifically, food availability on staging grounds may be synchronized with weight gain (Verkuil *et al.* 2006), and weight gain is typically associated with higher survival and reproductive success (Schneider and Harrington 1981). However, most shorebirds require specific foods

and habitats, which restrict staging sites for particular shorebird species (Verkuil *et al.* 2006). Furthermore, the abundance of typical foods for shorebirds, such as polychaetes and chironomids, are affected by many factors, including monsoonal rains, water quality, temperature (at least in the temperate zone) and intensity of predation by shorebirds or other predators (Dudgeon 1999; Jearakul 2000; Hongsing 2003; Tellioglu *et al.* 2008).

Despite the importance of stopover sites for shorebirds, little is known regarding food

availability for shorebirds in Southeast Asia, particularly at staging and wintering sites with large concentrations of shorebirds, in a region where wetlands are under significant threat particularly from habitat loss from beach development (BirdLife International 2004). Greater understanding of how shorebirds respond to seasonal changes in food supply and how food supply varies in relation to habitat type may assist decision makers in prioritizing sites for conservation as well as restoration (Goss-Custard *et al.* 1984; Maron and Myers 1985).

The objective of this study was to determine how seasonal variation in relative food abundance affected the foraging of the Long-toed Stint (*Calidris subminuta*). The Long-toed Stint is a small shorebird (22-26 g) that breeds in northern Asia and winters in South and Southeast Asia to Australasia (BirdLife International 2013). During the non-breeding season, Long-toed Stints are mainly found on shallow inland wetlands, and freshwater, brackish, or saline ponds on salt farms, only rarely occurring on intertidal mudflats (Higgins and Davies 1996; BirdLife International 2013). We examined prey capture rates, rates of aggressive interaction among Long-toed Stints (chasing rates), step rates, and body mass. We selected the Long-toed Stint as a target species because individuals occur regularly in the region and could be relatively easily captured for study. They are a common winter visitor to Southeast Asia and are currently listed as a species of Least Concern (Birdlife International 2013). We predicted that during periods of higher food density, shorebirds (all species as well as Long-toed Stints) should be more abundant based on previous studies that showed that shorebirds track resources through time (Schneider and Harrington 1981), are heavier (Verkuil *et al.* 2006), and have higher foraging (defined here as feeding attempts) rates (Goss-Custard 1977b; Goss-Custard *et al.* 1984). As actual foraging success is often difficult to measure (Beauchamp 2012), we also looked at step rates, which we predicted to be inversely correlated with increasing prey density (i.e., more foraging attempts per distance traveled; Goss-Custard and

Durell 1987; Wilson and Vogel 1997; Minderman *et al.* 2006; Santos *et al.* 2006). We expected aggressive interactions between birds to be more common when bird density was high and food density was low as birds should then be more likely to compete for patchy resources (Groves 1978; Goss-Custard *et al.* 1984). Furthermore, if juveniles are less proficient at foraging than adults, outside of molting periods we would expect them to have lower body weights (Johnson 1985; Goss-Custard and Durell 1987; Verkuil *et al.* 2006).

METHODS

Study Area

The Inner Gulf of Thailand is an important shorebird staging and wintering site on the East Asian-Australasian Flyway. It is a wetland complex of international priority and is classified as an Important Bird Area (BirdLife International 2004), consisting of 800-1,000 km² of mudflats, coastal salt-pans, prawn-capture ponds and unused coastal flats (Erftemeijer and Jugmongkol 1999; Manopawitr and Round 2004). At least 56 shorebird species have been recorded in the Gulf, 19 of which occur in internationally important concentrations (Round 2006; Round *et al.* 2007; Round and Gardner 2008). The study was conducted from August 2006-April 2008 at the Laem Phak Bia Environmental Research and Development Project (Laem Phak Bia), Phetchaburi Province (13° 02' 59.75" N, 100° 05' 13.64" E) in south central Thailand (Fig. 1), a site known to harbor one of the highest diversities of shorebirds in the Inner Gulf (Sripanomyom *et al.* 2011). Habitats within and around Laem Phak Bia consisted of wastewater treatment

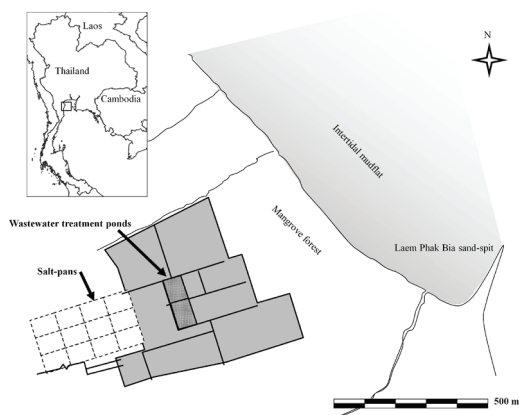


Figure 1. Map of the Laem Phak Bia study area. Salt-pans and wastewater treatment plots are noted with arrows.

plots, small mudflat ponds ($75 \times 200 \text{ m}^2$), salt-pans, small grasslands ($50 \times 100 \text{ m}^2$), mangroves, and intertidal mudflats. The wastewater treatment plots and salt-pans were separated by 0–18 cm deep ponds of a lagoon wastewater treatment system. Many shorebirds, especially Long-toed Stints, used the wastewater treatment plots for roosting and feeding throughout their non-breeding season. Six species of mangroves occur naturally in the study area: *Avicennia alba*, *A. officinalis*, *A. marina*, *Rhizophora apiculata*, *R. mucronata* and *Bruguiera cylindrica* (Hongsing 2003). Three of these (*R. apiculata*, *A. marina* and *B. cylindrica*), together with another species, *Ceriops tagal*, were planted perpendicular to the seashore in the wastewater treatment lagoons beginning in April 1997 (Jearakul 2000). The planted *B. cylindrica* and *C. tagal* remained small ($< 1 \text{ m}$ in height) and generally failed to grow (Fig. 1). The area contained mostly muddy ponds, with standing water up to 5 cm deep depending on rainfall and management, leaving approximately 50–70% of the area sufficiently shallow for Long-toed Stint foraging depending on the tides and the season. There was a sparse cover of shoots ($< 1 \text{ m}$ tall) from the mangrove trees. Differences in food density, foraging activities and weights (based on this study and from banding data collected during 2000–2007; P. D. Round, unpubl. data) were compared among three seasonal periods: April (spring migration), July–September (autumn migration), and November–February (wintering).

Benthos Sampling

Macrozoobenthos sampling was conducted monthly at the wastewater treatment plot. Samples were collected from 10 systematically selected 1 m^2 plots; initially due to logistical constraints, sampling was conducted once per month in August and October 2006, and February, April, and May 2007, and then every month from August 2007–April 2008. Within the 1 m^2 plots, invertebrates were sampled using cores (15 cm diameter, 10 cm depth), and passing the material through a 0.5 mm sieve adapted from Schneider and Harrington (1981). Samples were taken to a depth of 10 cm because while the Long-toed Stint bill is only about 2 cm in length (P. D. Round and S. Nimnuan, unpubl. data) and most of the target invertebrates in the diet were at the surface, some potential prey such as polychaetes are known to move vertically in the substrate (Howes and Bakewell 1989). Sampling points were each separated by 5 m within the treatment ponds, with three replicates within each 1 m^2 sampling unit. This method was used to examine the density of prey items from the surface to 10 cm below the surface. The invertebrates were preserved in 95% alcohol for identification in the laboratory. We identified invertebrate samples using aquatic insect identification keys (McCafferty 1981; Dudgeon 1999). Invertebrate densities were defined as the number of individuals per m^2 . One individual invertebrate was defined as equal to one prey item. Invertebrate samples were also collected three times during August 2006 to April 2008 (10 October 2007, 29 January 2008 and 19 March 2008) in nearby (100 m) salt-pans using the same method as the treatment ponds.

Foraging Observations and Morphometrics

Counts of all shorebirds in the wastewater treatment plots and salt-pans were conducted 30 min before starting focal observations of Long-toed Stint activities. Counts were made at least once per week using a 30x spotting scope.

Seasonal changes in activities of Long-toed Stints, including peck rate (number of pecks per min), step rate (number of steps per min), and chasing rate (number of chases or fights with other birds per min), were assessed throughout the study period by focal sampling of specific Long-toed Stint individuals and 1-min activity scans following Howes and Bakewell (1989). Each foraging movement involving contact of the bird's bill with the substrate in search of food was recorded as a "peck." Pecks included unsuccessful attempts to capture single prey items. This behavior also included rapid pecks at a single point (referred to as "stitching" following Cramp and Simmons (1983) as cited in Ward and Bullock (1988)), although not all such pecks could be recorded due to the rapidity of their motion. Therefore, stitching in one location was defined as one peck. As we could rarely observe prey being consumed because it appeared to be small or perhaps because handling was fast, we assumed that peck rate was positively correlated with prey capture rate and prey density, but this relationship remains unclear (McCurdy *et al.* 1997). We observed randomly selected focal individuals on two wastewater treatment plots and 15 salt-pans at various tidal levels using a spotting scope. After locating a focal individual, peck rates were recorded (number of pecks per min). Observations were repeated for as long as we could follow the individuals but for no longer than 5 min per activity for the same individual. For the same bird, we also counted steps in 1-min periods and again for a total of 5 min, as well as the number of chases/fights in 1-min intervals up to a possible total of 15 min. Seasonal differences in peck rates, step rates and chasing rates were tested by comparing the frequency distribution of rates in 1-min periods. Weights were compared for the above three monthly periods using Kruskal-Wallis tests and Wilcoxon matched-pairs tests with JMP Discovery Statistics (SAS Institute, Inc. 2002). We also examined the ratio of pecks to steps because a higher rate of pecks per step may occur when food density is higher, or when birds are feeding by touch rather than by sight (Elner *et al.* 2005). Although not specifically tested, it is likely that Long-toed Stints find their prey via touch (Kuwaie *et al.* 2012).

All observations were conducted on uniquely color-banded individuals. Adult and juvenile Long-toed Stints were distinguished on plumage features and molt status in the early part of the study. Thereafter, once a sufficient proportion had been marked, adults and first-winter birds were distinguished through recognition of color-banded individuals. Although banding of a variety of species, including Long-toed Stints, has been conducted over multiple years since 2000 (P. D. Round, unpubl. data), Long-toed Stints were targeted and captured only on the treatment ponds approximately 15 days per month during July 2006 to July 2007 by opening previously set mist nets in the feeding areas during the early morning, from

05:00 to 11:00 hr. Before release, captured birds were weighed and marked with two color leg flags, two regular color bands, and one uniquely numbered metal band. We also recorded a fat score following Redfern and Clark (2001), wing length (maximum chord), tarsus length and bill length from feathering (all to the nearest 0.1 mm). Adults could be easily distinguished in the hand because they were molting primaries during autumn and early winter (Round *et al.* 2012). Once primary molt was completed, adults had distinctly fresher primaries than first-year birds, which retained their juvenile primaries (Prater *et al.* 1997).

Seasonal differences in body weight were tested by comparing the weights for the same three monthly periods using Kruskal-Wallis tests and Wilcoxon matched-pairs tests with JMP Discovery Statistics (SAS Institute, Inc. 2002). We also report body weight means and standard deviations.

RESULTS

Food Abundance

Five families of invertebrates together with eight unidentified groups of invertebrates were collected from the wastewater treatment

plots and from salt-pans during August 2006 to April 2008. These included larval Chironomidae (blood worms/midges, 2-8 mm), larval Hydrophilidae (water scavenger beetles, 2-6 mm), larval (although a few imagoes were also observed) Stratiomyidae (aquatic soldier flies, 2-8 mm), larval Ephydriidae (shore flies, 4-10 mm), and larval Helodidae (marsh beetles, 2-8 mm). The unidentified groups (4-10 mm) comprised approximately 0.1% of the samples. Chironomidae were the most abundant invertebrates in the wastewater treatment plots, and Ephydriidae were the most abundant in the salt-pans. Because the potential prey were too small to observe being eaten, we were unable to assess whether foraging behavior changes were in response to differences in prey types between habitat types or in response to some other variable. The abundance of invertebrates among the three periods (April, July-September and November-February) was significantly different (Kruskal-Wallis test, $P < 0.001$; Fig. 2).

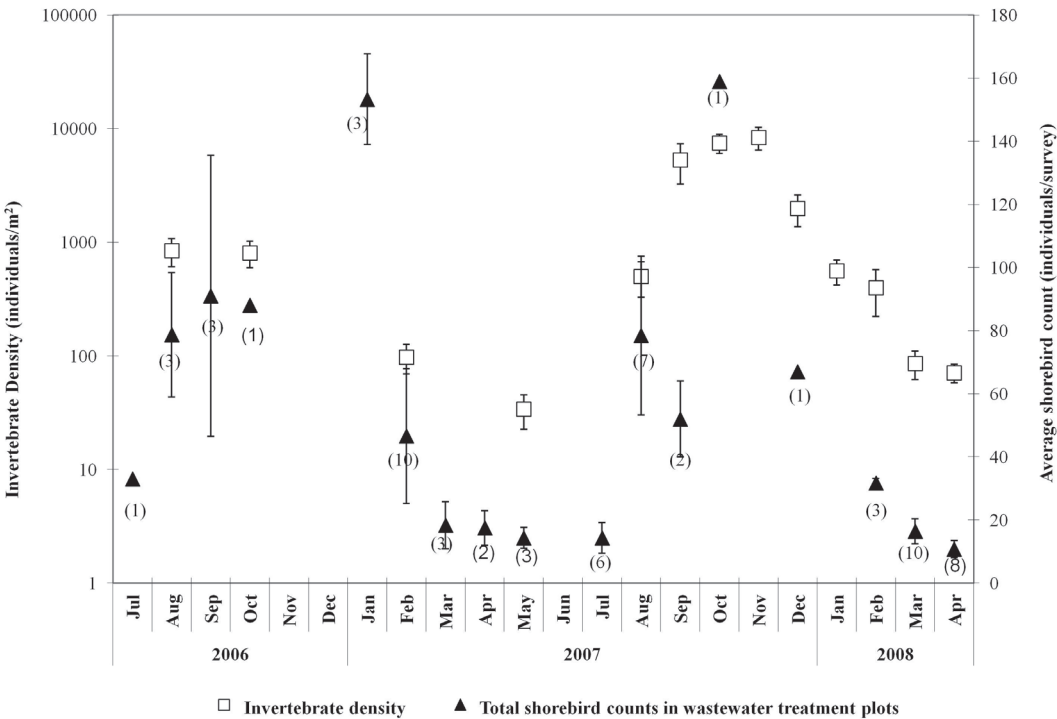


Figure 2. Seasonal variation in log mean invertebrate density (individuals/m²) in the wastewater treatment plots and average shorebird (all species) count (individuals/survey) during 2006-2008 (numbers in parenthesis indicate number of counts).

July-September had a higher invertebrate density than April (Mann-Whitney test, $P < 0.001$). Densities of invertebrates did not differ significantly between the July-September and November-February periods. The wastewater treatment plots had higher invertebrate densities than the salt-pans (Wilcoxon matched-pairs test, $Z = -16.244$, $P < 0.001$). In the treatment ponds, 98.8% of the invertebrates were either Chironomidae (95.1%) or Hydrophilidae (3.7%). The relative abundance of these two groups was weakly correlated ($r_s = 0.49$, $P = 0.075$) across 14 months of sampling. In the salt-pans, we only collected data during three periods (October, January, March), thus trends were less clear; however, overall 95% of the prey sampled were Ephydriidae, while 5% were Chironomidae. The dominant invertebrates in the salt-pans varied notably in time: Ephydriidae (94.7%) in October, Chironomidae (96.9%) in January and Chironomidae (47.3%) in March. Gross energy values were available from the literature for four of the five families found in our study. Three of the invertebrate groups, including the two most dominant, were relatively similar: Chironomidae, Ephydriidae, and Stratiomyidae were 3.9, 3.8, and 3.6 kcal/g, respectively (Anderson and Smith 1998). Hydrophilidae appeared to be approximately 1.4 times higher (5.5 kcal/g) (Anderson and Smith 1998). From the few fecal samples available, we were only able to confirm the consumption of Hydrophilidae.

There was a significant positive correlation between food density and average number of all species of shorebirds observed in the treatment plots ($r_s = 0.82$, $P < 0.001$, $n = 11$), but data were insufficient to assess this relationship for the salt-pans. Of note, shorebirds arrived as the food density appeared to be increasing (August) and departed in the spring as the food density was declining (March/April) (Fig. 2), although we did not examine whether shorebirds were responsible for the latter decline in prey. Long-toed Stints began arriving in late July (earliest arrival 19 July) and departed in early May (latest departure 5 May).

Forty-nine Long-toed Stints were captured and color-banded during the course

of the study from 29 July 2006 to 6 April 2007. The proportion of late-captured Long-toed Stints (those initially captured and marked after October 31) that were subsequently re-sighted within the same season was higher than the proportion of re-sighted early-captured birds subsequently re-sighted ($\chi^2_1 = 5.41$, early capture and not re-sighted $n = 15$, early capture and re-sighted $n = 5$, late capture and not re-sighted $n = 12$, late capture and re-sighted $n = 17$, $P < 0.05$), suggesting that a higher proportion of those captured earlier were either passage migrants that moved on to winter elsewhere or individuals that otherwise dispersed from Laem Phak Bia after arrival.

Long-toed Stint Body Weights

A total of 152 Long-toed Stints were banded during 2000-2007, 49 birds during this study (July 2006-April 2007) and 103 birds from previous work (September 2000-April 2006). Overall, body weights of adults and juveniles were not significantly different (Table 1). Body weights of juvenile and adult Long-toed Stints did not differ significantly among the three periods tested (Kruskal-Wallis, $Z = -1.263$, $P = 0.207$). However, the body weights of Long-toed Stints (adults and juveniles combined) caught in April were significantly higher than those captured in November-February (Table 1, Fig. 3). November-February weights were also significantly lower than weights from July-September. However, April and July-September body weights were not significantly different (Table 1). In addition, molting birds did not differ significantly in body weight from those not in molt (Table 1). No correlation could be demonstrated between food density and combined (adult and juvenile) Long-toed Stint body weights ($r_s = 0.15$, $P = 0.35$, $n = 9$). Fat score data were limited, but suggested little variation for both adults and first-year Long-toed Stints: fat score = 0 had 48 adults and 13 first-year; fat score = 1 had one adult and one first-year; fat score = 2 had one adult.

Table 1. Body weights of adult (combined with second-year birds) and juvenile Long-toed Stints using data collected between 2000 and 2007 (both means and standard deviation and medians are included for some tests). Seasonal differences use all age classes combined. Molt data include only adults and second-year birds. Medians with different associated letters are significantly different ($P < 0.001$) based on Mann-Whitney tests. Medians without superscript are not significantly different.

Variable	n	Body Weight (g)	
		$\bar{x} \pm \text{SD}$	Median
Adult	94	24.12 \pm 2.00	24.00
Juvenile	52	25.24 \pm 3.73	24.25
July-September	78	24.72 \pm 2.64	25.40 ^a
November-February	28	23.07 \pm 1.56	22.80 ^b
April	18	25.65 \pm 2.63	25.80 ^a
Molting	75		24.15
Non-molting	64		23.80

A total of 83 Long-toed Stint feeding observations in the wastewater treatment plots and 65 observations in the salt-pans were made between September 2006 and April 2008. In the wastewater treatment plots, no significant correlation could be demonstrated between food density and step rates ($r_s = -0.524$, $P = 0.091$, $n = 8$), peck rates ($r_s = -0.571$, $P = 0.069$, $n = 8$) or chase rates ($r_s = 0.144$, $P = 0.367$, $n = 8$).

Seasonal Differences in Foraging Rates

There was no seasonal difference in the peck rates of Long-toed Stints in the treatment plots (Kruskal-Wallis test, $H = 3.159$, $P = 0.206$). However, during February-April Long-toed Stints had higher step rates than

during September-January in both the treatment plots and the salt-pans (Mann-Whitney test, $U = 447$, $P < 0.05$, $n = 16$ and $n = 86$ for September-January and February-April, respectively.). Prey species composition appeared to be relatively similar within sites across months, while prey density appeared to be notably lower February-April.

Habitat Differences (Wastewater Treatment Plots vs. Salt-pans)

Step rates of Long-toed Stints in the salt-pans were higher than in treatment plots (Table 2, Fig. 4); however, there was no significant difference in peck rates between treatment ponds and salt-pans (Table 2, Fig. 5). There was a negative correlation between peck and step rates of Long-toed Stints in the salt-pans (Table 2, Fig. 6), but there was no correlation between peck and step rates in the wastewater treatment plots (Table 2). The overall pecks per step ratio in the treatment plots was higher than in the salt-pans (Table 2). The pecks per step ratio in the treatment plots was also higher than in the salt-pans in mid-winter (November-February) but not during July-September or April (Table 2), probably reflecting higher food densities in the wastewater treatment ponds compared to the salt-pans. We had few observations between July-September to compare habitats with sufficient power (Table 2). These differences were unlikely due to differences in prey composition as the relative energy values of the respective prey species appeared to be roughly equivalent on a per gram basis.

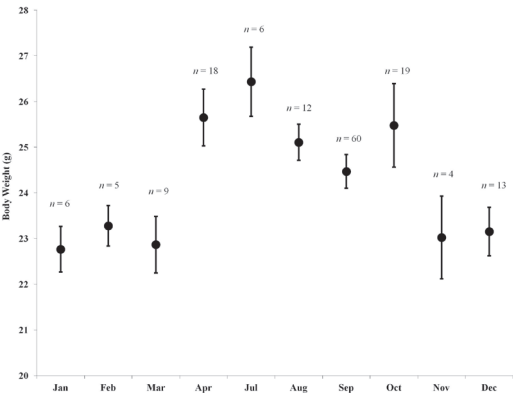


Figure 3. Mean weights and standard errors of Long-toed Stint during 2000-2007. Monthly samples size (total $n = 152$) ranges from September ($n = 60$) to November ($n = 4$).

Table 2. Foraging patterns (step rates, peck rates, pecks/step) for Long-toed Stints between two habitats (wastewater treatment ponds and salt-pans). Pecks/step were also compared among seasons between habitats. Medians with different letters are significantly different ($P < 0.05$) between habitats (Mann-Whitney test). n = the number of individuals observed. Medians without superscripts are not significantly different.

Variable	Median		Median	
	Wastewater Treatment Ponds	n	Salt-pans	n
Steps/min	72.30 ^a	72	111.40 ^b	61
Pecks/min	61.50	72	56.40	61
Pecks/step	0.86 ^a	72	0.54 ^b	61
Pecks/step				
July-September	2.23	2	—	0
November-February	0.53 ^a	14	0.26 ^b	16
April	0.64	14	0.56	15

DISCUSSION

This study represents only the second published survey of invertebrate food abundance in relation to shorebird abundance and behavior in tropical Asia despite the

importance of the region to shorebirds and the level of threat (Manopawitr and Round 2004). Overall, total shorebird abundance at our site appeared to be associated with invertebrate abundance. The wastewater treatment site appears to be relatively pro-

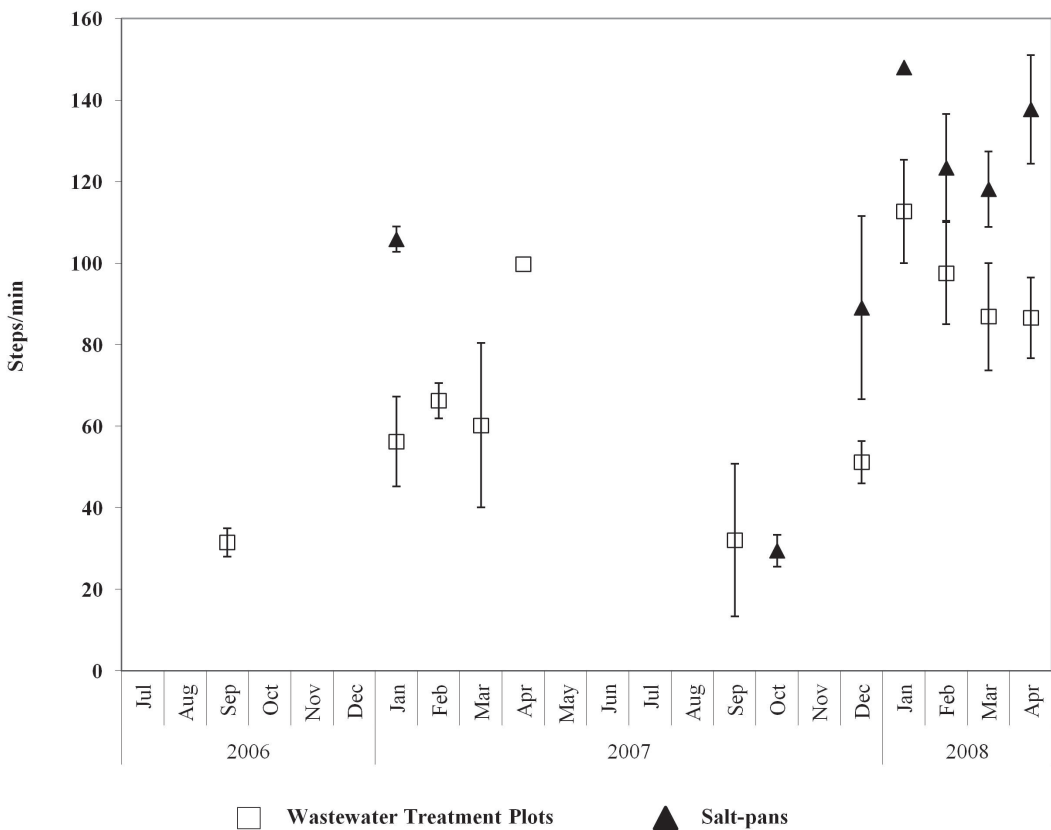


Figure 4. Mean pace rates (steps/min) of Long-toed Stint in the wastewater treatment plots and salt-pans. Step rates in salt-pans were higher than in wastewater treatment plots (Wilcoxon matched-pairs test, $Z = -2.201$, $P = 0.014$) (error bars represent standard errors of pace rates, no error bars indicate only one individual was sampled).

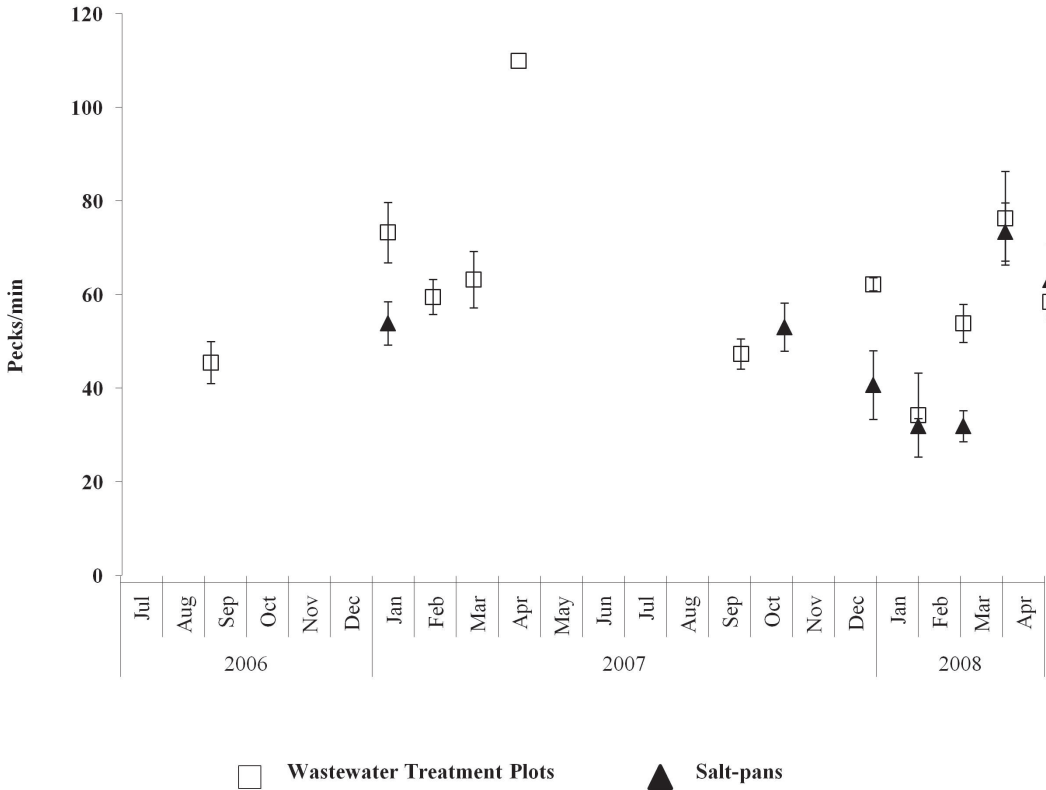


Figure 5. Mean peck rates (pecks/min) of Long-toed Stint in wastewater treatment plots and salt-pans. There was no significant difference in peck rates in wastewater treatment plots and salt-pans (Wilcoxon matched-pairs test, $Z = -1.121$, $P = 0.155$) (error bars represent standard errors of peck rates).

ductive consistent with findings from other studies of wastewater treatment wetlands (Murray and Hamilton 2010) at least during the southward migration in the autumn.

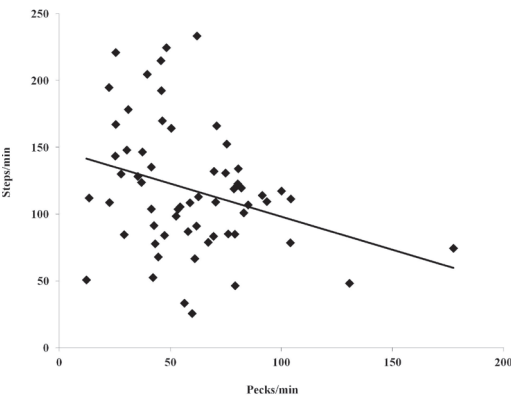


Figure 6. Correlation between peck and step rates in the salt-pans ($r_s = -0.27$, $P < 0.05$, $n = 61$).

With respect to individual foraging patterns, our Long-toed Stints appeared to have lower step rates in the wastewater treatment ponds where there was probably higher invertebrate abundance compared to the salt-pans, although salt-pans are also thought to be suitable human-modified habitat for shorebirds of the region (Yasue and Dearden 2009; Sripanomyom *et al.* 2011). However, we found that food abundance tended to wane toward the end of the migration period (February–April) in both habitats regardless of the differences in prey species composition.

The seasonality of tropical Asian zoobenthos is generally thought to be caused by monsoonal rains (late April/early May–late October) combined with variations in the intensity of predation, but the timing of life-cycle events will also influence population densities and community composition of invertebrates (Connors *et al.* 1981; Dudgeon

1999). Based on previous work on macrofauna in the wastewater treatment ponds of this study area (Hongsing 2003), the major environmental factor that appears to influence invertebrate abundance is salinity, which was highest in April when invertebrate abundance was low and lowest in December when invertebrate abundance was higher in both wastewater treatment ponds and salt-pans (salinity data not shown). We do not have equivalent macrofauna data for the salt-pans. As far as we are aware, there are no published data on other possible environmental factors, such as temperature, and their effects on shorebird prey in the tropics.

The strong correlation between invertebrate density and numbers of shorebirds in the wastewater treatment plots suggested that the shorebird community closely tracked food supply. Higher invertebrate density during September–November provided food for shorebirds during the southward passage migration. Invertebrate density declined dramatically from November to April, probably due in part to consumption by shorebirds (although we did not experimentally test this), reductions in water levels and the consequent increases in salinity. During March and April, low food abundance in our study area appeared to limit the use of this site by shorebirds. This was similar to the findings of Schneider and Harrington (1981) in Massachusetts, USA, where food availability declined significantly during southward migration at least in part due to predation by birds. Shorebird body mass increases have also been shown to be greater when shorebirds arrive at stopover sites during periods of peak or higher food density (Verkuil *et al.* 2006). However, no correlation could be demonstrated between Long-toed Stint body mass and food density in our study area, perhaps because of the availability of other surrounding habitats that may have supported higher food densities during the northward migration. It is possible that while our study ponds became too dry to support adequate invertebrate prey, nearby deeper salt-pans may have retained sufficient water to contain more prey than our areas (Yasue and Dearden 2009);

however, we have no observations to support this speculation. Body masses were lowest during the mid-winter months, possibly reflecting the steady depletion/reduction in prey over the course of this period. There are probably two co-occurring mechanisms involved in the weight changes observed here, one related to prey abundance/prey depletion and the other related to the physiology of migration (Goss-Custard 1977b).

Goss-Custard and Durell (1987) and Groves (1978) found that juvenile Eurasian Oystercatchers (*Haematopus ostralegus*) and Ruddy Turnstones (*Arenaria interpres*) had lower foraging rates and were less efficient foragers than adults. However, both of these species appear to require some experiential learning to become efficient foragers of their preferred prey. In contrast, this might not be the case for Long-toed Stints where such learning may play a reduced role in the development of foraging skills, and, therefore, first-year birds may obtain relatively similar weights to adults as observed here. To our knowledge, all first-year Long-toed Stints migrate northward in spring as we never observed over-summering birds unlike some other shorebirds (e.g., Spoon-billed Sandpiper (*Eurynorhynchus pygmeus*); Eiam-ampai *et al.* 2011). Even if first-year birds were less efficient foragers, lack of demonstrable weight differences in any period might also have been due to higher energetic demands faced by adults during their complete molt, which occupied the period from late July until November. It is also possible that there is an optimal non-breeding weight for these Long-toed Stints and that they avoid getting too heavy because additional weight would increase the various costs of migration such as energetic demands and predation risk (Ydenberg *et al.* 2004; Taylor *et al.* 2007).

Failure to demonstrate any clear relationship between food density and peck rate was possibly due to a weak correlation between the number of pecks and the number of successful foraging bouts. This in turn could have been related to our inability to determine when the Long-toed Stints had successfully captured prey, as well as the difficulty of counting actual number of pecks when they

were feeding with the “rapid stitching” bill movements. It is also possible that other food items that we did not measure, such as mesofauna and biofilm (Sutherland *et al.* 2000; Elner *et al.* 2005; Kuwae *et al.* 2008, 2012), were important food sources. However, peck rates of the Long-toed Stints were similar in both wastewater treatment plots and salt-pan habitats even though prey abundance was lower in the salt-pans, although the relationship between foraging success and peck rate may not be reliable (McCurdy *et al.* 1997). The negative correlation between peck and step rates suggests that habitats with higher abundances of invertebrates may promote shorebird survival by reducing energy expenditure (fewer steps per unit time) through the winter period (Goss-Custard and Durell 1987). It is also possible that more steps per peck indicate a different foraging strategy, i.e., more visual foraging vs. tactile foraging (Sutherland *et al.* 2000). For example, in the wastewater treatment ponds the substrate was softer, lending itself to more tactile foraging, whereas in the salt-pans, with a harder substrate, birds may have had to switch at least partly to a more visual form of foraging, although we did not have clear evidence to support this switch.

Whether the food resources important for Long-toed Stints and other shorebirds in our study area (larval Chironomidae, Ephyridae and Hydrophilidae) are equally important in other sites in the Inner Gulf or elsewhere in the region is unknown. Chironomids are high quality food resources (51.5–56.0% protein) and relatively energy rich (3.9–6.1 kcal/g) (Armitage 1995; Anderson and Smith 1998) and were noted as a significant resource in the only other study in the region similar to ours (Yasue and Dearden 2009). However, our study found relatively few Chironomids during most months in the salt-pans compared to Yasue and Dearden (2009), suggesting significant intersite variation. The relationship between invertebrate density and numbers of shorebirds also suggests that, as elsewhere (Goss-Custard *et al.* 1977, 1984; Triplet *et al.* 1999), the number of birds using a site is in part related to the abundance of the food supply and that both first-year and

adult shorebirds spend most of their time feeding where prey density is high (Goss-Custard 1977a; Buchanan *et al.* 1985; Maron and Myers 1985; Goss-Custard and Durell 1987). Conservation plans for shorebird communities therefore may benefit by identifying and then predicting which physical features at the site level are associated with higher quality food resources. The development of such predictive models will require a broad-scale, comparative approach whereby multiple sites in the region representing a range of shorebird abundances and human disturbance levels are sampled for their invertebrate as well as biofilm abundance.

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