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ORIGINAL PAPER

Effects of exotic *Spartina alterniflora* on the habitat patch associations of breeding saltmarsh birds at Chongming Dongtan in the Yangtze River estuary, China

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Abstract Smooth cordgrass (*Spartina alterniflora*) is one of the most invasive exotic plants of saltmarshes worldwide. To understand the effects of smooth cordgrass invasion on the habitat use and selection by breeding saltmarsh birds, we compared species number and abundance of breeding birds in native reed (*Phragmites australis*) and smooth cordgrass-invaded habitats (reed-cordgrass mixed habitats and cordgrass monocultures) at Chongming Dongtan in the Yangtze River estuary, China. We further examined the similarity of bird communities in different habitats and habitat selection by dominant bird species. For saltmarsh generalists, species number and abundance did not differ among the habitats. For saltmarsh specialists, species number and abundance did not differ in reed monocultures and reed-cordgrass mixed habitats but were significantly lower in cordgrass monocultures than in reed monocultures and reed-cordgrass mixed habitats. ANOSIM indicated that the difference in bird communities was larger between cordgrass monocultures and the habitats with reed than between the habitats with reed. The saltmarsh specialists preferred reed monocultures, while saltmarsh generalists avoided reed monocultures. Most species indicated no selection (neither preferred nor avoided) on reed-cordgrass mixed habitats, and no species preferred the cordgrass monocultures. The use of cordgrass monocultures by the common saltmarsh birds was negatively related to their body size. This study suggests that the spread of exotic smooth cordgrass has greatly affected the species composition and structure of local bird communities and has been especially disadvantageous to the saltmarsh specialists.

Keywords Breeding birds · Habitat generalists · Habitat specialists · Exotic plants · Saltmarsh · Smooth cordgrass · *Spartina alterniflora*

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Introduction

Biological invasion is a severe threat to native biodiversity. Exotic species can affect the local biota both directly and indirectly, and direct effects include predation on, competition with, parasitism to, and hybridization with native species (e.g., Hilton and Cuthbert 2010; Kenis et al. 2009; Kerpez and Smith 1990; Rhymer and Simberloff 1996). Indirect effects include changes in the biotic and abiotic environment, trophic pathways, and ecological functions and services of ecosystems (Crooks 2002; Levis et al. 2006; Straube et al. 2009). Although the direct effects

of invasive species on the native biota have been well studied, the indirect effects of invasive species are very complex and thus remain elusive (Sax et al. 2005).

Exotic plants in particular represent an important group of invasive organisms that can strongly affect the biotic and abiotic characteristics of ecosystems (Crooks 2002; Li et al. 2009). The many organisms that can be affected by exotic plants include birds. Invasion by exotic plants not only changes the local plant communities, which constitute the major components of bird habitats, but also impact birds by changing food chains (Flanders et al. 2006; Ortega et al. 2006; Remeš 2003).

The success of breeding birds depends on suitable habitats (Gjerdrum et al. 2005). Although the invasion of exotic plants dramatically changes the habitats of local breeding birds, research on the impacts of exotic plants on breeding birds have produced equivocal results. Most studies have indicated that the invasions by exotic plants negatively affect local breeding birds by decreasing species richness and/or abundance of birds (Benoit and Askins 1999; Fandino et al. 2010; Flanders et al. 2006; Skórka et al. 2010), by causing the disappearance of some guilds (Ellis 1995; Hunter et al. 1988; Mitra and Sheldon 1993), by reducing breeding success (Borgmann and Rodewald 2004; Mermoz and Reboreda 1998; Nordby et al. 2009; Remeš 2003; Schmidt and Whelan 1999), by decreasing the growth rate of nestlings (Lloyd and Martin 2005), and by reducing nest-site fidelity (Ortega et al. 2006). Other studies, however, have indicated that exotic plants could provide alternative or new breeding habitats for the local birds (Schmidt et al. 2005; Sogge et al. 2008; Whitt et al. 1999) and that the breeding success in exotic habitats is equal to or even higher than that in native habitats (Kennedy et al. 2009; Schlossberg and Kings 2010). Moreover, some birds in previously degraded ecosystems might depend on the exotic plants completing life histories (Fleishman et al. 2003; Heckscher 2004; Safford 1997). Overall, the impacts of exotic plants on breeding birds seem to be region- and species-dependent. Birds are more likely to prefer the exotic habitats in those regions where suitable native habitats are limited, whereas the exotic plants are more likely to be detrimental to those birds that depend on native plants for their habitats and food (e.g., Flanders et al. 2006; Hunter et al. 1988; Safford 1997; Skórka et al. 2010; Sogge et al. 2008). Although invasion by exotic plants might not have obvious effects on the species richness and/or abundance of local bird communities, species composition and structure are generally altered (e.g., Flanders et al. 2006; Fleishman et al. 2003).

Cordgrasses (*Spartina* spp.) are among the most invasive exotic plants in saltmarshes worldwide. Studies in North America (Buchanan 2003), Europe (Goss-Custard and Moser 1988), Australia (Simpson 1995), and East Asia (Gan et al. 2009) have indicated that cordgrass invasion degrades or eliminates habitats for nonbreeding migratory shorebirds. This might be related to the dense populations of cordgrass that could obstruct shorebird movement and foraging. However, the effects of exotic cordgrass on breeding saltmarsh birds were largely unexplored. Recent studies in San Francisco Bay indicate that although some birds can nest in the cordgrass-invaded saltmarshes, the breeding success is lower in exotic cordgrass habitats than in native vegetation (Nordby et al. 2009).

In China, smooth cordgrass (*Spartina alterniflora*) was intentionally introduced in 1979. After natural spread and intentional introductions over the past three decades, smooth cordgrass is distributed widely along the east coastal and estuarine wetlands (An et al. 2007; Wang et al. 2006). In the Yangtze River estuary in east China, smooth cordgrass has become the dominant plant species in saltmarshes (Wang 2007). Smooth cordgrass can out-compete native sea bulrush (*Spartina mariqueter*) and form dense monocultures, and can also form mixed mosaics with native reed (*Phragmites australis*) (Li et al. 2009; Wang et al. 2006). Thus, the invasion of smooth cordgrass has substantially changed the plant composition and structure of saltmarshes in the Yangtze River estuary, and such changes might affect habitat use and habitat selection by breeding birds.

Saltmarshes are important habitats for breeding birds in the Yangtze River estuary. Some species, such as reed parrotbills (*Paradoxornis heudei*) and oriental great reed warblers (*Acrocephalus orientalis*), exclusively depend on the reed communities for their breeding habitats (Xu and Zhao 2005). In this study, we attempted to determine how invasive smooth cordgrass affects habitat use and habitat selection by breeding birds at Chongming Dongtan saltmarshes in the Yangtze River estuary. We

hypothesized that the species composition and structure of bird communities are different between native habitats and in smooth cordgrass-invaded habitats, and that these differences result from different preferences for the native and smooth cordgrass-invaded habitats by the saltmarsh breeding birds.

Methods

Study sites

Chongming Dongtan (31°25′–31°38′N, 121°50′–122°05′E, Fig. 1) is located at the eastern end of Chongming Island in the Yangtze River estuary of eastern China, and encompasses a large area of estuarine wetlands (Fig. 1). The estuarine wetlands are composed of bare mudflats in the low tidal zone and vegetated saltmarshes in the middle and high tidal zones. The dominant native plants in the saltmarshes include sea-bulrush and common reed (hereafter reed) (Fig. 1a). Ongoing deposition of sediments in the estuary has gradually increased the elevation of the tidal flats so that they have become less affected by tides, resulting in a vegetation succession from pure sea-bulrush stands in the middle tidal zone to pure reed stands in the high tidal zone (Xu and Zhao 2005). The total area of saltmarshes at Chongming Dongtan was 4,000 ha in 2005 (Wang 2007). The sea-bulrush habitats support few breeding birds although many shorebirds forage in the sparse sea-bulrush habitats during migration (Gan et al. 2009). In contrast, the tall reed habitats support large numbers of saltmarsh birds in both breeding and nonbreeding seasons (Xu and Zhao 2005).

The bare intertidal zone and saltmarshes have been heavily colonized by introduced smooth cordgrass (hereafter cordgrass) at Chongming Dongtan. As of 2005, cordgrass occupied about 2,000 ha, i.e., about half of the vegetated portion of the intertidal area (Li et al. 2009; Wang 2007). In the middle tidal zone, cordgrass has out-competed sea-bulrush and formed pure stands, which has gradually led to a reduced range of sea-bulrush communities. In the high tidal zone, cordgrass invasion has fragmented the reed communities, resulting in the formation of either a mosaic of reed mixed with cordgrass or pure cordgrass stands (Wang 2007).

At Chongming Dongtan, the plant height of reed (2–3 m) is greater than that of cordgrass (1.5–2 m). With a large number of upstanding stems, cordgrass stands (284 ± 81 ind. m^{-2}) are much denser than reed stands (129 ± 9 ind. m^{-2}) (Gan 2009). According to the proportion of reed and cordgrass in the saltmarshes, we classified bird habitats into reed monocultures, reed-dominated community (reed area > 2/3 of total area), reed-cordgrass mixture (reed area about 1/3–2/3 of total area), cordgrass-

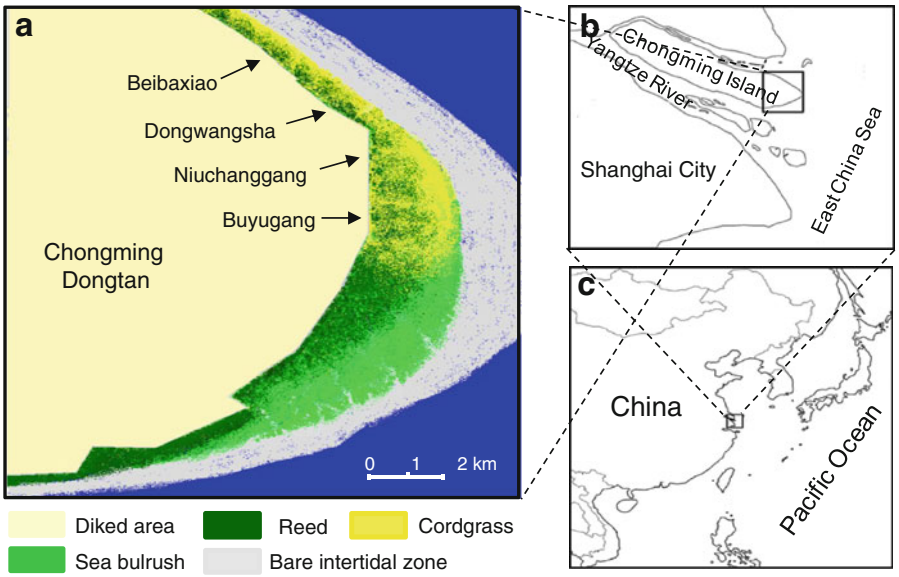

Fig. 1 The distribution of saltmarsh plants on the tidal flats at Chongming Dongtan (**a**) and the location of Chongming Dongtan in the Yangtze River estuary (**b**) and in China (**c**)

dominated community (reed area < 1/3 of total area), and cordgrass monocultures. Compared to cordgrass and reed, sea bulrush is relatively short (plant height < 0.5 m). It is distributed in the middle and low tidal zones and is frequently submerged by tidewater (Xu and Zhao 2005). Thus, sea bulrush habitats are not suitable for the saltmarsh birds during the breeding period, and we did not include the sea-bulrush habitats in this study.

Breeding bird surveys

Bird surveys were conducted in the north and east parts of Chongming Dongtan saltmarshes, where the cordgrass has invaded (Fig. 1). According to the separation of tidal channels and the origin of cordgrass, the surveyed area was divided into four regions from north to east: Beibaxiao, Dongwangsha, Niuchanggang, and Buyugang (Fig. 1a). The cordgrass at Beibaxiao naturally spread from north of the Yangtze River estuary in the middle 1990s; the cordgrass at Buyugang was intentionally planted in 2001 and then spread naturally; and the cordgrass at Dongwangsha and Niuchanggang was the consequence of natural spread from the Beibaxiao and Buyugang regions. During our surveys, reed and cordgrass were the dominant plant species in the intertidal zone in these four regions (Fig. 1a).

Fixed-radius point counts were used for bird surveys in May and June in 2008. Because it was difficult to walk on the muddy intertidal flats and dense vegetation zone, we set bird counting stations along the trails extending from the high to low tidal zones at each region; local fishermen used the trails to collect shellfish in the intertidal area. During our surveys, the trails were rarely used, and human disturbance was limited. To minimize overlapping observations from adjacent counting stations, we set adjacent counting stations with >250 m interval and 4–6 counting stations were set in each trail according to trail length. All the counting stations were >100 m from the dikes, which could avoid the disturbance of human activities on the dikes and edge effects. We located the counting stations with Global Positioning System (GPS, Garmin eTrex, accuracy <15 m), and recorded the habitat patch (reed monoculture, reed-dominant, reed-cordgrass mixture, cordgrass-dominant, or cordgrass monoculture) at each counting station according to the proportion of reed and cordgrass within a 30-m radius. Pre-surveys had indicated that birds within 30 m of a station could be detected based on visual and aural data (Cai et al. 2010).

Breeding bird surveys were conducted in the morning from sunrise and lasted for 3 h to minimize hourly variation in detection. Two investigators (XJG and YTC) conducted bird surveys using 8 × binoculars. We used range finders (Bushnell 20-2018) to calibrate the distance estimation of the investigators before the surveys. The numbers of bird species seen and heard within a 30-m radius of each counting station were recorded for 10 min. Upon arrival at a station, the investigators also recorded birds within 30 m of the station so as to include individuals that were flushed upon approach. Although bird densities might have been under- or overestimated, methods were consistent among study periods. To decrease the effects of changes in bird species and numbers during surveys, we conducted bird surveys in turn in the four regions, and selected three trails randomly in each region during each survey. A total of three surveys were conducted during the study periods, each survey lasted for 1 week and a minimum of 10 days separated the three surveys.

We included the aerial foragers (e.g., barn swallows *Hirundo rustica*) and nest parasites (e.g., common cuckoos *Cuculus canorus*) in the records because the food of aerial foragers is related to the vegetation, and the habitat condition affects the nest parasites indirectly by influencing the nest sites of the hosts. Birds that simply flew over the regions were excluded.

Data analysis

According to the habitat use of the saltmarsh birds, we classified the birds into saltmarsh specialists (those that depend on saltmarshes exclusively or primarily) and saltmarsh generalists (those that depend on both saltmarshes and other habitats) (Gan 2009; Xu and Zhao 2005). The number of species and abundance of species of saltmarsh specialists, saltmarsh generalists, and of all saltmarsh species (= specialists + generalists) were determined for each habitat. To reduce the bias of different sampling effort and sampling size among the habitats, we used Chao1 (abundance-based estimator of species richness) and Chao2 (incidence-based estimator

of species richness) statistics to estimate the species richness of each bird group in each habitat (Colwell and Coddington 1994). Software package EstimateS 8.2 (Colwell 2009) was used to compute the Chao1, Chao2, and randomized sample-based species accumulation curves for the observed species richness (using the Mao Tau procedure) with 50 randomizations in all calculations. In this study, sample size was the number of counting stations, with 40 in reed monocultures, 28 in reed-dominated community, 40 in reed-cordgrass mixture, 40 in cordgrass-dominated community, and 32 in cordgrass monocultures. Analyses of Variance (ANOVAs, Tukey-HSD tests followed if significant difference occurred) were further used to compare the differences in species richness among different habitat patches according to the Chao1 and Chao2 estimators.

To examine the similarity of bird communities in different habitats, we performed one-way analysis of similarities (ANOSIM) using PRIMER-E software (PRIMER-E, Plymouth, United Kingdom). The ANOSIM generates an R statistic that is scaled between -1 and 1, with $R > 0.75$ indicating quite different communities, $R > 0.5$ indicating overlapping but clearly different communities, and $R < 0.25$ indicating communities with substantial similarity (Clarke and Warwick 2001). Bird species and their numbers in the four survey regions were gathered, respectively, before analysis. Ordinations by nonmetric multidimensional scaling (MDS) were performed with the MDS module of PRIMER-E based on the Bray-Curtis similarity matrix.

Repeated-measures ANOVAs (Zar 1999) were used to compare the number of bird species and number of individuals recorded per counting station in different habitats with survey time as within group factor, survey region as covariate, and habitat patch as between group factor. Tukey-HSD tests were used for post-hoc comparison if the differences were significant. There was no significant interaction between time and patch type ($P > 0.1$ for both), and thus the comparisons were feasible.

We selected those bird species with >100 detections during the surveys as common species for analysis of their habitat selection among the five habitat patches. Chi-squared goodness of fit was used to compare habitat use (percentage of birds observed in each habitat) and habitat availability (percentage of area of each habitat) of each bird species among the five habitat patches. If habitat use was significantly different from habitat availability, Bonferroni analyses were used to test the positive, null, and negative selection for the habitats by the birds (Byers et al. 1984; Neu et al. 1974).

Dense vegetation can obstruct the movements of birds, make prey inaccessible to them, and reduce their foraging efficiency (Benoit and Askins 1999; Vitz and Rodewald 2007). The obstacle of dense vegetation increases with the increase of birds' body size. In order to detect the use of dense cordgrass monocultures by the breeding birds, we used generalized linear regression to analyze the relationship between the body size of birds and their use of the cordgrass monocultures. Only common birds were involved in this analysis so as to decrease the observation bias. We used body mass of birds as an index of their body size. The body mass of birds was obtained from local bird-banding data (XJ Gan unpublished data).

Data for bird species and numbers were logarithmically transformed before analysis to reduce heteroscedasticity and improve normality. We performed all statistical analyses using version 6.0 of STATISTICA (StatSoft, Tulsa, Oklahoma) unless otherwise indicated, and used $\alpha < 0.05$ for statistical significance.

Results

Bird species

A total of 22 bird species were recorded during the study (Table 1). The largest number of species was recorded in reed monocultures (19 species), followed by the reed-dominated community and reed-cordgrass mixture (17 species for both), and cordgrass-dominated community (15 species). The smallest number of species was recorded in the cordgrass monocultures (11 species) (Table 2).

The species in the four habitats with reed (reed monocultures, reed-dominated community, reed-cordgrass mixture, and cordgrass-dominated community) consisted of a mix of saltmarsh generalists and specialists, while the species in cordgrass monocultures mainly consisted of saltmarsh generalists (Table 2). Of the 16 species of saltmarsh generalists recorded in this study, 13 species were recorded in reed monocultures, and 11, 11, 9, and 8 species were recorded in the reed-dominated community, reed-

Table 1 Birds species and their numbers (mean ± SD recorded per counting station) in the five habitats in the saltmarshes at Chongming Dongtan

Bird species	Scientific name	Habitat				
		RM	RD	RC	CD	CM
Ring-necked pheasant (G)	*Phasianus colchicus*	0.08 ± 0.27	–	0.03 ± 0.16	–	–
Intermediate egret (G)	*Egretta intermedia*	–	–	0.08 ± 0.27	–	–
Little egret (G)	*Egretta garzetta*	0.10 ± 0.30	0.07 ± 0.26	0.15 ± 0.43	0.08 ± 0.28	0.06 ± 0.25
Black-crowned night heron (G)	*Nycticorax nycticorax*	0.05 ± 0.22	–	–	–	0.03 ± 0.18
Chinese little bittern (G)	*Ixobrychus sinensis*	0.35 ± 0.62	0.25 ± 0.52	0.38 ± 0.67	0.22 ± 0.48	0.06 ± 0.25
Schrenck's little bittern (G)	*Ixobrychus eurhythmus*	–	–	0.03 ± 0.16	–	–
Cinnamon bittern (G)	*Ixobrychus cinnamomeus*	–	0.04 ± 0.19	–	–	–
Common moorhen (G)	*Gallinula chloropus*	0.03 ± 0.16	–	–	–	–
Slaty-breasted banded rail (S)	*Rallus striatus*	0.18 ± 0.71	0.07 ± 0.26	0.08 ± 0.27	0.11 ± 0.32	–
Common cuckoo (G)	*Cuculus canorus*	0.43 ± 0.71	0.54 ± 0.69	0.55 ± 1.04	0.64 ± 0.11	0.03 ± 0.18
Barn swallow (G)	*Hirundo rustica*	0.80 ± 1.14	0.29 ± 0.53	0.53 ± 1.18	0.28 ± 0.81	0.09 ± 0.30
Red-rumped swallow (G)	*Hirundo daurica*	0.18 ± 0.45	0.21 ± 0.42	0.10 ± 0.30	0.03 ± 0.17	0.03 ± 0.18
Long-tailed shrike (G)	*Lanius schach*	0.08 ± 0.27	0.11 ± 0.31	–	0.03 ± 0.17	–
Vinous-throated parrotbill (G)	*Paradoxornis webbianus*	0.15 ± 0.36	0.50 ± 0.79	0.88 ± 1.32	1.17 ± 1. 48	0.78 ± 0.83
Reed parrotbill (S)	*Paradoxornis heude*i	2.90 ± 2.64	1.75 ± 1.69	1.18 ± 1.38	1.81 ± 1.65	0.22 ± 0.55
Zitting cisticola (G)	*Cisticola juncidis*	0.28 ± 0.55	0.71 ± 0.76	1.13 ± 1.04	1.14 ± 1.13	1.13 ± 0.87
Manchurian bush warbler (G)	*Cettia canturians*	0.03 ± 0.16	0.04 ± 0.19	–	–	–
Black-browed reed warbler (S)	*Acrocephalus bistrigiceps*	0.18 ± 0.38	0.11 ± 0.42	0.03 ± 0.16	0.03 ± 0.17	–
Oriental great reed warbler (S)	*Acrocephalus orientalis*	3.58 ± 2.14	2.21 ± 2.06	1.25 ± 1.60	1.22 ± 1.22	–
Blunt-winged warbler (S)	*Acrocephalus concinens*	0.03 ± 0.16	0.04 ± 0.19	–	0.06 ± 0.23	–
Marsh grassbird (S)	*Megalurus pryeri*	0.05 ± 0.22	0.71 ± 0.90	1.05 ± 1.01	1.28 ± 1.23	0.91 ± 0.86
Tree sparrow (G)	*Passer montanus*	0.08 ± 0.27	0.18 ± 0.61	0.05 ± 0.32	0.31 ± 1.12	–
Saltmarsh generalists		2.60 ± 1.88	2.93 ± 2.04	3.89 ± 2.29	5.71 ± 0.90	2.25 ± 1.27
Saltmarsh specialists		6.90 ± 3.47	4.89 ± 2.44	4.50 ± 2.25	0.68 ± 0.21	1.16 ± 1.05
All saltmarsh species		9.5 ± 4.14	7.82 ± 3.59	8.39 ± 3.44	6.96 ± 1.03	3.41 ± 1.27

The saltmarsh specialists is referred to as specialists in this region

RM reed monocultures, *RD* reed-dominated community, *RC* reed-cordgrass mixture, *CD* cordgrass-dominated community, *CM* cordgrass monocultures, *G* saltmarsh generalist, *S* saltmarsh specialist

Table 2 Observed (S_{obs}) and estimated (Chao1 and Chao2) bird species richness in the five saltmarsh habitats

		Habitat				
		RM	RD	RC	CD	CM
All birds	S_{obs}	19	17	17	15	11
	Chao1	20.0 (1.8)	18.0 (1.8)	20.0 (4.2)	19.5 (7.2)	11.8 (1.4)
	Chao2	20.0 (1.8)	17.7 (1.4)	20.8 (6.8)	19.5 (6.2)	11.7 (1.4)
Saltmarsh generalists	S_{obs}	13	11	11	9	8
	Chao1	13.5 (1.9)	11.5 (1.3)	13.0 (3.7)	10.0 (2.5)	8.3 (0.7)
	Chao2	13.5 (1.7)	11.5 (1.3)	13.9 (4.5)	10.0 (2.2)	8.2 (0.7)
Saltmarsh specialists	S_{obs}	6	6	6	6	3
	Chao1	6.0 (0.3)	6.0 (0.3)	7.0 (2.2)	6.0 (0.3)	3.0 (0.4)
	Chao2	6.0 (0.2)	6 (0.2)	7.0 (2.2)	6.0 (0.2)	3.0 (0.4)

The values in the parentheses indicate the SD. Sample size was 40, 28, 40, 36, and 32 for RM, RD, RC, CD, and CM

RM reed monocultures, *RD* reed-dominated community, *RC* reed-cordgrass mixture, *CD* cordgrass-dominated community, *CM* cordgrass monocultures

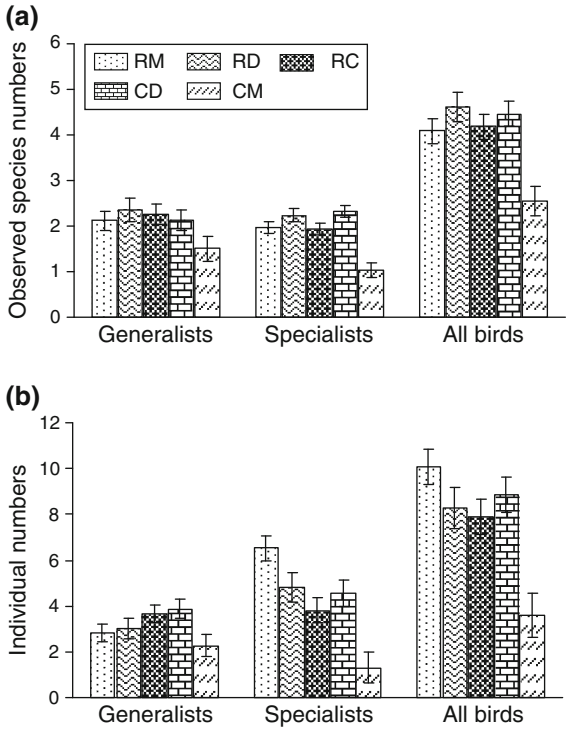

Fig. 2 Mean number of bird species (**a**) and mean number of birds (**b**) recorded per counting station in the five habitats. All birds = saltmarsh specialists + saltmarsh generalists. *RM* reed monocultures, *RD* reed-dominated community, *RC* reed-cordgrass mixture, *CD* cordgrass-dominated community, *CM* cordgrass monocultures. The vertical bars indicate the SE

cordgrass mixture, cordgrass-dominated community, and cordgrass monocultures, respectively. All six species of the saltmarsh specialists were recorded in the four habitats with reed, while only three were recorded in the cordgrass monocultures (Table 2).

Based on the data for all saltmarsh birds (specialists + generalists), repeated-measures ANOVAs indicated a significant difference in the number of species recorded in the five habitats ($F = 6.40$, df = 4, $P = 0.001$); the number of species was significantly lower in the cordgrass monocultures than in other four habitats, while species number did not significantly differ among the four habitats with reed (Fig. 2a). The distribution of saltmarsh specialists indicated a similar pattern, with fewer species in cordgrass monocultures than in the other habitats ($F = 11.63$, df = 4, $P < 0.001$) (Fig. 2a). The number of species of saltmarsh generalists, however, did not significantly differ ($F = 1.52$, df = 4, $P = 0.23$) among the five habitats (Fig. 2a).

The cumulative curves of observed species richness approached an asymptote after 20 samples in all bird groups in the five habitats. The cumulative curves of observed species richness of all birds and saltmarsh specialists were similar among the habitats with reed but were consistently lower in the cordgrass monocultures than in the other four habitats. For the saltmarsh generalists, the cumulative curves of observed species richness were similar among the five habitats, although the species number was higher in the reed monocultures than in the other habitats.

Comparison between observed species richness and the Chao estimators indicated that detection probabilities were >75% (76.9–100%) for all bird

groups in different habitats (Table 2). The Chao1 and Chao2 estimators for species richness indicated the same trends as the cumulative curves of observed species richness, with more species of all birds (18–21) and saltmarsh specialists (6–7) in the four habitats with reed than in the cordgrass monocultures (12 for all birds and 3 for saltmarsh specialists), and a similar number of species of saltmarsh generalists (9–14) in the five habitats (Table 2). Tukey-HSD tests followed ANOVAs based Chao1 and Chao2 estimators also indicated that the species numbers of all saltmarsh birds and saltmarsh specialists were significantly lower in the cordgrass monocultures than in other four habitats ($P < 0.01$ for all), and there was no significant difference in the species numbers of saltmarsh generalists among the five habitats ($P > 0.05$ for both).

Bird detections

A total of 1,384 birds were recorded in the saltmarshes during the study. The most abundant species was the oriental great reed warbler (*Acrocephalus orientalis*, 299 birds, 21.6% of the total), followed by the reed parrotbill (284 birds, 20.5% of the total). They were the dominant species in the reed monocultures (35.6 and 28.9%) and reed-dominated community (26.7 and 21.1%). However, they were rarely recorded in the cordgrass monocultures (no oriental great reed warblers and only seven reed parrotbills). The most abundant species recorded in the cordgrass monocultures was the zitting cisticola (*Cisticola juncidis*, 30.0%), followed by the marsh grassbird (*Megalurus pryeri*, 24.2%) and the vinous-throated parrotbill (*Paradoxornis webbianus*, 20.8%) (Table 1). The highest density of all saltmarsh birds was recorded in the reed monocultures (10.1 birds per counting station). The reed-dominated community, reed-cordgrass mixture, and cordgrass-dominated community had similar bird densities (8.3, 7.9, and 8.8 birds per counting station, respectively). The lowest bird density was recorded in the cordgrass monocultures (3.8 birds per counting station).

Of the 553 individuals of saltmarsh generalists recorded during this study, the highest density occurred in reed-cordgrass mixture and cordgrass-dominated community (3.9 birds per counting station for both) (Fig. 2b). Of the 755 individuals of saltmarsh specialists recorded during this study, the highest density occurred in reed monocultures (6.9 birds per counting station) (Fig. 2b). The cordgrass monocultures had the lowest densities of both saltmarsh generalists (2.3 birds per counting station) and saltmarsh specialists (1.2 birds per counting station) (Fig. 2b).

Repeated-measures ANOVAs indicated that the mean number of individuals of all saltmarsh birds differed among the five habitats ($F = 7.52$, df $= 4$, $P < 0.001$); the number of individuals was significantly lower in the cordgrass monocultures than in the other four habitats, while there was no significant difference in the mean number of individuals among the four habitats with reed (Fig. 2b). The distribution of saltmarsh specialists had a similar pattern, with fewer individuals ($F = 9.11$, df $= 4$, $P < 0.001$) in cordgrass monocultures than in the other habitats. The mean number of saltmarsh generalist individuals, however, did not significantly differ ($F = 2.17$, df $= 4$, $P = 0.11$) among the five habitats (Fig. 2b).

Similarity of bird communities in different patch types

One-way ANOSIM indicated a significant difference in the bird communities among the five habitats (Global test R $= 0.64$, $P = 0.001$). The difference in bird communities was larger between the cordgrass monocultures and the four habitats with reed (R $= 0.94$–1.0, $P < 0.05$ for all) than between the four habitats with reed (R $= 0.17$–0.85, $P = 0.03$–0.8), although significant differences were detected between the reed monocultures and reed-cordgrass mixture ($P = 0.03$) and between reed monoculture and cordgrass-dominated community ($P = 0.03$). The MDS ordination plot indicated the same pattern (Fig. 3).

Habitat selection of common birds

Habitat use and habitat availability significantly differed for the five common bird species (χ^2 tests, $P < 0.05$ for all). The oriental great reed warbler and reed parrotbill preferred reed monocultures and avoided cordgrass monocultures. The zitting cisticola, vinous-throated parrotbill, and marsh grassbird avoided reed monocultures and had no selection (neither preferred nor avoided) on the cordgrass monocultures. Most birds had no selection on the

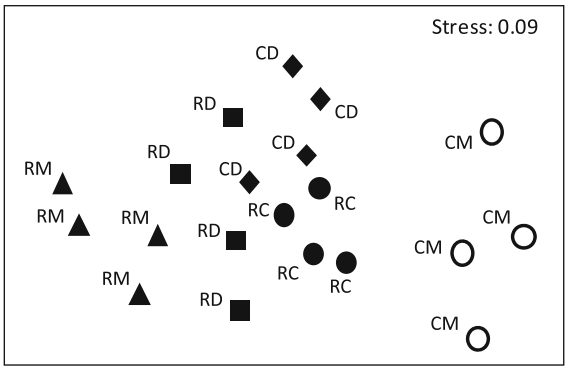

Fig. 3 Non-metric multidimensional scaling (NMDS) ordination of bird communities in the five habitats in the four sampling regions. *RM* reed monocultures, *RD* reed-dominated community, *RC* reed-cordgrass mixture, *CD* cordgrass-dominated community, *CM* cordgrass monocultures

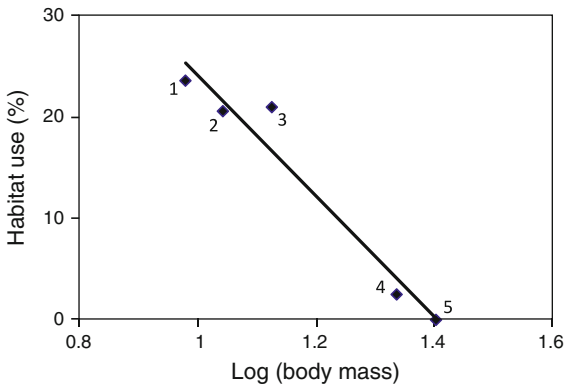

Fig. 4 The relationship between the body mass (g) of five common saltmarsh birds (*1* Zitting cisticola, *2* Vinous-throated parrotbill, *3* Marsh grassbird, *4* Reed parrotbill, *5* Oriental great reed warbler) and their use of cordgrass monocultures (Habitat use $= -59.5 \times \log(\text{body mass}) + 83.6, R^2 = 0.95, P = 0.01$)

reed-dominant, reed-cordgrass mixed, and cordgrass-dominant habitats, except that the oriental great reed warbler had negative selection and the vinous-throated parrotbill and marsh grassbird had positive selection on the cordgrass-dominant habitats (Table 3). Linear regression indicated that body size was related to the association of cordgrass monoculture patches among the five common bird species, with the proportions of birds in the cordgrass monocultures decreasing with the increase of body mass (Fig. 4).

Discussion

We detected no statistical differences in number of species or abundance of saltmarsh birds (specialists and generalists) among the four habitats with reed, while species number and abundance were lower in the cordgrass monocultures than in the habitats with reed. Although the distribution of saltmarsh generalists did not significantly differ among the habitats, species number and abundance of saltmarsh specialists were lower in the cordgrass monocultures than in the other habitats. Moreover, the preferred habitats differed among the common bird species, and no birds preferred the cordgrass monocultures. These results suggest that the cordgrass monocultures are not suitable habitats for the breeding birds, especially for the saltmarsh specialists. Although different species could have various detection probabilities in different habitat patches, the detection probability of species richness was >75% for all bird groups in different habitat. This suggests our results are reliable.

The study was conducted in a single season without replication through different years. However,

Table 3 Habitat use (%) and selection by common bird species in the five habitats

Bird species	Habitat patch				
	RM	RD	RC	CD	CM
Oriental great reed warbler	47.8 (+)	20.7 (0)	16.7 (0)	14.7 (−)	0.0 (−)
Reed parrotbill	40.8 (+)	18.3 (0)	17.5 (0)	20.9 (0)	2.5 (−)
Zitting cisticola	7.2 (−)	13.1 (0)	29.4 (0)	26.8 (0)	23.5 (0)
Vinous-throated parrotbill	4.9 (−)	11.5 (0)	28.7 (0)	34.4 (+)	20.5 (0)
Marsh grassbird	1.4 (−)	14.4 (0)	30.2 (0)	33.1 (+)	20.9 (0)

The '+', '0', and '−' in the parentheses indicate positive, null, and negative selection, respectively

Habitat patches and availabilities (%): *RM* reed monocultures (22.7), *RD* reed-dominated community (15.9), *RC* reed-cordgrass mixture (22.7), *CD* cordgrass-dominated community (20.5), *CM* cordgrass monocultures (18.2)

the use of different habitat patches by birds might vary among different years. Moreover, some birds can adapt themselves to the cordgrass-invaded habitats after some time (Kennedy et al. 2005). Further research is needed to understand the yearly variation and track the long-term trajectory of bird responses to invasive cordgrass.

Many studies have indicated that plant species composition (floristics) affects bird species composition, and that some plant species determine whether birds can use the habitats (Flanders et al. 2006; Fleishman et al. 2003). At Chongming Dongtan, the number of bird species and abundance were lower in the cordgrass monocultures than in the habitats with reed, while there was no significant difference in species number and abundance among the habitats with reed. This suggests that the reed is a key species determining habitat use by breeding saltmarsh birds. This finding is similar to that in previous studies of pine-invaded forests, where the presence of native vegetation is related to the composition of bird communities and habitat use by native birds (Estades and Temple 1999; Lantschner et al. 2008). This result also supports previous studies indicating that the breeding performance of birds is not reduced by the low and moderate invasion of exotic plants (Grant et al. 2004; 2006; Kennedy et al. 2009; Wilson and Belcher 1989) but is reduced in the highly invaded habitats (Davis and Duncan 1999; Flanders et al. 2006; Lloyd and Martin 2005).

The spread of exotic cordgrass changed not only the local plant species composition but also the vegetation structure of the invaded communities. At Chongming Dongtan, stem density (number of stems per unit area) is greater for cordgrass than reed (Gan 2009). In breeding periods, birds frequently move through stems to care for the nests, eggs, and nestlings. Thus, a dense stand of stems might be unsuitable for the breeding birds (Stanevièius 2002). Gan et al. (2010) also indicated that the high density of cordgrass stems is one of reasons for the lower bird density in cordgrass habitats than in reed habitats in winter. Walker (2008) has indicated that both species composition and community structure are associated with bird community organization, with species composition being related to the potential food and nesting sites for birds and community structure being related to the habitat availability and usability. Because the cordgrass community is denser and shorter than the reed community, the spread of cordgrass changed both the species composition and structure of the local vegetation and thus could greatly affect the local bird communities.

The replacement of native plants by exotic plants also changes the functional relationship between birds and their food resources (Benoit and Askins 1999; Flanders et al. 2006). During breeding periods, saltmarsh birds consume a large amount of animal food, especially arthropods, to meet their nutritional and energy requirements. Given the lack of coevolution between the native fauna and exotic plants, arthropod diversity is generally lower on the exotic plants than on the native ones (Flanders et al. 2006). This reduces the quantity of animal food for birds in the exotic habitats. Recent study on the arthropod communities in the saltmarshes at Chongming Dongtan has indicated that the arthropod densities were substantially higher in the reed monocultures and in the reed-cordgrass mixture than in the cordgrass monocultures (Wu et al. 2009). This is consistent with the distribution of breeding birds in these habitats. Consequently, the lack of food resources might be one of the reasons for the low number of species and individuals of saltmarsh birds in the cordgrass monocultures.

Nest predation is also a major selection pressure affecting breeding success of birds in saltmarshes (Greenberg et al. 2006). Many studies have compared nest predation in native and exotic habitats, and the results are inconsistent (e.g., Borgmann and Rodewald 2004; Ortega et al. 2006; Remeš 2003; Schmidt and Whelan 1999; Schmidt et al. 2005). Schlossberg and King (2010) concluded that nests in monocultures of exotic plants experienced relatively high predation rates, while nests in mixed plant communities with native and exotic plants tended to survive at least as well as those in native plant communities. This suggests that the dense cordgrass monocultures might increase nest predation at Chongming Dongtan. In addition, the nests established in cordgrass monocultures might be more susceptible to attack by carnivores on the ground because the plant height is lower for cordgrass than reed (Borgmann and Rodewald 2004; Graveland 1999).

Tidal flooding is another key factor restricting the diversity of breeding birds (Reinert 2006) and greatly affects the breeding success of birds that nest in saltmarshes (Greenberg et al. 2006). At Chongming Dongtan, reed can only grow in the high tide zone in

the tidal flats, while cordgrass, which can endure long periods of inundation, can grow over the entire tidal flat, including the middle and low tide zones (Wang et al. 2006). Moreover, cordgrass plants are shorter than reed plants (Gan et al. 2009), and therefore the nests built in the cordgrass are more likely to be submerged by tidewater than those in the reed. Nordby et al. (2009) have indicated that the nests of the Alameda song sparrow (*Melospiza melodia pusillula*) built in exotic cordgrass were more likely to fail from tidal flooding than those built in native vegetation in San Francisco Bay because the exotic cordgrass occurred at lower elevations relative to the tides. Thus these cordgrass habitats are ecological traps for the birds (Guntenspergen and Nordby 2006; Nordby et al. 2009). Gan (2009) also recorded breeding failure caused by the inundation of nests in the cordgrass vegetation at Chongming Dongtan. Because exotic plants can have conflicting effects on different parts of the life history of birds (Heckscher 2004), the influence of cordgrass invasion on the breeding performance of birds in native and cordgrass-invaded habitats requires additional study.

Compared to habitat specialists, habitat generalists have broad niches, high adaptability to various environments, and wide distributions across habitats. The spread of exotic plants changes local habitats, and these changes affect the habitat specialists more than the habitat generalists (Ceia et al. 2009). At Chongming Dongtan, the species number and abundance of saltmarsh generalists did not differ among different habitats, but species number and abundance of saltmarsh specialists were lower in cordgrass monocultures than in the other habitats. Habitat selection of common birds also indicated that the saltmarsh specialists (oriental great reed warblers and reed parrotbills) preferred reed monocultures and avoided cordgrass monocultures. In contrast, two saltmarsh generalists that can use diverse habitats including shrubs and nearby grasslands (the zitting cisticolas and vinous-throated parrotbills) had no selection (neither preferred nor avoided) to cordgrass monocultures. This suggests that the saltmarsh specialists but not generalists are strongly affected by the invasion of exotic cordgrass.

Although the marsh grassbird is a saltmarsh specialist at Chongming Dongtan, it avoided reed monocultures and was found mainly in the cordgrass-invaded habitats. Gan (2009) indicated that the marsh grassbird established nests exclusively in the cordgrass communities. Unlike the relatively thick and hard stems of reeds, the thin and flexible stems of cordgrass provide suitable nest sites and materials for this species. The marsh grassbird is a new species that was first recorded at Chongming Dongtan in the early 2000s (Gan et al. 2006). Its population has increased rapidly since then. Because the marsh grassbird depends on the cordgrass communities for breeding habitat, its occurrence at Chongming Dongtan is apparently related to the cordgrass invasion and spread (Gan et al. 2006).

Our results indicate that the use of cordgrass monocultures by the common breeding birds was negatively related to their body size. We suggest three hypotheses to explain this result. First, the stems of cordgrass, which are dense and soft, may provide better nest sites for small birds than for large birds. The small saltmarsh birds generally build nests among plant stems, and supports on the nest base are needed; in contrast, large birds can hang their nests directly on the more rigid stems of reed plants (Graveland 1999). Second, highly dense vegetation can reduce movements and food availability of birds, and this reduction is likely to be greater for large than for small birds. Third, large birds may out-compete small birds in the optimal saltmarsh habitats. Many studies have indicated that strong interspecific competition occurs among saltmarsh birds because their niches are similar (Edington and Edington 1972; Catchpole 1973). Generally, large birds are dominant in bird communities and occupy the optimal habitats (Luck and Daily 2003). The interspecific competition might force the small birds to use the sub-optimal cordgrass-invaded habitats.

The area invaded by exotic cordgrass has expanded exponentially in the saltmarshes at Chongming Dongtan over the past decades (Wang et al. 2006). Cordgrass cannot completely out-compete reed in the high tidal zone but it can take over the middle and low tidal zones and form a cordgrass monoculture at the expense of native sea-bulrush. Moreover, the cordgrass monocultures cannot be invaded by native plants (Wang 2007). Thus, the invasion of cordgrass will change plant succession and eventually change the saltmarsh plant communities at Chongming Dongtan. Although saltmarsh birds can use the cordgrass-invaded habitats and although cordgrass monocultures support similar species and

individual numbers of saltmarsh generalists as other habitats, cordgrass monocultures are not suitable for the saltmarsh specialists. This might cause a homogenization of bird communities in saltmarshes and other habitats, and eventually decrease the local bird diversity. Controlling the spread of exotic cordgrass and maintaining the native habitats for the saltmarsh birds, especially for the saltmarsh specialists, is urgently needed.

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