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Female tidal mudflat crabs represent a critical food resource for migratory Red-crowned Cranes in the Yellow River Delta, China

DONGLAI LI, YUQING DING, YING YUAN, HUW LLOYD and ZHENGWANG ZHANG

Summary

Staging sites are vital for large-sized migratory cranes, which require high-protein food sources during migration. In this study, we used field surveys and faecal analysis to determine the migration patterns and dietary composition of the globally threatened Red-crowned Crane *Grus japonensis* population that migrates and stages at the Yellow River Delta Nature Reserve (YRDNR), Eastern China. Analysis of 135 faecal samples collected during the migration season in 2008, 2010 and 2011 showed that 78.8% of the faeces comprised > 90% dry mass of tidal mudflat crab *Helice tientsinensis* remains, suggesting that tidal mudflat crab was an important source of food for these Red-crowned Cranes. Smaller percentages of two other crab species (*Eriocheir sinensis*, *Macrophthalmus dilatatum*), fish remains, ragworms *Hediste diversicolor* and vegetation were also detected in the faecal samples. Consumption of tidal mudflat crabs was found to increase from autumn through to spring. Surveys of tidal mudflat crabs from YRDNR revealed that female crabs have significantly smaller body size (dry mass) but higher energy reserve ratio (ash-free dry mass per body mass) compared to males. Red-crowned Cranes fed predominantly on small and medium-sized female crabs, with a female to male ratio of 5:1 in the diet, compared with the 1:2 ratio of female to male crabs found within the coastal wetland crab population. Our findings suggest that tidal mudflat crabs represent a critical food source for the migratory Red-crowned Crane population in YRDNR, and future crane conservation strategies should encompass the necessary measures to conserve the tidal mudflat crab population at this staging site.

Introduction

Migration staging sites are vital for many waterbird populations as they allow the birds to develop large quantities of fat and proteins to fuel their migration journeys (Myers *et al.* 1987, Placyk and Harrington 2004). Migratory waterbirds are constrained not only by the narrow window of opportunity to refuel but also because so few staging sites along their migratory routes have the necessary extent of habitats and food resources (Morrison and Harrington 1979). Staging sites are also highly vulnerable to commercial development, expansion of agricultural practices and land reclamation (Pfister *et al.* 1992, Yang *et al.* 2011), threats which are linked to the decline of many waterbird populations (van de Kam *et al.* 2004, Catry *et al.* 2011). To date, there remain large gaps in our knowledge of the diet and foraging ecology of these threatened waterbirds, particularly larger-bodied omnivorous species such as cranes. Cranes may depend on a wider range of vegetation (for fats) and animal (for protein) food resources to complete their migration (Avilés *et al.* 2002, Ma *et al.* 1999). However, with such a lack of basic empirical data regarding the dietary composition of cranes, our ability to assess the population response of these migratory species to numerous anthropogenic pressures is somewhat limited.

This study involved the characterisation of the predominant food resource for a highly threatened bird species at a critical migratory staging site along the flyway of its continental population. Red-crowned Crane *Grus japonensis* is globally 'Endangered' (BirdLife International 2012), having undergone a serious population decline in China from more than 1,200 individuals in 2000 to less than 500 in 2011 in one of the most important wintering areas (Yancheng Nature Reserve; Su and Zou 2012). This decline has been linked to the extensive loss and degradation of its primary breeding grounds in north-east China due to agricultural reclamation and irrigation (Su and Wang 2010). Extensive tidal land reclamation, invasion by *Spartina alterniflora*, and the expansion of oilfield production in coastal tidal areas and river estuaries that serve as important wintering and staging sites also present serious challenges for the migratory crane population (Cao and Liu 2008, Ma *et al.* 2009).

The diet of both the migratory and wintering populations is poorly quantified. Anecdotal evidence suggests that the cranes feed predominantly on marine invertebrates, frogs, fishes, polychaetes, sedge tubers and cereal grains (Ma *et al.* 1999). In winter, this species is thought to feed on marine snails (e.g. *Oncomelania* spp., *Bullacta exarata*), bivalve mollusks (e.g. *Venerupis* spp.) and *Hemigrapsus* or *Sesarma* crabs at their wintering grounds in Yancheng Nature Reserve (Lu 2008). Some authors have suggested that in areas of severe coastal wetland degradation, cranes may have become more dependent on agricultural rice fields (Lee *et al.* 2007, Wang *et al.* 2011). However, Red-crowned Cranes were observed feeding predominantly on tidal mudflat crabs *Helice tientsinensis* in November–December 2008 and March 2009 during a recent study on avian wetland communities in the Yellow River Delta Nature Reserve (Li *et al.* 2011). The tidal mudflat crab is widely distributed along the coastal zones of eastern China, and is the most abundant crab species in the estuarine wetlands of the Yellow River Delta (Dai and Yang 1991). In winter, they tend to hibernate in burrows, but individuals are often found along creeks during low tide in late December, and also when they become stranded from their burrows. They emerge from their burrows and become more active from early March, which coincides closely with the arrival of the migrating Red-crowned Cranes.

In this study, we assessed the dietary composition of Red-crowned Cranes at the Yellow River Delta Nature Reserve (YRDNR) using faecal analysis. Our first objective was to identify the critical food resource for staging and wintering Red-crowned Cranes to determine whether tidal mudflat crabs are an essential food source for these birds during this period. We then determined whether there is any connection between prey-size selection and the energy reserves of the crab. Finally, we discuss the innate conservation value of these predominant prey types for this highly endangered species.

Methods

Study site

This study was conducted in the Yellow River Delta Nature Reserve (37.64°–38.15°N, 118.62°–119.37°E) in Shandong Province, Eastern China (Figure 1). This nature reserve consists of extensive estuarine wetlands formed by rapid land accretion, driven by high sediment deposition at a rate of more than 2.7 km^2 /year since 2002 (Li *et al.* 2009). Extensive estuarine mudflats and *Suaeda salsa* salt marshes form the principal foraging habitats for Red-crowned Cranes, especially in winter, as other inland wetland habitats are often frozen. At other times, some individuals might also forage on aquaculture fish ponds and the actively restored reed marsh habitat (Li *et al.* 2013). The delta is also host to the second largest oil field in China. Further details regarding the threats to these wetland habitats and their biodiversity are given in the reports by Cao and Liu (2008) and Li *et al* (2011).

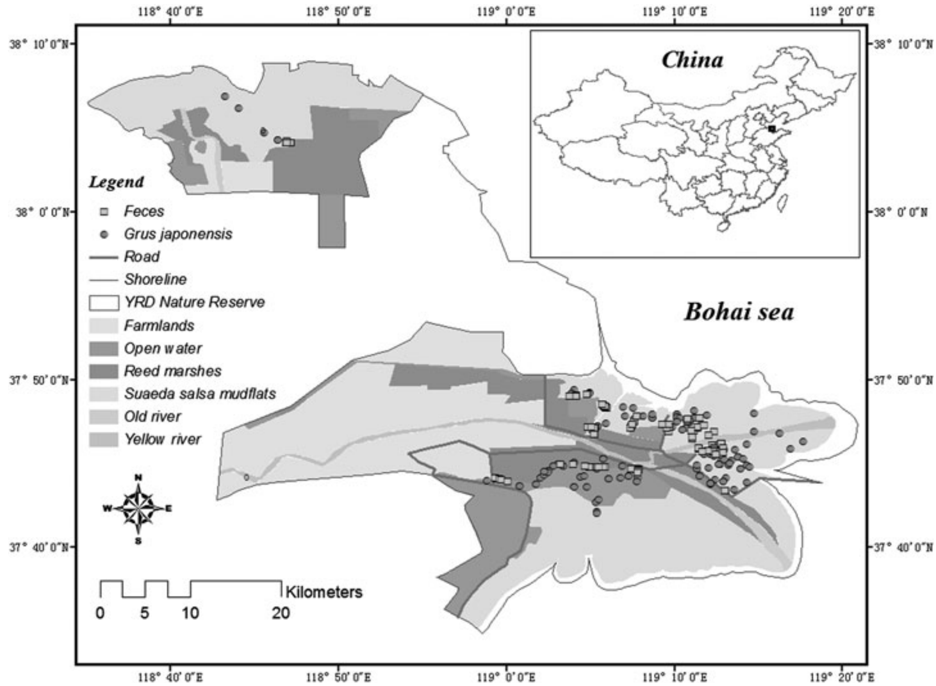

Figure 1. Location of the YRDNR study site on the east coast of China, showing the distribution of Red-crowned Cranes and faecal sampling locations.

Faecal and food specimen collection and analysis

Fresh faeces of Red-crowned Cranes were collected during three seasons: autumn (12–18 November, 2010); winter (20–27 December, 2011); and spring (5–26 March, 2008 and 6–8 April, 2011). We collected fresh faeces and possible food specimens in known feeding and roost sites based on the tracks left by the birds. The entire faeces were scraped off the surface and preserved in 95% ethanol. We limited the number of samples collected from each site to reduce bias of pseudo-replication.

Faecal analysis was conducted following the protocol devised by Hunt and Slack (1989). Samples were disinfected by ultraviolet light for 30 min, and then placed over a 0.3 mm sieve and scoured under tap water for 10 min to separate soil and other matter. Indigestible parts were analysed using a stereomicroscope and food items were identified to the lowest possible taxonomic level, aided by comparisons with collected food specimens. We classified faecal content into four groups: crabs, fish, vegetation and other unidentified food matter. Since fragments of unknown food type were rare, and formed only a tiny proportion of the total recorded, we removed them from subsequent statistical analysis. All identified prey items were dried to a constant weight at 70°C. Crane diets were quantified using frequency of occurrence and aggregate percentage of dry mass for each food (Rodway and Cooke 2002). Seasonal variation in the abundance of crabs in the cranes' diet was examined by first quantifying the number of the claw dactyl and pollex and walking leg tips found in the faecal samples.

Collections and analysis of tidal mudflat crabs

We collected random samples of tidal mudflat crabs from the preferred foraging site of Red-crowned Cranes using several 1-m^2 quadrats and digging the burrows. A total of 104 tidal mudflat crabs

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were collected, with 23, 34 and 44 crabs captured on 22 December (2010), 18 November (2011) and 6 December (2011), respectively. All crabs were placed in labelled plastic bags and stored at -10°C in a laboratory freezer. For subsequent laboratory analysis, crabs were washed clean of any debris and dried to constant weight at 70°C for 48 hours in a drying box. The dry mass of crabs was weighed to 0.001 g and the remains carefully separated into three categories: dactyl of the claws, carapaces and chelipeds, and indigestible parts. The length and width of intact dactyls collected in the faecal samples and those from crabs were measured with callipers to 0.01 mm. Dactyl length was defined as the maximum length of the dactyl from the tip to the top, while width was measured as the maximum width of the dactyl from the first ridge on the top side. Indigestible parts were incinerated in a muffle furnace at 550°C for 5 h to obtain the ash-free dry mass (AFDM) of each crab. We used the dry crab mass as a measure of prey size and AFDM as a measure of energy reserve (Dekinga and Piersma 1993, Van Gils *et al.* 2005). To compare the variation in the crab energy reserve, we presented AFDM ratio as the percentage of AFDM per dry mass.

Male and female crabs were easily distinguished by examining the shape of the abdomen. Female crabs have a noticeabl wide abdomen, whereas male crabs have much narrower abdomens. There are also significant known differences between male and female crabs with respect to the size (length and width) of their dactyls (Spivak and Sánchez 1992). Consequently we used the length and width of dactyls to further discriminate between male and female crabs found in the faecal samples.

Statistical analysis

We found no significant differences in the dactyl length (Student's T-test: t = -0.143, df = 197, P = 0.886) and dactyl width (t = -0.04, df = 201, P = 0.968) between right and left claws. Therefore we used the mean dactyl length and width in subsequent analyses. There were no significant difference in the dry mass (Mann-Whitney U: z = 866.5, P = 0.611) or sex ratio (Chi-square test: χ^2 = 0.078, P = 0.768) between years, so all data were pooled together. We also found no evidence for annual changes in the percentage of dry mass of both crabs (mean % ± SE: 95.6 ± 3.0 in 2008, 97.5 ± 1.4 in 2011; t = -0.561, df = 84, P = 0.576) and fish (mean % ± SE: 4.3 ± 3.0 in 2008, 2.4 ± 1.4 in 2011; t = -0.556, df = 84, P = 0.580) or in the number of identified crabs claws and tips per faecal samples (all P > 0.573). Consequently, we also pooled all the data for subsequent analysis.

All variables were examined for normality using Kolmogorov–Smirnov tests. Where data were normally distributed, Student's T-tests were used to compare differences between sexes and groups, otherwise non-parametric Mann-Whitney U tests were used. One-way ANOVA with Tukey post-hoc tests were used to determine seasonal variation in diet composition as the percentage dry mass of crabs, fish, and vegetation, and the relative importance of crabs in the food composition of the crane's diet with the number of dactyl and pollex, and walking leg tips. Discriminant Function Analysis (DFA) was used to classify the sex of crabs with dactyl length and dactyl width as independent factors. Chi-square (χ^2) tests were used to examine differences between the sex ratio of tidal mudflat crabs found in crane faeces and those found in natural samples collected from the habitat. Prey size (dry mass) and AFDM were estimated from linear regressions of dactyl length or width derived from male and female reference crabs. All statistical analyses were conducted using STATISTICA, version 6.0 (StatSoft, Tulsa, OK, USA). The statistically significant P value was set as 0.05 and all data were expressed as mean ± SD, unless otherwise stated.

Results

Red-crowned Crane migration and habitat use

The migratory Red-crowned Cranes arrived at the YRDNR from late October to early December and from late February to mid-March (Figure 2). The largest observed populations were 173 and 123 individuals in the 2007–2008 and 2008–2009 migration seasons, respectively. The majority of

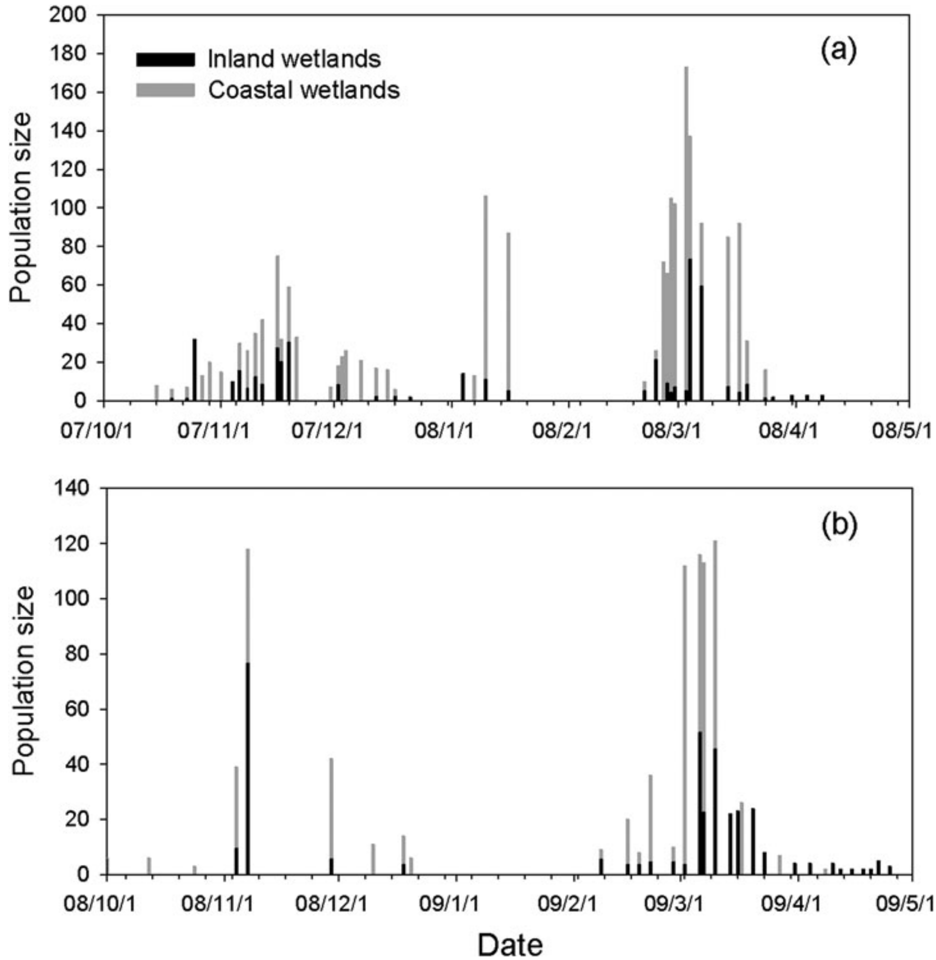

Figure 2. Red-crowned Crane migration and habitat use at YRDNR; (a) migration seasons between October 2007 and May 2008; (b) migration seasons between October 2008 and May 2009.

individual cranes (75.8% in 2007–2008 season and 63.8% in 2008–2009 season) were recorded from coastal intertidal mudflats, *Suaeda salsa* salt marshes, and estuaries, particularly during the winter (Figure 2). Inland freshwater reed marshes and fish ponds were used by individual cranes primarily during the autumn (36.5% in 2007; 53.6% in 2008). No Red-crowned Cranes were found using the farmlands (rice or wheat fields) around the reserve.

Description of faecal samples and diet composition

Most faecal samples (n = 106 or 78.5%) contained a large proportion (> 90% dry mass) of crab remains (Figure 3), indicating that crabs were a critical food resource. The majority of identified claws (dactyl and pollex) and carapaces belonged to tidal mudflat crab, with only four samples containing the remains of Chinese mitten crab *Eriocheir sinensis* and seven samples containing claws of *Macrophthalmus dilatatum*. Fourteen faecal samples contained a significant amount of vegetable matter, primarily algae, corn, seeds of *Suaeda salsa* and various grasses (Table 1). Unidentified fish bones and otoliths (but no scales) were found in only 13 samples. We found no

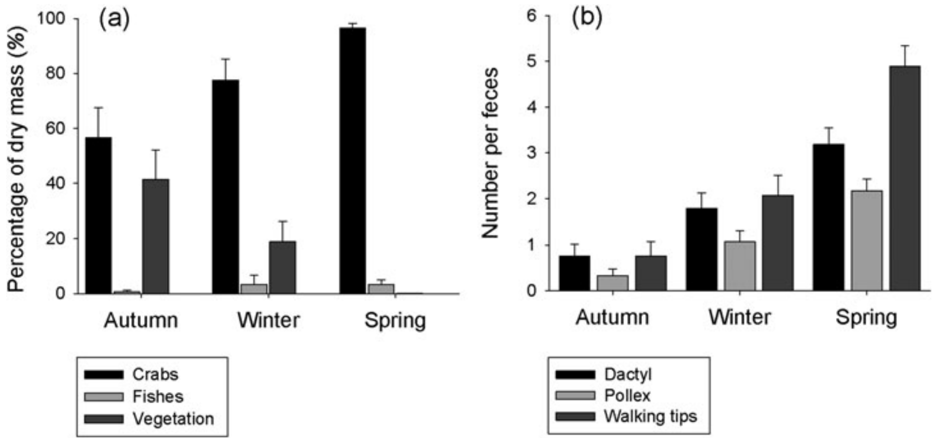

Figure 3. Seasonal variations in the main food types of Red-crowned Cranes at YRDNR, China. (a) the percentage dry mass of the main food items; (b) the three unique cheliped parts of crab prey in the faecal samples of Red-crowned Crane. Multiple comparison Tukey post-hoc tests for crab food items: Autumn vs Winter, $P = 0.04$; Autumn vs Spring, $P < 0.0001$; Winter vs Spring, $P = 0.01$. Vegetation: Autumn vs Winter, $P = 0.008$; Autumn vs Spring, $P < 0.0001$; Winter vs Spring, $P = 0.003$); Dactyl: Autumn vs Winter, $P = 0.420$; Autumn vs Spring, $P = 0.002$; Winter vs Spring; $P = 0.061$. Pollex: Autumn vs Winter, $P = 0.419$; Autumn vs Spring, $P = 0.001$; Winter vs Spring, $P = 0.036$. Tips: Autumn vs Winter, $P = 0.412$; Autumn vs Spring, $P < 0.0001$; Winter vs Spring, $P = 0.001$.

mussel or snail shells in any of the faecal samples, but jaw remains of ragworm *Hediste diversicolor* were recorded from nine samples.

Seasonal variations in food items

Pronounced seasonal variations were found in two main food types in the crane's diet (Figure 3a), with a significant increase of crab remains (ANOVA: $F_{2,\,132} = 17.1$, $P < 0.0001$) and a significant decline in plant matter ($F_{2,\,132} = 14.2$, $P < 0.0001$) from autumn to the following spring. An increase in crab remains was also evident in the percentage occurrence within faecal samples (Table 1). Of the vegetation food items, only algae and corn showed evidence of a decline in their occurrence in the crane's diet. There was no significant variation in the dry mass of fish remains ($F_{2,\,132} = 0.3$, $P = 0.759$) despite recording a slight increase in occurrence (Table 1). A strong seasonal increase in crab prey in the diet of Red-crowned Cranes was also suggested by the number of dactyls ($F_{2,\,132} = 7.5$, $P = 0.001$), pollex ($F_{2,\,132} = 8.5$, $P < 0.0001$) and tips of walking legs ($F_{2,\,132} = 14.9$, $P < 0.0001$) found per faecal sample (Figure 3b).

Prey size and sex selection

The sex ratio of female to male crabs from the foraging habitats of Red-crowned Cranes was close to 1:2. DFA revealed that male and female crabs were easily distinguished based on the size of the dactyls, with a success rate of 90.3% (Wilks' lambda = 0.454, df = 2, $P = 0.0001$). The predicted sex ratio of female-to-male tidal mudflat crabs in crane faeces was 5:1 (Fisher's linear discriminant functions), which was heavily skewed toward the number of females (119 out of 143). This indicated that cranes showed a significant preference for female crabs in their diet (Chi-square test: $\chi^2_{\ 1} = 57.7$, $P < 0.0001$; Figure 4). Regression analysis revealed significant variations between male and

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Table 1. Percentage (%) occurrence of food remains in the faeces of migratory Red-crowned Cranes at the YRDNR.

Food types		Percentage (%) occurrence			
		Autumn (n = 21)	Winter (n = 28)	Spring (n = 86)	Total (n = 135)
Crabs	*Helice tientsinensis*	61.9	89.3	98.8	91.1
	Eriocheir sinensis	19.0	3.5	0.0	3.7
	Macrophthalmus dilatatum	14.3	0.0	4.6	5.1
Fishes	Fish bones and otoliths	19.0	10.7	7.0	9.6
Polychaeta	Jaws of Ragworm (*Nereis* spp.)	23.8	3.5	4.6	6.7
vegetation	Corns	9.5	21.4	0.0	5.9
	Seeds of *Suaeda salsa*	19.0	17.9	25.6	23.0
	Seeds of grasses	38.1	7.1	14.0	16.3
	Leaf of *Tamarix chinensis*	0.0	0.0	4.7	3.0
	Unidentified plant materials	47.6	46.4	52.3	50.4
	Algae	28.6	0.0	0.0	4.4
Others	Unidentified food matter	38.1	3.6	10.5	13.3

female prey size (dry mass), dactyl length and dactyl width (male: R^2 = 0.814, F = 219.2, P < 0.0001; female: R^2 = 0.908, F = 692.9, P < 0.0001), and between AFDM, dactyl length and dactyl width (male: R^2 = 0.461, F = 42.8, P < 0.0001; female: R^2 = 0.825, F = 329.3, P < 0.0001; Figure 5).

Cranes showed a significant prey-size preference for smaller tidal mudflat crabs, with the dry mass of crabs consumed (3.44 ± 1.52, n = 143) being significantly smaller than that of crabs sampled from the YRDNR (4.92 ± 1.52, n = 104; Student's T-test: t = 7.07, df = 245, P < 0.0001; Figure 6). Although there was a significantly higher AFDM per male crab (1.73 ± 0.49, n = 72) than female crab (1.46 ± 0.53, n = 32; t = 2.589, df = 102, P = 0.011), the female crabs provided more energy per body weight (AFDM ratio: 0.38 ± 0.07, n = 32) than males (0.34 ± 0.06, n = 72; t = -3.879, df = 102, P < 0.0001). Collectively, the AFDM ratio of crabs consumed by Red-crowned Cranes (0.37 ± 0.12, n = 143) was significantly higher than the average AFDM ratio of tidal mudflat crabs sampled in the YRDNR wetlands (0.34 ± 0.07, n = 104; t = -2.527, df = 245, P = 0.012).

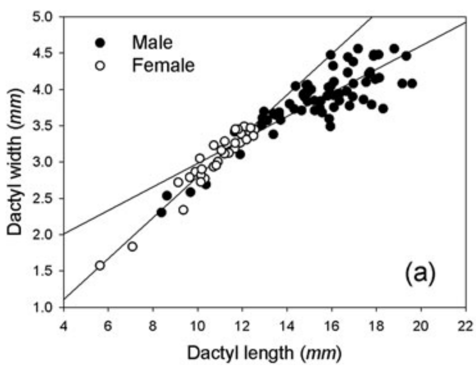

Figure 4. Difference in length and width of male and female dactyl of *Helice tientsinensis* crabs: (a) represents crabs sampled from tidal land habitats; (b) represents predicted sex of crabs from dactyls in faecal samples.

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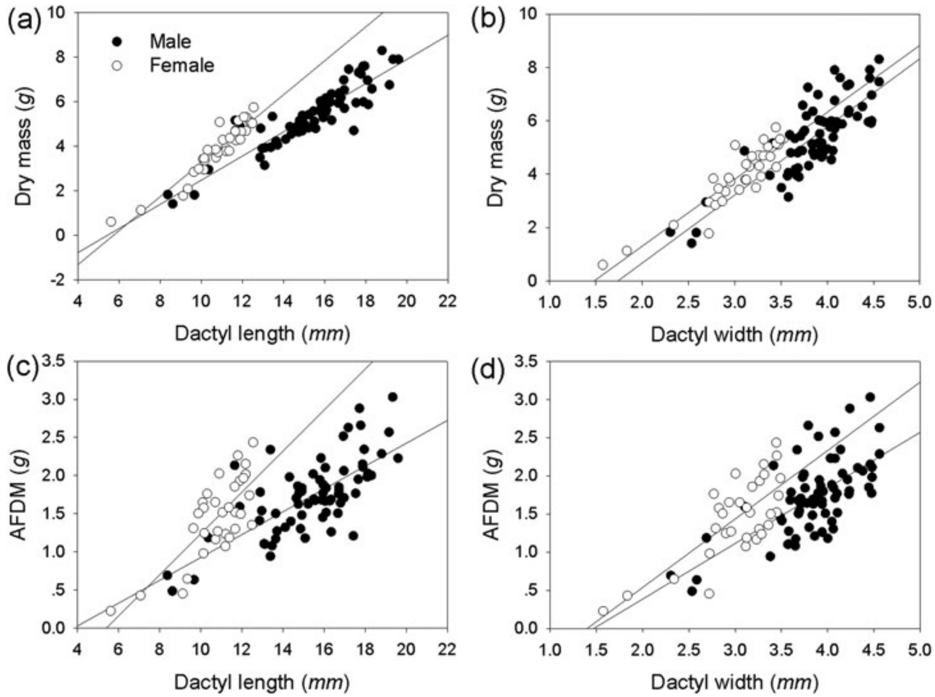

Figure 5. Variation in the relationships of the dry mass (7a and 7b) and AFDM (Ash-free dry mass, 7c and 7d) of male and female *Helice tientsinensis* crabs with length and width of dactyls. Linear regressions between prey size (dry mass) and dactyl length and dactyl width for males: Dry mass = -3.579 + 0.469 x Length + 0.456 x Width; $R^2 = 0.814$, F = 219.2, $P < 0.0001$; females: Dry mass = -4.377 = 0.778 x Length -0.051 x Width; $R^2 = 0.908$, F = 692.9, $P < 0.0001$), and between AFDM, dactyl length and dactyl width for males: AFDM = -0.864 + 0.115 x Length + 0.215 x Width; $R^2 = 0.461$, F = 42.8, $P < 0.0001$; females: AFDM =-1.456 + 0.231 x Length + 0.126 x Width; $R^2 = 0.825$, $F = 329.3$, $P < 0.0001$).

Discussion

This is the first detailed report on the dietary composition of endangered Red-crowned Cranes in the Yellow River Delta, eastern China. Using faecal analysis we found that tidal mudflat crabs, particularly adult females from coastal *Suaeda salsa* salt marsh habitat and intertidal mudflats, represent a critical food resource for the Red-crowned Cranes at YRDNR, since the majority (78.8%) of the samples contained over 90% dry mass of mudflat crab remains. Faecal analysis is not without bias, and the use of samples did not enable us to fully reconstruct the complete composition of the cranes' diet due to differential digestibility of different prey items (Hunt and Slack 1989, Rodway and Cooke 2002). Thus it could be argued that the significance of crabs in the diet may be exaggerated since crabs contain a higher proportion of hard part than other prey types (e.g. fish), and would remain undigested and appear in the faeces (Hunt and Slack 1989). However, faecal analysis is a proven and reliable approach for estimating the main prey types and their relative proportions in the diets of some carnivorous and omnivorous bird species (Dekinga and Piersma 1993, Rodway and Cooke 2002).

Previously it was thought that migratory Red-crowned Cranes in China fed on various fish, crustaceans, molluscs and other macro-benthos species during the migration and wintering period (Yan 1991, Ma *et al.* 1999). We did find a small percentage of fish bone and otoliths, along with

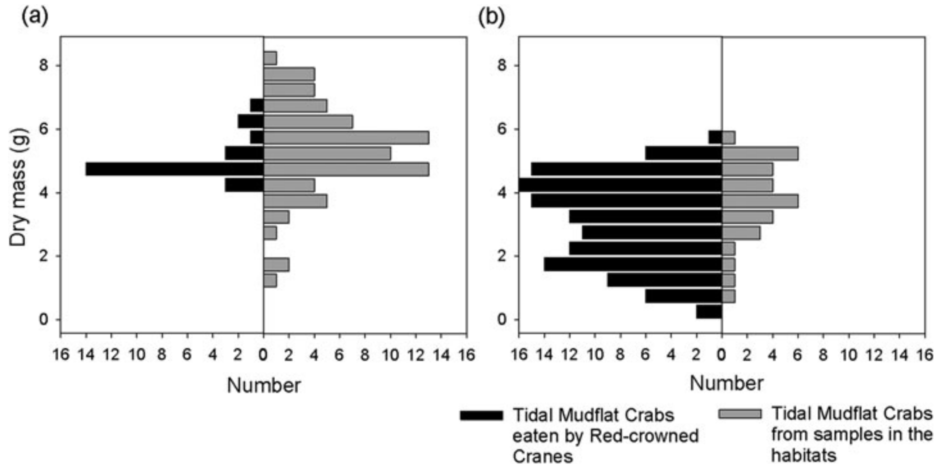

Figure 6. Sexual variation in the frequency of tidal mudflat crab dry mass from samples in tidal land habitats and those eaten by Red-crowned Cranes. (a) males; (b) females.

some small jaws of ragworm in the faecal samples, but there was no evidence of other animal material e.g. shrimps, snails or bivalve molluscs, all of which have some percentage of indigestible hard parts that can be easily identified in the diets of waterbirds through faecal analysis (e.g. Moreira 1994, Rodway and Cooke 2002). Furthermore it is unlikely that the Red-crowned Cranes have adopted special feeding strategies that can split the soft tissues from the hard parts of their prey as previous observations from YRDNR have revealed that Red-crowned Cranes often swallow the whole prey, following a brief handling time (Li *et al.* unpublished data).

There was no evidence in the diet to indicate that the cranes fed on molluscs, a finding which is surprising given that YRDNR is known for the high diversity and biomass of several mollusc species (Zhao and Song 1995). We did record small percentages of vegetable matter such as corn and *Suaeda salsa* seeds in some of the faecal samples. Rather interestingly, we did not record any evidence of rice or wheat in the faecal samples. Unpublished faecal analysis of the Yancheng wintering population has revealed a predominance of indigestible sheaths of rice in the wintering cranes diet (Li *et al.* unpubl. data). There are areas of rice fields around YRDNR, which attract some population of White-naped Crane *Grus vipio*) and Common Crane *G. grus*, but so far there have been no records of Red-crowned Cranes foraging in YRDNR rice fields. Our results therefore showed that Red-crowned Cranes preferred to eat animal food (crabs and fish) rather than vegetable matter (e.g. rice) during their migration at YRDNR. Future studies would address the underlying reasons for selecting crabs as a main food resource in the light of trade-off between individual nutrient requirement and efficient foraging for these different food types at a large geographic scale during migration process.

To our knowledge, this is the first empirical documentation of the importance of a single food resource, specifically tidal mudflat crabs, for any known population of Red-crowned Cranes. Previous studies at Yancheng Nature Reserve have indicated that *Hemigrapsus* and *Sesarma* crab species represent one of several important animal food sources for wintering Red-crowned Cranes (Yan 1991), but these studies did not note the presence of tidal mudflat crabs even though the species is commonly found within the reserve (Ren *et al.* 1986). Globally, crabs in coastal mudflats are known to serve as important prey for shorebirds and gulls (e.g. Zharikov and Skilleter 2004, Ellis *et al.* 2012), but the importance of tidal mudflat crabs in the diet of cranes has not been recorded previously. Only one other species of crane is known to be dependent on a specific crab species for food (Hunt and Slack 1989). Blue crab *Callinectes sapidus* makes up 80–90% of the diet of Whooping Crane *G. americana* when it becomes available at Texas coastal wetlands in the

USA (Chavez-Ramirez 1996). Noticeable reductions in the availability of blue crab during one particular winter caused high winter mortality and low breeding success of Whooping Cranes in the following year (Stehn 2008).

The increased proportion of crabs in the cranes' diet from the autumn stage to winter and spring stages was significant. For cranes, this shift may be related to seasonal variation in crab availability, or result from some vegetable food sources becoming exhausted or a reduction in the availability of other animal prey (e.g. fish). During their southern migration, Red-crowned Cranes have opportunities to feed in a greater range of wetland habitats, including restored reed marsh wetlands, natural shallow water habitats and aquaculture ponds (Li *et al.* 2011). However, foraging opportunities and prey availability during winter and spring may be severely restricted due to some of these habitats becoming frozen or dry. Despite this, there was some evidence to suggest that tidal mudflat crabs are still active during winter. Unpublished data from experimental trap nets (0.25 m radius x 4 m length) set in creeks in the intertidal zones trapped 75 crabs after two days of sampling in December, and frozen crabs are occasionally found along these creeks (Li *et al.* unpubl. data). In spring, flocks of Red-crowned Cranes arrive at YRDNR during late February and early March, migrating to their northern breeding grounds approximately 10–20 days later. This period corresponds to the time when tidal mudflat crabs are beginning to emerge from their winter hibernation and are more sluggish and conspicuous to predators. Tidal mudflat crabs therefore represent a highly nutrient-rich food resource for the migratory Red-crowned Cranes, fulfilling the need for increased body fats to continue further their migration and the formation of eggs.

More interestingly, we found that the Red-crowned Cranes at the YRDNR displayed a specific prey selection by exhibiting a preference for small and medium-size female tidal mudflat crabs. Several ecological studies have revealed important insights into prey-size selection strategies by birds and other taxa (Estrella and Masero 2010, Suraci and Dill 2011). For instance, Olrog's Gull *Larus atlanticus* is known to select small and medium-sized crabs due to the poor digestibility of carapaces and a higher risk associated with capturing large crabs (Berón *et al.* 2011). However, few studies have demonstrated that waterbirds specifically select prey of a particular sex. Our results showed that tidal mudflat crabs were sexually dimorphic, and although females were smaller than males, they had a much higher energy reserve ratio than males, having a higher AFDM ratio. The selection of small and medium-size female crabs is consistent with the Digestive Rate Model (DRM) (Verlinden and Wiley 1989) as female crabs provide more energy per body weight than males. However, the DRM may only be relevant for cranes and other foraging organisms when they face digestive constraints related to prey availability and handling time (Van Gils *et al.* 2005). Based on the contingency model of Belovsky (1984), the prey choice of a foraging crane may also be determined by its profitability, i.e. the net energy intake per handling time that a foraging crane should maximise when its foraging time is divided between the time required for searching and handling prey (Farnsworth and Illius 1998). Small female crabs may simply be easier to handle or to swallow than larger male crabs, so further data are required to quantify the prey-handling time and to determine whether the profitability of female crabs is greater than male crabs. How cranes recognise and select female crabs over males is not yet known, and future studies should determine whether cranes select female crabs based on differences in behaviour between females and males, whether there are differences in the size and depth of burrows of males and females, or whether it is simply a secondary effect of selecting small and medium prey items. Further studies are also needed to determine whether this highly selective pattern exhibited by migratory Red-crowned Cranes at the YRDNR is evident across other populations.

Conservation implications

Both the crane and tidal mudflat crab populations at YRDNR face significant anthropogenic threats such as tidal reclamation, pollution, oil production, and fish harvests at known crane staging and wintering sites. The potential impact of the recent invasion by *Spartina alterniflora* on tidal mudflat crabs within the YRDNR, which is known to adversely impact crab populations (Cui *et al.* 2011) merits further detailed investigation since this could impact the capacity of the YRDNR to serve as an important staging ground for the Red-crowned Crane populations along the western flyway in China. Conservation management actions within these coastal habitats that focus on maintaining and boosting the population and habitats of tidal mudflat crabs may prove invaluable for the conservation of Red-crowned Cranes in China.

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DONGLAI LI[1], YUQING DING, YING YUAN & ZHENGWANG ZHANG*
State Key Laboratory of Earth Surface Processes and Resource Ecology; Ministry of Education Key Laboratory for Biodiversity Sciences and Ecological Engineering; College of Life Sciences, Beijing Normal University, Beijing 100875, China.
[1]*Present address: College of Life Sciences, Liaoning University, Shenyang 110036, China.*

HUW LLOYD
Division of Biology and Conservation Ecology, School of Science and the Environment, Manchester Metropolitan University, Chester Street, Manchester, England, United Kingdom M1 5GD.

**Author for correspondence, email: zzw@bnu.edu.cn*

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