

Reed Parrotbill nest predation by tidal mudflat crabs: Evidence for an ecological trap?

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Abstract. Understanding the relationships between nesting habitat quality and predation risk is essential for developing appropriate conservation management for threatened species. This is particularly relevant where anthropogenic pressures could decouple the environmental cues used by birds to assess nesting habitat quality from increased predation risk. In this study, we conducted a series of surveys and nest experiments to examine the nest predation rates of Reed Parrotbill (*Paradoxornis heudei*) a passerine bird between inland and tidal reed-bed wetland habitats, at Yellow River Delta National Nature Reserve, Eastern China during 2008, and 2010–2012. We found significant differences in the habitat structural characteristics between the two adjacent wetland habitats that are critical for Reed Parrotbill nest-site selection. Experimental trials using recently constructed and abandoned Reed Parrotbill nests as ‘artificial nests, quail eggs and predator-exclusion measures, revealed that tidal mudflat crab (*Helice tientsinensis*) was the primary cause of Reed Parrotbill egg predation in tidal reed-bed habitat. Annual predation rates of real nests from inland reed-bed habitat varied from 35% to 68%, and predation rates of artificial nests were much lower than those from real nests. Pitfall sampling revealed that the abundance of tidal mudflat crabs was significantly higher in tidal reed-bed habitat. Our data suggested that Reed Parrotbills breeding in tidal reed-bed habitats may be highly vulnerable due to extremely high rates of nest predation (up to 100%), caused primarily by the high density of tidal mudflat crabs. The incongruence between nest-site habitat preference and nest survival indicated an ecological trap scenario, which requires further studies on its proximate and ultimate causes as well as the development of effective conservation management for the Reed Parrotbill.

Key words: artificial nest trials; ecological trap; *Helice tientsinensis*; nest-site selection; nest survival rate; *Paradoxornis heudei*; Reed Parrotbill; tidal mudflat crabs; Yellow River Delta.

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INTRODUCTION

birds should prefer habitats that maximize their fitness during nest-site selection (Cody 1985).

The theory of habitat selection predicts that Birds are able to exploit various habitat quality

components such as structural habitat characteristics to serve as cues for aspects of nest site selection (Jaenike and Holt 1991, Clark and Shutler 1999) including nest placement (Rodewald et al. 2010), nesting substrate and architecture (Schmidt and Whelan 1999), level of anthropogenic disturbance (Que et al. 2015), and for concealment against predation risk (Martin 1993). Under this premise, the cues of habitat quality (i.e., habitat structure) that birds use should expect to reduce the risk from predation and therefore directly correlate to the birds' nest survival rate during the breeding season (Martin 1993). However, birds sometimes face an abrupt and rapid change in environmental conditions (Anteau et al. 2012), decoupling the cues used to assess nesting habitat quality, from the true quality of potential nesting sites (Schlaepfer et al. 2002, Borgmann and Rodewald, 2004). Consequently, they may select or 'settle for' much poorer quality habitats for nesting - a phenomenon referred to as an 'ecological trap' (Dwernychuk and Boag 1972, Battin 2004, Abrams et al. 2011).

Nest predation has long been considered as one of the most important factors influencing the breeding success of many bird species (Ricklefs 1969, Zheng et al. 1985, Martin 1993, Sieving and Willson 1998). Nest predation rates are related to the richness and abundance of predators within the selected breeding habitat (Fontaine and Martin 2006, Cox et al. 2012). However, there may be no significant relationship between the structural characteristics of the preferred breeding habitat and predation risk (Rangen et al. 1999, Schmidt and Whelan 1999, Borgmann and Rodewald, 2004) when the abundance and composition of the local predator community is impacted by anthropogenic changes to the extent and quality of habitat (Misenhelter and Rotenberry 2000, Weatherhead et al. 2010). Several studies have found that songbirds select breeding habitat subject to elevated predation rates and reduced nest survival (Misenhelter and Rotenberry 2000, Robertson and Hutto 2006). Such ecological traps often arise because anthropogenic pressures have disrupted the nest predator behavior, predator distribution and predator community composition in ways that are not recognized by the birds selecting the nest sites (Shochat et al. 2005, Latif et al. 2011).

Nest predators such as reptiles, mammals, and other avian species have received much attention in the bird nesting literature (Ricklefs 1969, Thompson and Burhans 2003, Weatherhead and Blouin-Demers 2004), but there are few documented cases of bird nest predation caused by invertebrate animals, such as crabs (but see Yang et al. 2014). In this study we investigated nest predation rates of Reed Parrotbill (*Paradoxornis heudei*) caused by the tidal mudflat crab (*Helice tientsinensis*) (Brachyura: Varunidae). The Reed Parrotbill is a vulnerable passerine species that is restricted to reed-bed habitat along inland and coastal wetlands in China and Far Eastern Russia (del Hoyo et al. 2007). Although the species may be locally abundant in some parts of its range, its global population is in declining due to the loss and degradation of its wetland habitat (Lei and Lu 2006) and the species is listed as Near-threatened (Birdlife International 2012). Previous studies have revealed the importance of reedbeds in providing suitable nesting habitat for the Reed Parrotbill (Boulord et al. 2011), as well as nest materials and food resources (Xiong and Lu 2013). Density of dry reed stems is the most important habitat cue for nest site selection, whilst the species avoids nesting in green reed stems >2.5 m height, preferring instead medium high reed stems between 1.5 m and 2.5 m in height (Li et al. 2015). Winter reed harvesting by local people is thought to have had a pronounced negative effect on reed habitat quality and nest site selection (Boulord et al. 2012). The tidal mudflat crab is a widely distributed species along the coastal waters of the West-Pacific, where it is abundant and highly dependent on coastal or estuarine tidal reed marsh habitat (Dai et al. 1986). It is also the most abundant crab species on the estuarine wetlands in the Yellow River Delta of China (Li et al. 2014). The previous studies had found several nests of Reed Parrotbill were predated by the crabs in the coastal wetland of the Yellow River Delta (Li 2012).

In this study, we conducted surveys and nest experiments to examine the predation rates of Reed Parrotbill nests between inland and tidal reed-bed wetlands on the Yellow River Delta National Nature Reserve (N 37.754°, E 119.178°; YRD hereafter). First, we surveyed the structural habitat characteristics of both reed-bed habitats and the abundance of tidal mudflat crabs within

the Yellow River Delta. Second, we performed standardized searches for Reed Parrotbill nests in both habitats and compared the nest survival rates between them. Finally, we carried out a series of novel trials using recently constructed but abandoned Reed Parrotbill nests as ‘artificial nests’ containing quail eggs, and predator-exclusion measures to show that tidal mudflat crab is the primary cause of Reed Parrotbill egg predation in tidal reed-bed habitat and how this habitat may represent an ecological trap for the species.

METHODS

Study site

This study was conducted during May to July 2008, and 2010–2012. This region is characterized by a temperate continental monsoon climate with distinct seasons: the rainy season is mainly during June to August, mean annual temperature is 12.6°C, and mean annual precipitation is c.600 mm (see Li et al. 2011 and Li et al. 2013 for more details). The YRD is the second largest estuarine wetlands in China with extensive areas of reed habitats in different successional stages. Inland freshwater reed-bed (*Phragmites australis*) covers c. 70% of the reed-bed habitat within the reserve, with tidal reed-beds covering the remaining 30%. Tidal reed-bed habitat, dominated by *P. australis* with small patches of *Suaeda salsa*, is located primarily on the southern riverside of the YRD mouth where newly formed mudflats provide opportunities for new reed growth with daily brackish water flooding from the river mouth. Tidal reed plants are generally more robust, but are shorter and less dense than the inland freshwater reeds.

Approximately 80% area of the reed habitats are harvested in large patches by local people, with the assistance of manually operated harvester during the winter months (Li et al. 2015). Inland reeds, which are more homogenous and occur on more flat terrain, are typically harvested earlier and more intensely (almost approaching 100% in some area) due to their high productivity and the ease of operation. As a result, tidal reeds provide a temporary yet important winter shelter for many inland parrotbills during this early harvesting stage. Unpublished observations reveal that parrotbills then return to the inland

reeds in the early spring when there is a greater abundance and growth of green reed stems. However, a small proportion of individuals opt to remain and breed in this habitat (D. Li, *personal observation*). Since 2010, the tidal reed-bed habitat at YRD has been further impacted by reduced freshwater flooding due to infrastructure development, particularly road building near the entrance of one tributary that floods the tidal zone of the reserve. This has resulted in a reduction in the extent and quality of tidal reed-bed habitat, whereas the inland reed-bed habitats have not been impacted.

Nest sampling and monitoring

We systematically searched the nests of Reed Parrotbill in both habitats (tidal reed: 250 ha, inland reed: 450 ha) by using observations of male territorial behavior. For each active nest found we recorded its location using a Garmin GPS unit (GPSMAP 62sc, Shanghai) and categorized the ‘nest stage’ as follows: nest building, egg-laying, incubating or nestling. We also measured the egg size or body weight of the chicks. Nests were revisited every 2–5 days to determine the fate of the nest: 2–5 days = egg-laying stage; incubation until hatching = 12 days; nestling stage until fledging = 11–13 days (Li 2012). For non-active nests, we recorded the GPS position and checked for obvious signs of nest failure, e.g., damage to nesting material, evidence of nest predation e.g., broken eggs or egg-shell fragments. Nesting success was inferred by evidence of the obvious scurf—remains of feather sheaths and excrement at the base of the nest—caused most possible by fledged young birds. Unpublished observations show that the base of the nest is quite clean of excrement when the chicks are younger than 7–8 days, due to regular removal of these by the parent birds. When the chicks are >10 days old, feather sheaths and excrement tends to build up in the nest. We acknowledge that this method may overestimate nesting success, as some predated nests containing older chicks may be misclassified as being successful, but we think that this error is very low because parrotbill chicks >12 days old have a greater probability of escaping from the nest when they are disturbed.

Where it was not possible to determine the outcome, the nest was monitored for 7 days,

which corresponds to the typical time interval between nest-building and the egg-laying stage for the species (Li 2012). Nest failure due to predation was inferred when the intact nests contained no eggs for more than one week, as natural nest desertion is rare (D. Li, *personal observation*). Nest success was confirmed if more than one young fledging from the nest, and nest predation defined as the loss of all eggs or chicks within the typical 28–29 days breeding period, with no evidence of either natural or anthropogenic nest destruction. We calculated nest predation rate as the proportion of number of nests that were predated with total number of nests with confirmed nest fate (Martin 1987).

Nest-site habitat characteristics and estimates of crab abundance

The following habitat structural characteristics were recorded for each nest, using 0.5 m × 0.5 m quadrats placed within a 1-m radius of the nest: (1) density of dry reed stems per quadrat; (2) density of green reed stems per quadrat; (3) height of green reeds using the mean height (m) of 10 randomly chosen stems within the 1-m radius plots. We also recorded nest height and estimated the percentage of dry reed harvested within a wider (10-m radius) plot around each nest. All records were conducted only when the fate of the nest was known.

We used pitfall traps to sample the tidal mudflat crab population in this study. We positioned 20 cylindrical plastic buckets (30 cm in diameter, 25 cm deep) flush with the soil surface in each reed-bed habitat in June 2008. Each trap was placed 5 m apart along two perpendicular transect lines at 10 m apart. Pitfall traps in the inland reed-bed were positioned 5 m apart along the water edge. In order to prevent the buckets being washed away, a stone about 1 kg was put in each bucket. The crabs were counted and identified after the buckets were retrieved 48 h later. The crab density was defined as number of crabs per bucket.

Artificial nest trials of nest predation and predator exclusion

To estimate the frequency of nest predation, we randomly selected 15 natural and intact empty nests in 2008 in both reed habitats to serve as ‘artificial nests’. These nests were similar size in

the nest volume (mean ± SD: inland = 588.6 ± 156.5 cm³, tidal = 504.8 ± 107.6 cm³; $t = 0.904$, $df = 28$, $p = 0.374$) and nest height (inland = 0.65 ± 0.15 m, tidal = 0.60 ± 0.19 m; $t = 1.709$, $df = 28$, $p = 0.099$). Inside each nest we placed two quail eggs, a common surrogate for ‘real eggs’ used for artificial nest predation experiments (e.g., Marini and Melo 1998). To determine nest fate, we checked each nest for evidence of predation every two or three days for a two-week period, corresponding to the duration of the incubation stage. Nest predation was inferred when at least one quail egg was missing or broken. Nest success was inferred if both quail eggs were still intact at the end of the two-week period.

In June 2011, we conducted further ‘artificial nest’ trials to examine the predation by tidal mudflat crabs. Sixty intact and unused Reed Parrotbill’s nests were collected following the breeding season in 2010 and were randomly separated into three 20-nest groups. We placed an inverted bucket measuring 10 cm in radius, 35 cm in height around the base of the reeds to prevent the crabs from approaching the artificial nests, which were attached to 2–4 reed stems about 0.5 m high. Twenty artificial nests were positioned in the tidal reed marshes in two parallel transect lines placed 10 m apart. We randomly selected 10 nests to protect from predators and 10 nests to act as controls (with no bucket excluders). We placed two quail eggs inside each nest and then checked the nests every two days for one week. Nest fate was determined using the previous criteria. We repeated the same experimental design for the inland reed habitats on two occasions to control for any possible effect of nest predation from different types of predator.

Statistical analysis

All statistical analysis was conducted using R software version 3.0.3 (R Core Team 2014). Independent sample t-tests were used to compare differences in habitat characteristics and crab density between inland and tidal reed-bed habitats where data satisfied criteria for normality from Shapiro-Wilks test, otherwise, nonparametric Mann-Whitney *U*-tests were used. Chi-square tests were used to analyze predation rates between habitats, years and trials, except when >20% of the expected values in the contingency

Table 1. Gross structural habitat characteristics and density of crabs in the tidal and inland reed marshes, Yellow River Delta, China.

Characteristic	Tidal reed habitat	Inland reed habitat	T value	<i>p</i> value
n	35†	76		
Nest height (m)	0.58 ± 0.16	0.64 ± 0.17	1.748	0.083
Density of dry reed stems‡	9.29 ± 0.67	10.61 ± 8.98	0.776	0.439
Density of green reed stems‡	11.37 ± 10.22	17.13 ± 9.99	2.803	0.006
Vegetation height (m)	1.63 ± 0.34	1.98 ± 0.30	5.536	0.0001
Percentage dry reed harvested	42.86 ± 26.82	41.51 ± 26.81	0.238	0.812
Density of crabs	8.15 ± 3.89	0.20 ± 0.52	9.073	0.0001
n	20	20		

Note: Significant values appear in boldface.

† Six nests in the tidal-reed habitat were not measured due to the river-flooding.

‡ Density is per 0.5 m × 0.5 m quadrat.

table were <5, in which case we used Fisher exact tests. We calculated the daily survival rate (DSR) for nests in each habitat or trial using the Mayfield estimator (Mayfield 1961) using MARK 6.1 software (White and Burnham 1999). Cumulative nest survival rate (NSR) was defined as daily nest survival rate multiplied by the combined number of days of nest exposure (Dinsmore et al. 2002). We estimated DSR and NSR of nests in 2008 from different reed habitats separately, but for 2010–2012 we pooled the data and did not include nests from tidal reed marsh habitat. All statistical tests were two-tailed and data expressed as mean ± SD. Significant levels were set as $p < 0.05$.

RESULT

Nest-site habitat characteristics and crab abundance

Both inland and tidal reed-bed habitats had similar densities of dry reed stems but significant differences on density of green reed stems and reed vegetation height (Table 1). Both habitats were subjected to successive winter harvesting, but we found no significant difference in the percentage of dry reeds harvested between habitats. We captured 155 individual crabs, 95.1% of which were tidal mudflat crabs, whilst the remaining eight individuals belonged to *Macrophthalmus japonicas* and *Eriocheir sinensis*. The number of crabs per trap in tidal reed-bed habitat (8.15 ± 3.89) was significant higher than that in the inland reed-bed (0.20 ± 0.52 ; $t = 9.073$, $df = 38$, $p < 0.0001$). Tidal mudflat crabs were often observed climbing the reed stems to eat green reed leaves (Fig. 1a). On a small number of

occasions we found Reed Parrotbill's nests containing tidal mudflat crabs (Fig. 1b), or evidence of their presence, e.g., pellets (Fig. 1c) or even predated quail eggs (Fig. 1d). No similar observations were made from the inland reed-bed habitats.

Predation and survival rates of natural nests

During 2008, we recorded 75 intact Reed Parrotbill nests; 40 of these were active, containing either eggs or chicks (Table 2). Of the 75 nests, 35 were found in tidal reed marshes and 40 in the inland reed habitats. Nests in tidal reed-bed habitat were positioned lower above the ground than nests from inland reed-bed habitat, but this difference was not significant (Table 1). All of the 35 tidal reed-bed nests (100%) failed due to predation. Twelve of the 13 active nests were predated during the first 3 days of the egg-laying stage, while one other nest was predated during the fifth day of the egg-laying stage. Nest predation rate for the inland reed-bed habitat was 50%, with no significant difference between active nests (47.8%) and non-active nests (53.8%; $\chi^2 = 0.1204$, $df = 1$, $p = 0.7286$). Nest predation rate was significantly lower than in tidal reed-bed habitats (100%; $\chi^2 = 23.443$, $df = 1$, $p < 0.0001$).

During the 2010–2012 year, only six nests (2 in 2010, 1 in 2011, and 3 in 2012) were found in tidal reed-bed habitat and all were predated. More than 100 active nests were recorded from the inland reed-bed habitats. We randomly selected 40 nests for the subsequent comparative analysis because the other nests formed part of an ongoing experimental study on cuckoo parasitism (Li et al., unpublished data). Predation rates of



Fig. 1. (a) Damage to reed leaves caused by feeding tidal mudflat crabs; (b) Reed Parrotbill nest with a tidal mudflat crab; (c) tidal mudflat crab pellets at the base of a nest; (d) quail eggs predated by tidal mudflat crab (the crab was removed for the purposes of the photo).

active nests varied between 35.7% and 68.8% during 2010–2012 but this variation was not significant ($\chi^2 = 3.301$, $df = 2$, $p = 0.192$; Table 2). Nest predation rate during 2010–2012 and the total nest predation rate during 2008–2012 in tidal reed-bed habitat were significantly higher than those from the inland reed-bed habitat (2010–2012: Fisher exact test: $p = 0.034$; 2008–

2012: $\chi^2 = 29.192$, $df = 1$, $p < 0.0001$; Table 2).

Daily survival rate (DSR) of tidal reed-bed nests (2008: 0.786 ± 0.054) was noticeably lower than inland reed-bed nests (2008: 0.959 ± 0.012 ; 2010–2012: 0.960 ± 0.009). Predicted accumulative nest survival rate (NSR) for tidal reed-bed nests declined to $<30\%$ after five egg-laying days. Accumulative curves of NSRs for inland

Table 2. The rate of nest predation of Reed Parrotbill nests in tidal reed-bed and inland reed-bed habitats during 2008 and 2010–2012.

Year	Nest status	Nests in the tidal reed-bed habitat			Predation rate (%)	Nests in the inland reed-bed habitat			Predation rate (%)
		Predation	Success	Total		Predation	Success	Total	
2008	active nests	13	0	13	100	11	12	23 [†]	47.8
	non-active nests	22	0	22	100	7	6	13	53.8
	total	35	0	35	100	18	18	36	50.0
2010	active nests	2	0	2	100	5	5	10	50.0
2011	active nests	1	0	1	100	11	5	16	68.8
2012	active nests	3	0	3	100	5	9	14	35.7
2010–2012	active nests	6	0	6	100	21	19	40	52.5
2008–2012	active nests	19	0	19	100	32	31	63	50.8
2008–2012	all nests	41	0	41	100	39	37	76	51.3

[†] Four active nests in the inland reed habitat were destructed by storm during egg stage, and then were excluded in the analysis.

reed-bed nests were relatively higher and remained fairly consistent between 2008 and 2010–2012 (Fig. 2).

Predation and survival rates of artificial nests

The predation rate of artificial nests in the tidal reed-bed (60%, $n = 15$) was significantly higher than that of inland reed-bed artificial nests (20%, $n = 15$; $\chi^2 = 5.000$, $df = 1$, $p = 0.025$). Nest predation rate in both habitats were significantly or almost significantly lower than those observed for natural nests (Tidal: $\chi^2 = 6.618$, $df = 1$, $p = 0.01$; Inland: $\chi^2 = 3.021$, $df = 1$, $p = 0.082$). Artificial nest DSR from tidal reed-beds (0.930 ± 0.023) were evidently lower than those from the inland reed-bed habitats (0.984 ± 0.009), with the predicted cumulative NSR decreasing at a much

faster rate (Fig. 3a), though the decline was not as steep as in the natural active nests (Fig. 2).

Predation rate of artificial tidal reed-bed nests with predator exclusion buckets (10%, $n = 10$) was marginally significantly lower than the control group (50%, $n = 10$, $\chi^2 = 3.810$, $df = 1$, $p = 0.051$). DSR and accumulate NSR for nests with predator exclusion buckets was higher than for nests without the exclusion (Fig. 3b) but we found no significant difference in nest predation rate between nests with exclusion buckets (25%, $n = 20$) and those without (20%, $n = 20$) for inland reed-bed habitat ($\chi^2 = 0.143$, $df = 1$, $p = 0.705$) with the accumulative NSR trends being almost identical (Fig. 3c).

DISCUSSION

Do tidal reed-bed habitats represent an ecological trap for Reed Parrotbill?

Our studies have revealed significant differences in the structural habitat characteristics between the two adjacent wetland habitats that are critical environmental cues for Reed Parrotbill nest-site selection. The incongruence between nest-site selection and low nest survival rates caused by crab predation suggested that an ecological mismatch exists between the environmental cues used by breeding parrotbills and features that influence breeding success. We suggest that the 100% predation levels from tidal reed-bed habitat in the YND represent an extreme ecological trap for the Reed Parrotbill population. This trap must be a recent phenomenon since no species would be able to persist for more than just a year or two in a habitat subject

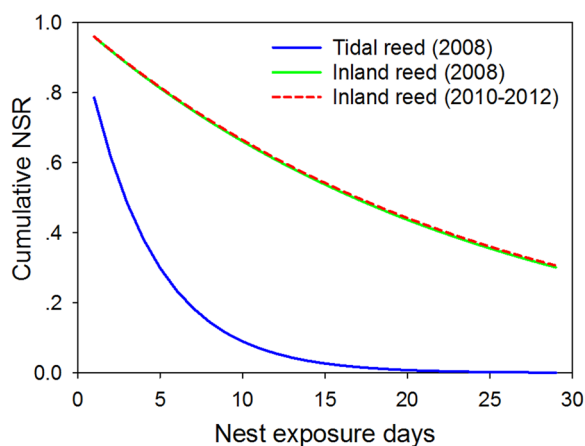


Fig. 2. Predicted cumulative nest survival rate (NSR) of Reed Parrotbill nests in tidal reed-bed and inland reed-bed habitat during 2008 and 2010–2012.

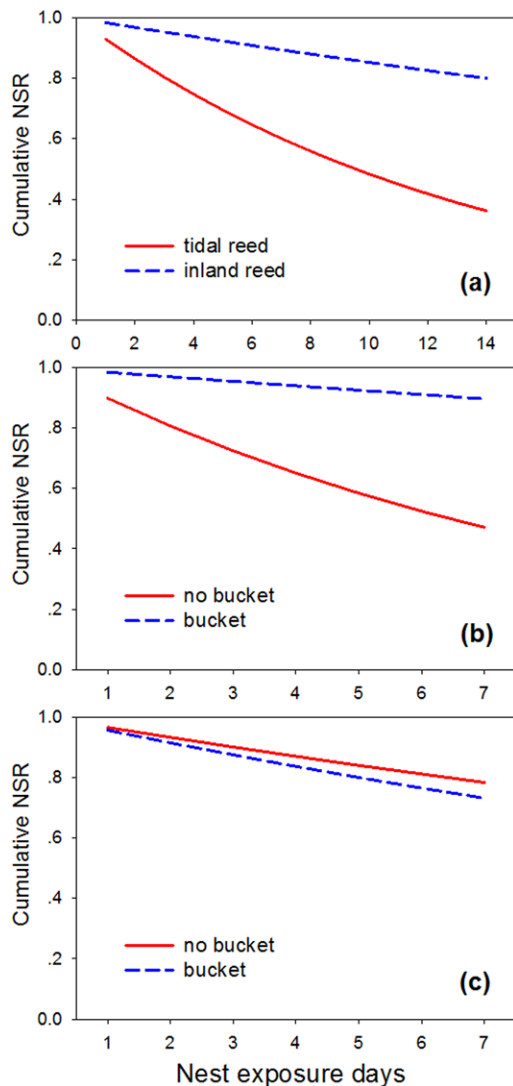


Fig. 3. Predicted cumulative nest survival rates (NSR) of 'artificial' Reed Parrotbill nests from three experimental trials: (a) artificial nest predation trials; (b) predator exclusion trials in the tidal reed marshes; (c) predator exclusion trials in the inland reed habitat, Yellow River Delta, China.

to such an extremely high predation rate. In a 'normal situation', Reed Parrotbills would not breed in this habitat since evolution and simple behavioral decision rules would lead them away from this trap. However, anthropogenic disturbances such as the changes to freshwater flooding and drainage, the loss and degradation of reed-bed habitat and reed-harvesting practi-

es, may have caused a boom in tidal mudflat crab populations, or may have led to the crab population becoming much more highly concentrated across a small number of areas within the YRD landscape. Under these premises, an ecological trap scenario becomes much more likely. Small-scale changes in the physical structure of mangrove forests caused by boardwalk and trail constructions are known to contribute toward localized increases in crab abundance (e.g., Kelaher et al. 1998a, Skilleter and Warren 2000), which have additional consequences for populations of other marine taxa in these disturbed areas (Kelaher et al. 1998b). Human-modified freshwater drainage and flooding strategies can also have spatial impacts on the distribution and abundance of resident crab populations (e.g., Lercari and Defeo 1999). Other studies have hypothesized that ecological traps could in fact benefit some components of bird species fitness rather than nest survival, if those benefits outweigh nest predation costs (Schmidt et al. 2008, Morosinotto et al. 2010, Latif et al. 2011). Brood size, adult and juvenile survivorship, and hatching success are fitness components that could potentially tradeoff with nest survival if any of these components were sufficiently elevated for parrotbills nesting in tidal reed-bed habitat, and this merits further investigation.

Reed Parrotbill nest predation by tidal mudflat crab

Reed Parrotbills that breed in tidal reed-bed habitats are highly vulnerable to extremely high rates of nest predation by tidal mudflat crabs. There were a numbers of reports of marine omnivorous marine crab species preying on other invertebrates (e.g., Quammen 1984, Brousseau et al. 2014), but few cases of crab predation on bird nests. Two previous studies have shown that some ground-nesting shorebird on open beaches were sometimes vulnerable to marine crabs. American Oystercatcher (*Haematopus palliatus*) and Least Tern (*Sternula antillarum*) eggs are known to have been predated by ghost crabs (*Ocypode quadrata*) (Sabine et al. 2005) and *Ocypode quadrata* crabs (Rodrigues et al. 2013), respectively. One recent study from China has reported very high predation rates of Oriental Reed Warbler (*Acrocephalus orientalis*) nests by mudflat crabs (*Chiromantes dehaani*) in tidal reed-

Table 3. Predation rates and daily survival rates (DSR) of 'artificial' Reed Parrotbill nests during both experimental trials.

Artificial nest trial	Habitat	Nests			Predation rate (%)	DSR (mean \pm SD)
		Success	Predation	Total		
Nest predation trial (14 days)	tidal reed-bed habitat	6	9	15	60.0	0.930 \pm 0.023
	inland reed-bed habitat	12	3	15	20.0	0.984 \pm 0.009
Predator exclusion trial (7 days)	tidal reed-bed habitat (with exclusion)	9	1	10	10.0	0.984 \pm 0.015
	tidal reed-bed habitat (without exclusion)	5	5	10	50.0	0.898 \pm 0.043
	inland reed marshes (with exclusion)	15	5	20	25.0	0.956 \pm 0.019
	inland reed marshes (without exclusion)	16	4	20	20.0	0.966 \pm 0.017

bed habitats of the Chongming islands (Yang et al. 2014). This study also suggested that predation rates were much lower in an inland Oriental Reed Warbler population nesting amongst inland reed-bed habitat in the Zalong wetlands, in Heilongjiang province where the crab is absent (Yang et al. 2014).

Nest predation rates from inland reed-bed habitat varied from year to year, from 35% to 68% (Table 2). Our nest trails also revealed that artificial nest predation rates from the same habitat were on the whole much lower than those observed for real nests during the study period, with crab exclusion measures having little impact in reducing the nest predation rate (Table 3). Other known predators of Reed Parrotbill nests from inland reed-bed habitat include Siberian weasel (*Mustela sibirica*), Northern Harrier (*Circus cyaneus*) and unidentified snake species (Li et al., unpublished data). These predators could easily be navigated around the exclusion bucket, and so would have little impact on the nest predation rate of experimental nests in the inland reed-bed habitats. To date, none of these species have been observed preying on parrotbill nests in tidal reed-bed habitat.

Daily survival rates of parrotbill nests could be improved by using a simple predator exclusion approach against tidal mudflat crabs and other possible small-bodied ground predators reaching the nests in the tidal reeds, but not in the inland reed-beds. For our experimental nest trials, we used actual Reed Parrotbill nests containing quail eggs that were positioned at known nest heights. We acknowledge however, that survival and mortality rates of artificial nests, particularly those using quail eggs, may not resemble those of real nests (Green 2004). Quail eggs are often 'easier' for predators to detect and consume (Craig 1998) or for some predators, may be more

difficult to consume, depending on what the target species is and its handling skill (Roper 1992). Predators often use detection or observations of parental birds in order to find nests (Martin et al. 2000), and this is lacking in artificial nests (Cresswell 1997). The lack of parent birds may have also influenced the results due to the lack of nest defense or detection by predators (Major and Kendal 1996) although we made significant efforts to control for this through group comparison within specific artificial nest trials.

In order to predate parrotbill nests, tidal mudflat crabs demonstrate considerable skill in climbing upward into the reed vegetation. Since these crabs habitually climb into the vegetation to eat the reed leaves, parrotbill nest predation may actually represent an opportunistic feeding opportunity during the crab's regular foraging ventures for reed leaves higher in the reed-bed habitat, rather than a deliberate feeding specialization. Tidal reed-beds are a common wetland habitat along the coastal regions of Shanghai, Jiangsu and Liaoning, and other populations of Reed Parrotbills may use this habitat for breeding. Conservation biologists must therefore determine whether these tidal reed-beds could lead to marked decreases in recruitment and rapid local extinction for any local parrotbill populations. Whether other sympatric bird species, i.e., Schrenck's Bittern (*Ixobrychus eurhythmus*) that breed in tidal reed-beds also face extreme nest predation rates by tidal mudflat crabs remains unknown, and this merits further investigation. Conservation efforts should consider prioritizing the maintenance and restoration of freshwater reed-bed habitats that lack significant tidal mudflat populations in order to increase the breeding success of parrotbills. Future conservation efforts would also benefit greatly from a

more explicit understanding of the relationship between the environmental cues used for nest-site selection and the 'true' quality of the reed-bed habitat.

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