

Low nest survival of a breeding shorebird in Bohai Bay, China

Pinjia Que · Yajing Chang · Luke Eberhart-Phillips ·
Yang Liu · Tamás Székely · Zhengwang Zhang

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Abstract Nest survival plays an important role in avian demography because of its influence on both individual fitness and population growth. It is also known to vary within species due to local factors such as climate, predation, substrate, and disturbance, among others. Therefore, an understanding of the relative influence of local factors on nest survival is of critical importance for the formulation of appropriate avian conservation and management policies/programs. Over the past 50 years the Yellow Sea has lost almost 65 % of its original intertidal habitats due to land reclamation and development. There has also been a concomitant and rapid decline in the populations of Kentish plover (*Charadrius alexandrinus*) in East Asia, but the

proximate causes of this decline are poorly understood. To gain a better understanding of this conservation issue, we investigated Kentish plover nest survival in Bohai Bay, China, using Program MARK to model the daily survival rate (DSR) of 417 nests. We found that in terms of nest survival, that for the Kentish plover populations in Bohai Bay [0.925 ± 0.004 (± 95 % confidence interval)] is the lowest reported worldwide for this species. The most common cause of nest failure was related to anthropogenic disturbance. We determined that nests occupying salt crystallization habitat had the highest hatching success and that initiation date, nest age, and nest density had quadratic effects on DSR. If low nest survival persists for consecutive years, fecundity will unlikely compensate for adult mortality, resulting in dramatic population declines of plovers in Bohai Bay. We therefore recommend that the Local Authority managers responsible for local environmental management act accordingly to create protected alternative nesting habitat for plovers in this region.

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P. Que · Y. Chang · Z. Zhang (✉)
Ministry of Education Key Laboratory for Biodiversity Sciences and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing 100875, China
e-mail: zzw@bnu.edu.cn

P. Que
e-mail: quepinjia@gmail.com

L. Eberhart-Phillips
Department of Animal Behaviour, Bielefeld University,
Morgenbreede 45, 33615 Bielefeld, Germany

Y. Liu
State Key Laboratory of Biocontrol and College of Ecology and Evolution, Sun Yat-sen University, Guangzhou 510275, China

T. Székely
Department of Biology and Biochemistry, University of Bath,
Bath, UK

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Zusammenfassung

Niedrige Überlebensrate von Nestern eines brütenden Watvogels in der Bohai-Bucht, China

Die Überlebensrate von Nestern spielt wegen ihres Einflusses auf individuelle Fitness und Populationswachstum eine wichtige Rolle für die Demographie von Vogelpopulationen. Es ist bekannt, dass die Überlebensrate von Nestern innerhalb einer Art aufgrund von Faktoren wie Klima, Prädation, Substrat und Störungen variiert. Daher ist das

Einschätzen von lokalen Einflüssen auf die Überlebensrate von Nestern von zentraler Bedeutung für das Erstellen von angemessenen Vogelschutz- und Managementplänen. Das Gelbe Meer hat über die letzten 50 Jahre beinahe 65 % seines ursprünglichen Habitats im Gezeitenbereich durch Landgewinnung und Entwicklung eingebüßt. Parallel hierzu sind Populationen des Seeregenpfeifers (*Charadrius alexandrinus*) in Ostasien schnell zurückgegangen, wobei die unmittelbaren Gründe hierfür nur unzureichend bekannt sind. Um diese Naturschutzproblematik zu bestätigen, untersuchten wir die Überlebensrate von Nestern des Seeregenpfeifers in der Bohai-Bucht, China. Wir nutzen das Programm MARK, um die tägliche Überlebensrate (DSR) von 417 Nestern zu modellieren, und fanden heraus, dass Nester von Seeregenpfeifern, die in der Bohai-Bucht brüten, die weltweit niedrigste bekannte Überlebensrate (0.925 ± 0.004 [± 95 % KI]) für diese Art aufweisen. Der häufigste Auslöser für das Scheitern eines Nestes war anthropogene Störung. Unsere Studie zeigt, dass Nester in Salzkristallisationshabitaten den höchsten Schlupferfolg aufwiesen und dass der Zeitpunkt des Nestbeginns, das Nestalter und die Nesterdichte quadratische Effekte auf DSR hatten. Sollte die niedrige Überlebensrate für mehrere aufeinanderfolgende Jahre anhalten, ist es unwahrscheinlich, dass die Fortpflanzungsrate die adulte Sterblichkeitsrate kompensiert, was zu dramatischen Bestandsrückgängen der Regenpfeifer in der Bohai-Bucht führen würde. Daher schlagen wir vor, dass Umweltmanager vor Ort entsprechend handeln und geschützte alternative Bruthabitate für die Regenpfeifer in dieser Region schaffen.

Introduction

Quantification of nest survival and determination of its environmental correlates are fundamental prerequisites to formulating effective conservation management programs for bird species at risk because both individual fitness and population growth can be affected by nest survival (Sæther and Bakke 2000). In many bird species, nest survival varies within and between breeding seasons due to variations in predation risk, climate, or differences in microhabitats (Rodríguez and Bustamante 2003; Maxson et al. 2007; Pieron and Rohwer 2010). For example, Grant et al. (2005) reported that nest survival of the Clay-colored Sparrow (*Spizella pallida*) and Vesper Sparrow (*Pooecetes gramineus*) declines throughout the breeding season, presumably due to an increase in predator abundance and activity. Drever and Clark (2007) estimated nest survival for five duck species (*Anas platyrhynchos*, *A. acuta*, *A. discors*, *A. clypeata* and *A. strepera*) and found that nest survival was positively correlated with spring temperatures. Nest density

is another factor which has been shown to have positive (e.g., enhancement of predator vigilance) and negative (e.g., nests are more conspicuous) effects on nest survival (Varela et al. 2007; Ringelman et al. 2014). Understanding the influence of human disturbance on nest survival is crucial for the development of successful management and conservation regimes, as shown in a study of Common Eider (*Somateria mollissima*) colonies by Bolduc and Guillemette (2003). These authors studied colonies visited by humans for down collection, research, and recreation and found that nest survival was associated with the date of the visit rather than the frequency of visits. This result provides important guidelines for formulating successful management policies by balancing the viability of eider populations and the interests of human traditions.

The Kentish plover (*Charadrius alexandrinus*) is a ground nesting species which breeds in coastal areas of East Asia, with a range that extends across the Palearctic (Marchant and Prater 1986). Up until 2011, the closely related Snowy plover (*C. nivosus*) of the Americas was considered to be the same species as *C. alexandrinus*, although behavioral and phylogenetic evidence suggest they are indeed separate species (Kupper et al. 2009). Increased human activity and predation pressure in breeding habitats of the USA, Europe, and Japan have been linked to population declines in both of these plover species, leading to the passage of laws providing protection in some regions (U.S. Fish and Wildlife Service 1993; Delaney et al. 2009; Amano et al. 2010, 2012). In East Asia, the Yellow Sea has lost almost 65 % of its original intertidal habitats over the past 50 years due to land reclamation and development. There has also been a concomitant and rapid decline in the populations of Kentish plover (*Charadrius alexandrinus*) in East Asia (Z. Ma, personal communication), but the proximate causes of this decline are poorly understood.

Nest survival plays an important role in avian demography because it can influence site fidelity (Haas 1998) and population viability (Fletcher et al. 2006). Compared to other vital rates, such as adult survival and movement, which require multiple years of resighting marked individuals, nest survival can be evaluated relatively easily and quickly to provide conservation managers with preliminary information on population status and/or habitat health. We have therefore investigated the nest survival of Kentish plovers nesting in Bohai Bay, China, where up to 4,000 nesting pairs have been estimated to breed (H. Yang and W. Lei, personal communication). The aims of our study were to (1) quantify nest survival of the Kentish plover, (2) identify the principle causes of nest failure, (3) explore environmental correlates of nest survival, and (4) assess patterns of density-dependence on nest survival.

Methods

Study site

We conducted fieldwork at the Nanpu wetland, in northern Bohai Bay, China (39°09'N, 118°09'E to 39°02'N, 118°19'E; Fig. 1) from April to October, 2012. Our study area encompasses many artificial salt ponds used for prawn aquaculture and salt processing. Beyond the seawall bordering the salt ponds, the coastline is dominated by tidal flats which are 1–3 km wide at low tide and completely submerged at high tide. The supratidal areas are no longer extant since the construction of the seawall in the 1950s. Little vegetation grows in this area, except for sparse patches of the common reed (*Phragmites australis*) along the seawall.

In Bohai Bay, Kentish plovers primarily nest in three habitats: (1) abandoned drilling platforms and the surrounding banks, (2) shrimp ponds, and (3) salt crystallization ponds. Each habitat is characterized by varying types of substrate, levels of human disturbance, and interactions with other wildlife. The drilling platforms, which were constructed for oil during the first years of the twenty-first century through the reclamation of former salt ponds, were abandoned in 2008. This habitat is characterized by mud, gravel, rock, and building debris substrates. We noted that some platforms collected standing water following heavy rainfall. Plovers nesting in this part of the study area breed amidst other birds, such as the Little Tern (*Sterna albifrons*), Pied Avocet (*Recurvirostra avosetta*), Black-winged Stilt (*Himantopus himantopus*), and Eurasian skylark (*Alauda arvensis*). Shrimp pond banks are 1–5 m wide and consist of fine gravel and broken shell substrates. Salt crystallization pond banks are 0.4–2 m wide and constructed of loosely arranged clay bricks. These latter two habitats are subject to a high degree of disturbance by humans who use the banks to commute by foot and by vehicles traveling between ponds for the commercial harvest of shrimp and salt.

Field methods

The first stage of the study was to systematically search for nests—by foot on the abandoned drilling platforms and along the banks of the crystallization ponds and on a motor bicycle to survey the banks of the shrimp ponds. Once a nest was discovered, its location was recorded with a handheld GPS and a photograph taken. We classified the microhabitat of the nest site as mud, rock, or brick. We took standard egg measurements and floated eggs to estimate the incubation stage and thus extrapolate the clutch initiation date and likely hatch date (Liu and Chen 2002). Nests were visited at 4–7 day intervals. After 22 days of

incubation had been recorded, we visited nests daily to check for signs of hatching (i.e., starring or pipping; Székely et al. 2008). We considered a nest to be “successful” if we found at least one chick, or if we observed 1- to 4-mm-long shell fragments in the immediate vicinity of the nest (Mabee 1997). Alternatively, we considered a nest to be “failed” when either: (1) eggs disappeared before 22nd days of incubation, (2) eggs were flooded, silted (i.e., covered with silt), or blown out of the nest scrape, (3) eggs were observed collected by humans, or (4) eggs remained in nest after 35 days of incubation. When nests did not meet the above criteria for success or failure, we classified them as being of “unknown fate” and did not use them in our subsequent nest survival analyses.

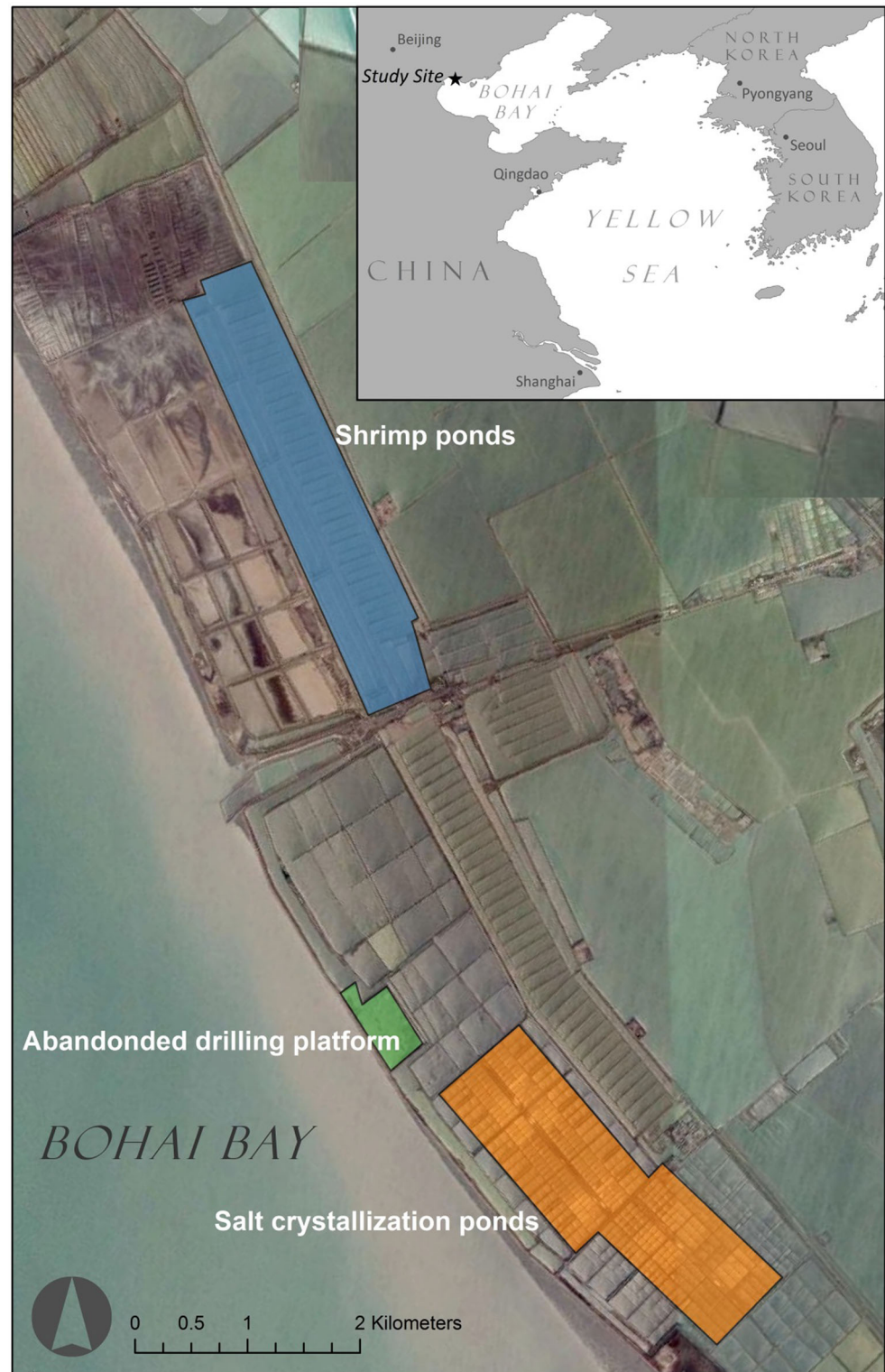
Statistical analyses

We estimated daily nest survival and evaluated environmental and temporal correlates of daily survival rate (DSR) using Program MARK (v7.1; Dinsmore et al. 2002; Cooch and White 2006). Program MARK ranks candidate models using corrected Akaike’s information criterion for small sample sizes (AIC_c) which assesses model likelihood and parameter parsimony given the data (Burnham and Anderson 2002). Our nesting season started when the first clutch was found and ended when the last nest was found. We constructed survival models using four chronological variables: (1) the day a nest was found, (2) the day it was last observed to be active, (3) the day it was last checked, and (4) its determined fate (i.e., success or failure). We then tested the influence of six environmental and temporal covariates on DSR and their interactions: (1) nest age since estimated initiation, (2) nest initiation date, (3) substrate of the nest (i.e., brick, mud, or rock), (4) nest habitat (i.e., abandoned drilling platform, shrimp ponds bank, or salt crystallization pond bank), (5) nearest-neighbor distance to conspecific nest, and (6) the density of plover nests within 200 m. We used ArcGIS 10.1 (ESRI, Redlands, CA) to estimate spatial covariates, and we also tested quadratic effects of our continuous covariates.

Results

We found the first Kentish plover nest on April 28 and the last nest on July 31, signifying a 94-day nesting period at our study site in Bohai Bay. In total, we found 485 plover nests and collected sufficient field data to determine the fate of 417 (85.98 %) of these, which were then included in subsequent analyses. Of these 417 nests, 95 were successful and 322 failed, resulting in an apparent nest survival of 0.228.

Fig. 1 Study site at Nanpu wetland in Bohai Bay, China. The three habitats surveyed for nesting Kentish plovers (*Charadrius alexandrinus*) are from north to south: shrimp pond banks, abandoned drilling platform, and salt crystallization banks, respectively



In our constant model, we estimated daily nest survival as 0.925 ± 0.004 [$\pm 95\%$ confidence interval (CI)]. The incubation period of the Kentish plover is usually 26 days (Liu and Chen 2002), and thus the average nest survival of plovers in our analysis was 0.131. The most common cause

of nest failure was related to anthropogenic disturbance (i.e., egg collection, irrigation, and trampling by pedestrians or vehicles; 22.67 %, $n = 73$). Other causes of nest failure included flooding and silting (11.80 %, $n = 38$), nest abandonment (9.94 %, $n = 32$), unviable eggs

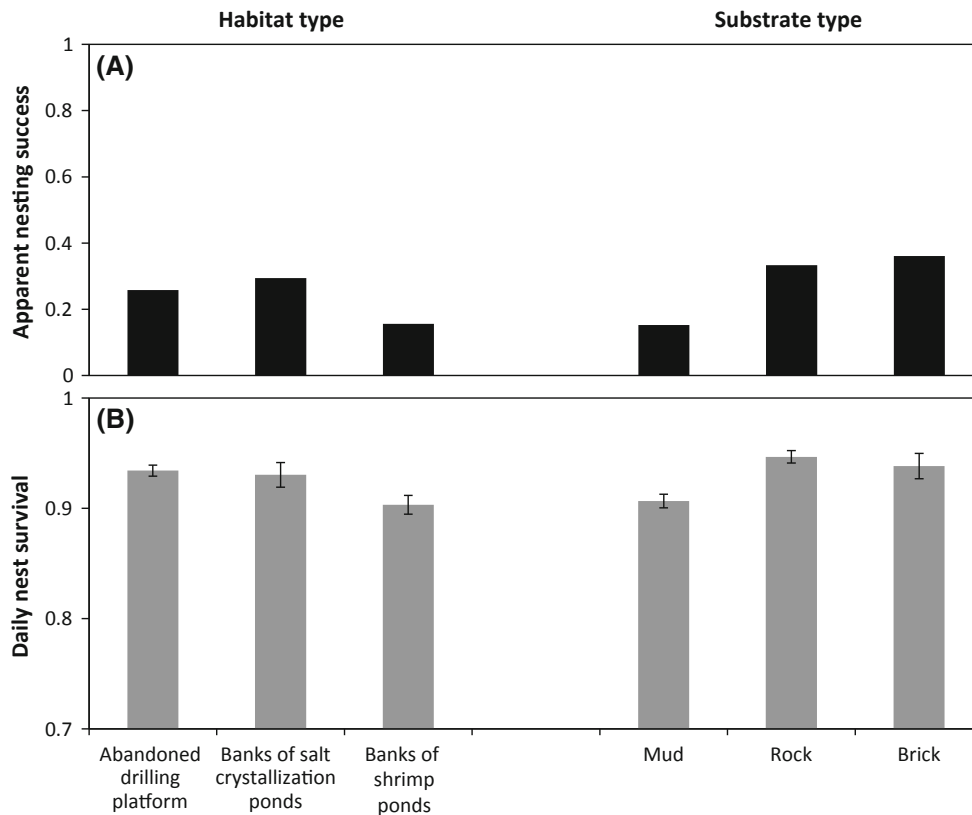


Fig. 2 Apparent nesting success (a) and daily nest survival (b) [$\pm 95\%$ confidence intervals (CI)] of Kentish plovers among different habitats and substrates at Bohai Bay, China

(6.52 %, $n = 21$), and predation (0.6 %, $n = 2$). The cause of nest failure in 48.45 % ($n = 156$) of the unsuccessful nests could not be determined.

Over half of nests with known fates identified in our study site were located in the abandoned drilling platform habitat (53.96 %, $n = 225$), followed by shrimp pond banks (33.81 %, $n = 141$) and salt crystallization pond banks (12.23 %, $n = 51$). Both of our measures of nest survival indicated that nests on the banks of the shrimp ponds had the lowest success among the three habitats (apparent 0.156, DSR 0.903 ± 0.009 ; Fig. 2), with nest survival higher on the banks of the crystallization ponds (apparent 0.294, DSR 0.930 ± 0.011) and the drilling platforms (apparent 0.258, DSR 0.934 ± 0.005 ; Fig. 2). In terms of nest substrate, 249 nests were build on a mud substrate, 132 on rock, and 36 on brick. Of these, nests on the mud substrate had the lowest survival (apparent 0.153, DSR 0.907 ± 0.006) compared to those on in rock (apparent 0.333, DSR 0.947 ± 0.006) or brick (apparent 0.361, DSR 0.938 ± 0.012 ; Fig. 2).

We constructed 45 candidate models of the environmental and temporal covariates describing variation in the DSR. Five competing models had ΔAIC_c of < 2 (Table 1); consequently, we modeled the averaged covariates

according to their respective AIC_c weight (w_1) to obtain robust estimates of the model parameters (Johnson and Omland 2004). After model averaging, the most important variables explaining variation in DSR (i.e., $w_1 = 1$) were habitat type and the linear and quadratic effects of nest initiation date and nest age (Table 2). The linear and quadratic effect of nest density was also a significant predictor but had a lower AIC_c weight than the aforementioned variables ($w_1 = 0.369$; Table 2).

Based on model-averaged estimates, eggs laid in nests in the banks of the salt crystallization ponds were most likely to hatch and initiation date, nest age, and nest density had quadratic effects on DSR (Table 2). Nest survival was highest during the peak of nest initiations from mid-May to mid-June, subsequently declining rapidly throughout the remainder of the nesting season (Fig. 3a). The relationship between nest age and DSR also showed a similar quadratic trend, but was less pronounced (Fig. 3b). A quadratic relationship between nest density and DSR was also found, such that nest survival was higher when nest density was at either end of the density continuum (i.e., sparse or dense; Fig. 3c). Nearest-neighbor distance and nesting substrate were not significant predictors of DSR (Table 2).

Table 1 Top five models ($<2 \Delta AIC_c$) predicting daily nest survival for the Kentish plover (*Charadrius alexandrinus*) in Bohai Bay, China

Model ^a	ΔAIC_c^b	w_i	K
$T^2 + NAge^2 + \text{habitat} + \text{density}^2$	0.000	0.202	9
$T^2 + NAge^2 + \text{habitat}$	1.324	0.104	7
$T^2 + NAge^2 + \text{habitat} + \text{substrate}$	1.436	0.099	9
$T^2 + NAge^2 + \text{habitat} + \text{density}^2 + \text{nearest}$	1.697	0.087	10
$T^2 + NAge^2 + \text{habitat} + \text{substrate} + \text{density}^2$	1.850	0.080	11

AIC_c , Akaike's information criterion for small sample sizes; w_i , AIC_c weight

^a T, Nest initiation date; NAge, nest age

^b AIC_c of the top model was 1682.678

Table 2 Model-averaged parameter estimates and descriptive statistics

Parameter	β	Standard error	Lower 95 % CI	Upper 95 % CI	w_i
Intercept	4.010	0.310	4.618	3.401	1.000
T	-0.010	0.008	0.006	-0.026	1.000
T^2	0.000	0.000	0.000	0.000	1.000
NAge	0.023	0.014	0.051	-0.005	1.000
$NAge^2$	-0.001	0.000	0.000	-0.002	1.000
Abandoned drilling platform	-1.661	0.236	-1.199	-2.123	1.000
Bank of shrimp ponds	-0.451	0.146	-0.165	-0.738	1.000
Mud	-0.009	0.068	0.124	-0.141	0.179
Rock	0.045	0.073	0.188	-0.099	0.179
Density	-0.006	0.003	-0.001	-0.011	0.369
$Density^2$	0.000	0.000	0.000	0.000	0.369
Nearest nest	0.000	0.000	0.000	0.000	0.087

T and NAge refer to nest initiation date and nest age, respectively

CI, Confidence interval

Discussion

Our study has identified an alarmingly low survival rate of a common breeding shorebird in Bohai Bay, Eastern China. Estimates of nest survival of Kentish plovers nesting in Bohai Bay based on our analysis are among the lowest reported for this species worldwide (Fig. 4), with an average nest survival of 0.131, which is second only to plovers breeding in the Farasan Islands of Saudi Arabia (AlRashidi et al. 2011). Our results are consistent with those of a previous study conducted in Bohai Bay in 2009 (apparent nest survival 0.319; average nest survival 0.138, $n = 133$; Lei 2010), suggesting that there may be little evidence of annual variation in nest survival. Estimates of plover nest survival for two adjacent breeding populations in Dalian, Northeast China (apparent nest survival 0.575, $n = 40$; Yu and Pei 1996) and Busan, Korea (apparent nest

survival 0.369, $n = 225$; (Hong and Higashi 2008) are reportedly higher than our estimates of nest survival at Bohai Bay, indicating that Bohai Bay could be the sink population in this region.

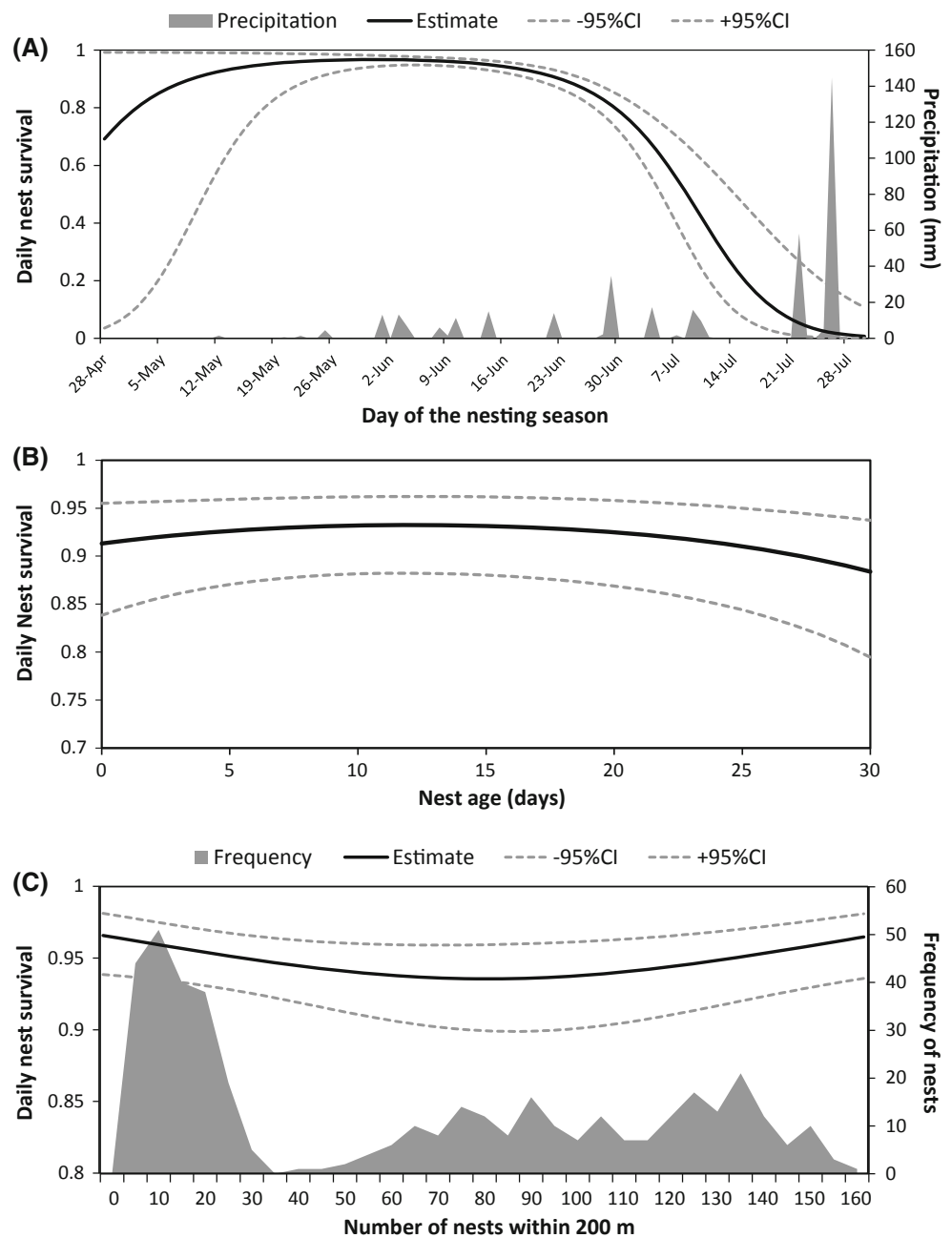
Although population growth in vertebrates is very sensitive to adult survival (Sæther and Bakke 2000), some studies have suggested that avian population dynamics coincide with nest survival rates (Pienkowski 1984; Byrd et al. 1994; Beauchamp et al. 1996; Tapper et al. 1996; Ronka et al. 2006; Fletcher et al. 2006). If population productivity becomes catastrophically low and is unsupported by immigrants from surrounding source populations, local extinction can occur in a relatively short period of time (Eberhart-Phillips and Colwell 2014). Human disturbance, habitat modification, and predation were identified as the main factors limiting the productivity and ultimate recovery of the closely related Snowy plover on the Pacific coast of the USA, which is listed as threatened under the US Endangered Species Act (USFWS 1993). Our results draw similar conclusions about the roles of human disturbance, habitat, and predation risk for Kentish plovers in Bohai Bay.

Variation in nest survival between habitats

Several studies have suggested that habitat plays an important role in nest survival (Stephens et al. 2005; Newmark and Stanley 2011), with intraspecific nest survival varying significantly between different nesting substrates, predation pressures, climates, or levels of human disturbance (Chase et al. 2005; Yasue and Dearden 2006; Cox et al. 2012). In our study, we found that variation in nest survival for the Kentish plover in Bohai Bay was also strongly related to differences in habitat characteristics.

In Bohai Bay, human disturbance was highest on the banks of the shrimp ponds, where employees frequently walked and/or drove vehicles between ponds to harvest shrimp (P. Que, personal observation). We believe that this high level of disturbance was the driving causal factor for the low nest survival observed on shrimp pond banks,

Fig. 3 Daily nest survival of Kentish plovers at Bohai Bay in relation to the 95-day nesting season (a), age of a nest (a), and nesting density (c)

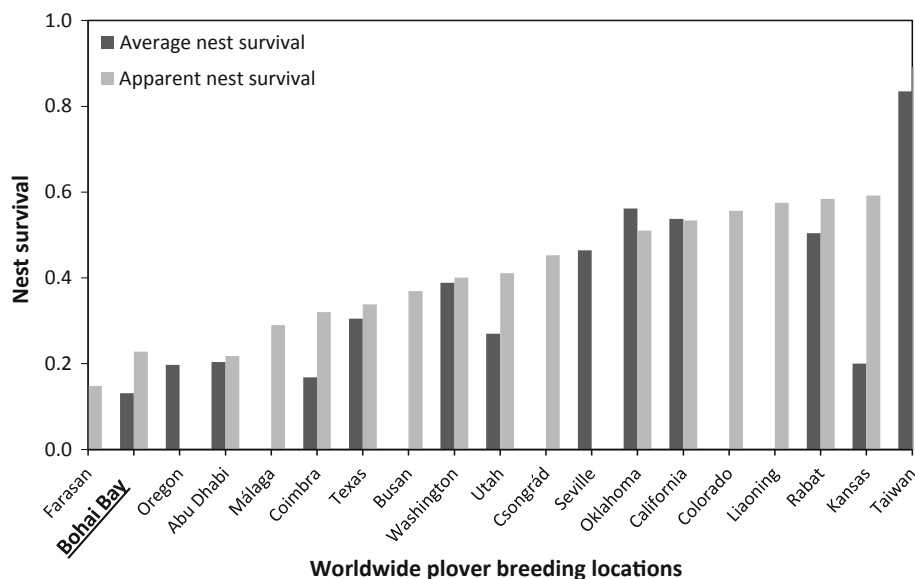


where almost half of the nests failed due to anthropogenic-related causes (i.e., collection, trampling of eggs, or parental abandonment after chronic disturbance). Consistent with our study, a high nest mortality has been reported for Kentish plovers nesting in human-made habitats in Central Europe (Szekely 1992; Szekely et al. 1994). In addition, the conflict between human recreation and plover nesting success has been well documented in other regions of the world, such Germany, USA, and Australia (Warriner et al. 1986; Buick and Paton 1989; Schulz and Stock 1993; Hardy and Colwell 2012).

Fine-scale micro-habitat heterogeneity could also play an important role driving variation in nest survival due to

the cryptic and percolating advantages that various substrates offer nesting plovers. We found that nest survival was highest in rocky substrates, which is likely due to the cryptic advantage that this heterogeneous habitat provides against predation or human collection. A similar finding was reported for Snowy plovers nesting in rocky riverine substrates versus homogenous sandy beaches in California (Colwell et al. 2011; Hardy and Colwell 2012). We also speculate that substrate type could aid in protecting nests from flooding and silting, which was the cause of almost one-quarter of all nest failures in Bohai Bay. Loose rocky substrates may allow adequate draining of water and silt that would otherwise submerge the eggs and provoke

Fig. 4 Comparison of nest survival at Bohai Bay (*underlined and in bold*) to published estimates of Kentish and Snowy plover nest survival worldwide. See Electronic Supplementary Material Table S1 for references



abandonment. None of the nests on the brick substrate of Bohai Bay failed due to flooding or silting, although these nests were relatively conspicuous. The mud substrate apparently offered no protection from flooding, silting, or human collection, which were all common causes of nest failure. Taken together, these findings demonstrate that there is most likely an interaction between the cryptic and draining abilities of various nesting substrates, which should be the subject of further studies on ground nesting birds. Lastly, the thermal properties of these different soil types (together with the nest materials that surround the eggs) may vary between different habitats and thereby influence the energetic costs of incubation (Szentirmai and Székely 2004).

Temporal variation in nest survival

It is common to observe temporal variation in nest survival across the incubation period and breeding season of many avian species, and this variation is often attributed to temporal variations in climate and predation pressure (Wilson et al. 2007; Smith and Wilson 2010). In our study, we found strong support for a seasonal quadratic effect on nest survival, such that nests initiated in the first half of the season had a much higher survival rate than those initiated near the end of the season. This trend was found to be associated with the sudden increase in daily precipitation at the end of the season (Fig. 3a) and was supported by our observations of more flooded and abandoned nests at the end of the season.

Shifts in predation pressure across the nesting season could also explain the sudden decline in nest survival. In Bohai Bay, we observed an increase in both the numbers of the

Black-tailed Gull (*Larus crassirostris*) and the number of predated nests throughout the season (P. Que, personal observation). Although this link is speculative, gulls have been identified as an important nest predator of shorebirds in many regions of the world (Nol and Brooks 1982; Rimmer and Deblinger 1990; Smith et al. 2007), and thus the temporal interaction between plover productivity and gull migration warrants further study. Nocturnal mammals (e.g., foxes, hedgehogs) may also take a substantial proportion of eggs (Székely 1992), although at this time we have no evidence linking mammals to nest predation in Bohai Bay.

Density-dependent nest survival

Colonial nesting provides benefits against predation risk, such as increased vigilance, more effective defense (e.g., mobbing), and the dilution effect (Götmark and Andersson 1984; Robinson 1985). The Snowy plover has been described as a semi-colonial breeder because it often nests in loose clusters but still defends its territories (Patrick 2013). Our nest survival models suggest that plover nests located in either dense or sparse colonies have the highest likelihood of survival, while those nesting in intermediate levels of density have the lowest survival rate. A possible interpretation of this evidence is the colony edge effect, such that nests located in the center of the colony (i.e., with the highest density) have the most protection from disturbance and predation compared to those on the proximity of the colony (i.e., with intermediate density). The effect of nesting success on the edge versus the center of a colony has been well documented in other colony-breeding bird species (Antolos et al. 2006; Ellis and Good 2006; Minias 2014). We also suspect that variation in the shape of the

available nesting habitat across the study area could (partly) explain the effect of nest density on survival. The abandoned drilling platform habitat had the highest nest densities (100.86 ± 32.02 nests within 200 m) and the nests showed a uniform distribution, presumably because the habitat was the most suitable. In contrast, the banks of the shrimp ponds had the lowest densities of nest (9.21 ± 5.22 nests within 200 m), presumably because nests were restricted to a linear arrangement of banks. A binomial distribution of nesting densities is a common finding among colonial nesting birds (Tinbergen et al. 1967; Sugden and Beyersbergen 1986; Martin 1988).

Conservation implications

We quantified various habitat features that were associated with low productivity, which we hope will provide valuable guidelines for management and conservation programs in this environmentally understudied—but economically booming—region of the world. Over the past 50 years, concomitant with the rise in China's economy, there has been a serious decrease in the size of the tidal flats of the Yellow Sea, with up to 65 % of the original tidal flats reclaimed, particularly in Bohai Bay (Yang et al. 2011; Murray et al. 2014). One of the results of this reclamation policy has been the loss or threatened loss of critical foraging and breeding habitats of the Kentish plover. In just 16 years, 450 km² of Bohai bay was reclaimed for industrial projects, including one-third of the original tidal habitat (218 km²) utilized by plovers (Yang et al. 2011). Habitat loss often forces birds to breed in sub-optimal environments or conditions (Bowler and Benton 2005), and we suggest that we have observed this response by plovers to tidal land reclamation in Bohai Bay, as exemplified by the poor success rate of only 15 % of 141 nests located on the banks of shrimp ponds where there was chronic human disturbance and poor substrates for egg crypsis. If this situation persists for consecutive years, fecundity will unlikely compensate adult mortality, resulting in dramatic population declines of plovers in Bohai Bay. In Europe, continent-wide declines in Kentish plover populations have largely been attributed to disturbance, destruction of breeding sites, and an increase in predation risk indirectly associated with human activities (Montalvo and Figuerola 2006; Delaney et al. 2009). Therefore, to minimize the risk of local extinction, we strongly recommend that environmental managers of the Bohai Bay region act accordingly to create protected alternative habitat for nesting plovers.

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References

- AlRashidi M, Kosztolanyi A, Shobrak M, Szekely T (2011) Breeding ecology of the Kentish plover, *Charadrius alexandrinus*, in the Farasan Islands, Saudi Arabia (Aves: Charadriiformes). *Zool Middle East* 53:15–24
- Amano T, Szekely T, Koyama K, Amano H, Sutherland WJ (2010) A framework for monitoring the status of populations: an example from wader populations in the East Asian–Australasian flyway. *Biol Conserv* 143:2238–2247
- Amano T, Szekely T, Koyama K, Amano H, Sutherland WJ (2012) Addendum to “A framework for monitoring the status of populations: an example from wader populations in the East Asian–Australasian flyway” *Biological Conservation*, 143, 2238–2247. *Biol Conserv* 145:278–295
- Antolos M, Roby DD, Lyons DE, Anderson SK, Collis K (2006) Effects of nest density, location, and timing on breeding success of Caspian terns. *Waterbirds* 29:465–472
- Beauchamp WD, Koford RR, Nudds TD, Clark RG, Johnson DH (1996) Long-term declines in nest success of prairie ducks. *J Wildl Manag* 60:247–257
- Bolduc F, Guillemette M (2003) Human disturbance and nesting success of Common Eiders: interaction between visitors and gulls. *Biol Conserv* 110:77–83
- Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol Rev* 80:205–225
- Buick A, Paton D (1989) Impact of off-road vehicles on the nesting success of Hooded plovers *Charadrius rubricollis* in the Coorong region of South Australia. *Emu* 89:159–172
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information—theoretic approach. Springer, New York
- Byrd GV, Trapp JL, Zeilemaker C (1994) Removal of introduced foxes: a case study in restoration of native birds. *Trans North Am Wildl Nat Resour Conf* 59:317–321
- Chase MK, Nur N, Geupel GR, Stouffer P (2005) Effects of weather and population density on reproductive success and population dynamics in a song sparrow (*Melospiza melodia*) population: a long-term study. *Auk* 122:571–592
- Colwell MA, Meyer JJ, Hardy MA, Mcallister SE, Transou AN, Levalley RR, Dinsmore SJ (2011) Western Snowy plovers *Charadrius alexandrinus nivosus* select nesting substrates that enhance egg crypsis and improve nest survival. *Ibis* 153:303–311
- Cooch E, White G (2006) Program MARK: a gentle introduction. Available at: <http://www.phidot.org/software/mark/docs/book/>
- Cox WA, Thompson F III, Faaborg J (2012) Landscape forest cover and edge effects on songbird nest predation vary by nest predator. *Landscape Ecol* 27:659–669
- Delaney S, Scott DA, Dodman T, Stroud DA (2009) An atlas of wader populations in Africa and Western Eurasia. Wetlands International Wageningen, Wageningen
- Dinsmore SJ, White GC, Knopf FL (2002) Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488

- Drever MC, Clark RG (2007) Spring temperature, clutch initiation date and duck nest success: a test of the mismatch hypothesis. *J Anim Ecol* 76:139–148
- Eberhart-Phillips LJ, Colwell MA (2014). Conservation challenges of a sink: the viability of an isolated population of the Snowy plover. *Bird Conserv Int* 24:327–341
- Ellis JC, Good TP (2006) Nest attributes, aggression, and breeding success of gulls in single and mixed species subcolonies. *Condor* 108:211–219
- Fletcher RJ, Koford RR, Seaman DA (2006) Critical demographic parameters for declining songbirds breeding in restored grasslands. *J Wildl Manag* 70:145–157
- Götmarm F, Andersson M (1984) Colonial breeding reduces nest predation in the Common gull (*Larus canus*). *Anim Behav* 32:485–492
- Grant TA, Shaffer TL, Madden EM, Pietz PJ, Johnson D (2005) Time-specific variation in passerine nest survival: new insights into old questions. *Auk* 122:661–672
- Haas CA (1998) Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk* 115:929–936
- Hardy MA, Colwell MA (2012) Factors Influencing Snowy plover nest survival on ocean-fronting beaches in coastal Northern California. *Waterbirds* 35:503–511
- Hong S, Higashi S (2008) Nesting site preference and hatching success of the Kentish plover (*Charadrius alexandrinus*) in the Nakdong Estuary, Busan, Republic of Korea. *J Ecol Field Biol* 31:201–206
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108
- Kupper C, Augustin J, Kosztolanyi A, Burke T, Figuerola J, Székely T (2009) Kentish versus Snowy plover: phenotypic and genetic analyses of *Charadrius alexandrinus* reveal divergence of Eurasian and American subspecies. *Auk* 126:839–852
- Lei WP (2010) Studies on migration and Habitat use of waterbirds at typical wetlands around Bohai Bay. MSc thesis, Beijing Normal University, Beijing, China
- Liu WT, Chen PH (2002) Hatching success and causes of hatching failure of Kentish plover *Charadrius alexandrinus* in Changhua Coastal Industrial Park. *Tunghai Sci* 4:85–101
- Mabee TJ (1997) Using eggshell evidence to determine nest fate of shorebirds. *Wilson Bull* 109:307–313
- Marchant J, Prater T (1986) Shorebirds: an identification guide to the waders of the world. A&C Black, London
- Martin TE (1988) On the advantage of being different: nest predation and the coexistence of bird species. *Proc Natl Acad Sci USA* 85:2196–2199
- Maxson SJ, Fieberg JR, Riggs MR (2007) Black tern nest habitat selection and factors affecting nest success in northwestern Minnesota. *Waterbirds* 30:1–9
- Minias P (2014) Evolution of within-colony distribution patterns of birds in response to habitat structure. *Behav Ecol Sociobiol* 68:851–859
- Montalvo T, Figuerola J (2006) The distribution and conservation of the Kentish plover *Charadrius alexandrinus* in Catalonia. *Revista Catalana d'Ornitologia* 22:1–8
- Murray NJ, Clemens RS, Phinn SR, Possingham HP, Fuller RA (2014) Tracking the rapid loss of tidal wetlands in the Yellow Sea. *Front Ecol Environ* 12:267–272
- Newmark WD, Stanley TR (2011) Habitat fragmentation reduces nest survival in an Afrotropical bird community in a biodiversity hotspot. *Proc Natl Acad Sci USA* 108:11488–11493
- Nol E, Brooks RJ (1982) Effects of predator exclosures on nesting success of Killdeer. *J Field Ornithol* 53:263–268
- Patrick AM (2013) Semi-colonial nesting in the Snowy plover. MSc thesis, Humboldt State University, Arcata, California
- Pienkowski MW (1984) Breeding biology and population dynamics of Ringed plovers *Charadrius hiaticula* in Britain and Greenland: nest-predation as a possible factor limiting distribution and timing of breeding. *J Zool* 202:83–114
- Pieron MR, Rohwer FC (2010) Effects of large-scale predator reduction on nest success of upland nesting ducks. *J Wildl Manag* 74:124–132
- Rimmer DW, Deblinger RD (1990) Use of predator exclosures to protect Piping plover nests. *J Field Ornithol* 61:217–223
- Ringelman KM, Eadie JM, Ackerman JT (2014) Adaptive nest clustering and density-dependent nest survival in dabbling ducks. *Oikos* 123:239–247
- Robinson SK (1985) Coloniality in the Yellow-rumped Cacique as a defense against nest predators. *Auk* 102:506–519
- Rodríguez C, Bustamante J (2003) The effect of weather on Lesser kestrel breeding success: can climate change explain historical population declines? *J Anim Ecol* 72:793–810
- Ronka A, Koivula K, Ojanen M, Pakanen V-M, Pohjoismäki M, Rannikko K, Rauhala P (2006) Increased nest predation in a declining and threatened Temminck's stint *Calidris temminckii* population. *Ibis* 148:55–65
- Sæther B-E, Bakke Ø (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653
- Schulz R, Stock M (1993) Kentish plovers and tourists: competitors on sandy coasts. *Wader Study Group Bull* 68:83–91
- Smith PA, Wilson S (2010) Intra-seasonal patterns in shorebird nest survival are related to nest age and defence behaviour. *Oecologia* 163:613–624
- Smith PA, Gilchrist HG, Smith JNM (2007) Effects of nest habitat, food, and parental behavior on shorebird nest success. *Condor* 109:15–31
- Stephens SE, Rotella JJ, Lindberg MS, Taper ML, Ringelman JK (2005) Duck nest survival in the Missouri Coteau of North Dakota: landscape effects at multiple spatial scales. *Ecol Appl* 15:2137–2149
- Sugden LG, Beyersbergen GW (1986) Effect of density and concealment on American crow predation of simulated duck nests. *J Wildl Manag* 50:9–14
- Székely T (1992) Reproduction of Kentish plover *Charadrius alexandrinus* in grasslands and fish-ponds: the habitat mal-assessment hypothesis. *Aquila* 99:59–68
- Szekely T, Karsai I, Williams TD (1994) Determination of clutch-size in the Kentish Plover *Charadrius alexandrinus*. *Ibis* 136:341–348
- Székely T, Kosztolányi A, Küpper C (2008) Practical guide for investigating breeding ecology of Kentish plover *Charadrius alexandrinus*. University of Bath, Bath
- Szentirmai I, Székely T (2004) Diurnal variation in nest material use by the Kentish plover *Charadrius alexandrinus*. *Ibis* 146:535–537
- Tapper SC, Potts GR, Brockless MH (1996) The effect of an experimental reduction in predation pressure on the breeding success and population density of grey partridges *Perdix perdix*. *J Appl Ecol* 33:965–978
- Tinbergen N, Impeken M, Franck D (1967) An experiment on spacing-out as a defence against predation. *Behaviour* 28:307–321
- US Fish and Wildlife Service (USFWS) (1993) Endangered and threatened wildlife and plants; determination of threatened status for the Pacific coast population of the western Snowy plover; final rule. *Fed Regist* 58:12864–12874
- Varela SAM, Danchin E, Wagner RH (2007) Does predation select for or against avian coloniality? A comparative analysis. *J Evol Biol* 20:1490–1503

- Warriner JS, Warriner JC, Page GW, Stenzel LE (1986) Mating system and reproductive success of a small population of polygamous Snowy plovers. *Wilson Bull* 98:15–37
- Wilson S, Martin K, Hannon SJ (2007) Nest survival patterns in Willow Ptarmigan: influence of time, nesting stage, and female characteristics. *Condor* 109:377–388
- Yang HY, Chen B, Barter M, Piersma T, Zhou CF, Li FS, Zhang ZW (2011) Impacts of tidal land reclamation in Bohai Bay, China: ongoing losses of critical Yellow Sea waterbird staging and wintering sites. *Bird Conserv Int* 21:241–259
- Yasue M, Dearden P (2006) The potential impact of tourism development on habitat availability and productivity of Malaysian plovers *Charadrius peronii*. *J Appl Ecol* 43:978–989
- Yu Y, Pei X (1996) Studies on the breeding ecology of *Charadrius alexandrinus dealbatus*. In: *Study on Chinese ornithology*. China Forestry Publishing House, Beijing, pp 305–308