

Simultaneous declines in summer survival of three shorebird species signals a flyway at risk

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Summary

1. There is increasing concern about the world's animal migrations. With many land-use and climatological changes occurring simultaneously, pinning down the causes of large-scale conservation problems requires sophisticated and data-intensive approaches.
2. Declining shorebird numbers along the East Asian–Australasian Flyway, in combination with data on habitat loss along the Yellow Sea (where these birds refuel during long-distance migrations), indicate a flyway under threat.
3. If habitat loss at staging areas indeed leads to flyway-wide bird losses, we would predict that: (i) decreases in survival only occur during the season that birds use the Yellow Sea, and (ii) decreases in survival occur in migrants that share a reliance on the vanishing intertidal flats along the Yellow Sea, even if ecologically distinct and using different breeding grounds.
4. Monitored from 2006–2013, we analysed *seasonal* apparent survival patterns of three shorebird species with non-overlapping Arctic breeding areas and considerable differences in foraging ecology, but a shared use of both north-west Australian non-breeding grounds and the Yellow Sea coasts to refuel during northward and southward migrations (red knot *Calidris canutus piersmai*, great knot *Calidris tenuirostris*, bar-tailed godwit *Limosa lapponica menzbieri*). Distinguishing two three-month non-breeding periods and a six-month migration and breeding period, and analysing survival of the three species and the three seasons in a single model, we statistically evaluated differences at both the species and season levels.
5. Whereas apparent survival remained high in north-west Australia, during the time away from the non-breeding grounds survival in all three species began to decline in 2011, having lost 20 percentage points by 2012. By 2012 *annual* apparent survival had become as low as 0.71 in bar-tailed godwits, 0.68 in great knots and 0.67 in red knots. In a separate analysis for red knots, no mortality occurred during the migration from Australia to China. In the summers of low summer survival, weather conditions were benign in the Arctic breeding areas.
6. We argue that rapid seashore habitat loss in the Yellow Sea is the most likely explanation of reduced summer survival, with dire (but uncertain) forecasts for the future of these flyway populations. This interpretation is consistent with recent findings of declining shorebird numbers at seemingly intact southern non-breeding sites.

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7. Policy implications. Due to established economic interests, governments are usually reluctant to act for conservation, unless unambiguous evidence for particular cause–effect chains is apparent. This study adds to an increasing body of evidence that habitat loss along the Yellow Sea shores explains the widespread declines in shorebird numbers along the East Asian–Australasian Flyway and threatens the long-term prospects of several long-distance migrating species. To halt further losses, the clearance of coastal intertidal habitat must stop now.

Key-words: bar-tailed godwit *Limosa lapponica menzbieri*, China, coastal conservation, East Asian–Australasian Flyway, global change, great knot *Calidris tenuirostris*, intertidal land claims, migration, red knot *Calidris canutus piersmai*, seasonal survival

Introduction

We live during times in which humans have ever greater effects on the biota of the Earth. Among many concerns, there have been voices of fear that the world's great animal migrations are in danger of disappearance (Wilcove & Wikelski 2008). One such potential extinction wave is signalled by the current declines of many long-distance migrating shorebirds in the East Asian–Australasian Flyway (Amano *et al.* 2010; Wilson *et al.* 2011; MacKinnon, Verkuil & Murray 2012; Minton *et al.* 2012; Conklin, Verkuil & Smith 2014; Ma *et al.* 2014; Hansen *et al.* 2015). Many authors have argued that the documented declines are likely caused by coastal wetland losses in the Yellow Sea of China and the Korean Peninsula (Rogers, Moores & Battley 2006; MacKinnon, Verkuil & Murray 2012; Ma *et al.* 2014; Murray *et al.* 2014; Wang *et al.* 2014; Aharon-Rotman *et al.* 2015; Hua *et al.* 2015), which are critical foraging habitats that migrating shorebirds rely on during both northward and southward migration (Barter 2002; Rogers *et al.* 2010; Battley *et al.* 2012; Ma *et al.* 2013).

Despite this increasing consensus, the cause-and-effect chain (i.e. that the loss of tidal flats in China and Korea, see Plate 1, directly leads to bird losses in Australia and New Zealand) remains to be demonstrated. The large-scale nature of the phenomenon makes the assemblage of such proof daunting, but we already have the following ingredients: (i) anywhere along the flyway, species showing declining numbers are the ones that rely most on the Yellow Sea (e.g. Amano *et al.* 2010), (ii) at the receiving end of the flyway, declining numbers are not explained by local habitat loss (e.g. Minton *et al.* 2012), and (iii) there are no widespread declines in breeding success (Aharon-Rotman *et al.* 2015). To these arguments we would like to add (iv) a demonstration that decreases in survival of the migrants occur only during the season of use of the Yellow Sea, (v) showing that these decreases in survival similarly occur in ecologically distinct species with different breeding grounds that share coastal staging areas along the Yellow Sea, in the knowledge that (vi) intertidal habitat loss in the area and in the season with reductions in survival are ongoing.

In this contribution, we present evidence for the latter three empirical building blocks of a causal pathway

towards possible extinction. We provide an analysis of seasonal survival patterns over a seven-year period (2006–2012) in three shorebird species that share non-breeding grounds in north–west Australia and intertidal staging areas in the Yellow Sea and present habitat loss data adding to Murray *et al.* (2014) and Wang *et al.* (2014). The three species, bar-tailed godwit *Limosa lapponica menzbieri*, great knot *Calidris tenuirostris* and red knot *C. canutus piersmai* (with small numbers of the subspecies *rogersi*) are all endemic to the East Asian–Australasian Flyway (Conklin, Verkuil & Smith 2014). Birds of each population go their separate ways to non-overlapping breeding areas in northern and north-eastern Siberia (Fig. 1). The three species show clear differences in breeding habitat (bar-tailed godwits use wet lowland marshy tundra, great knots breed on alpine tundra, and red knots breed on lowland tundra; Lappo, Tomkovich & Syroechkovskiy 2012). In the non-breeding areas they are also trophically distinct, with the two knot species counting as hard-shelled mollusc specialists (Piersma 2007; Ma *et al.* 2013; Yang *et al.* 2013), whereas bar-tailed godwits, though sometimes relying on molluscs too, have a more versatile diet (Duijns, Hidayati & Piersma 2013).

Bar-tailed godwits were recently heralded as the migrant bird species with the most surprising and unique long-distance migration lifestyle (Gill *et al.* 2009; Hedenström 2010; Piersma 2011). With respect to their general use of the Yellow Sea, amongst the three species the two knots occur in the most concentrated numbers and at the smallest number of sites (Conklin, Verkuil & Smith 2014), i.e. they are the most geographically 'bottlenecked' (Iwamura *et al.* 2013). In their use of the north-western Yellow Sea, red knots especially use the shores of Bohai Bay (Rogers *et al.* 2010; Yang *et al.* 2011) and the multi-year observation efforts here enabled a survival analyses over four rather than three seasons for this species. Many great knots pass through the Yangtze estuary near Shanghai and fuel up in the northern Yellow Sea (Ma *et al.* 2013) but also in the Koreas (Moores *et al.* 2007), whereas the bar-tailed godwits, at least in 2008, used areas around much of the Yellow Sea (Battley *et al.* 2012).

The dramatic reductions in survival during the time away from their north–west Australian non-breeding

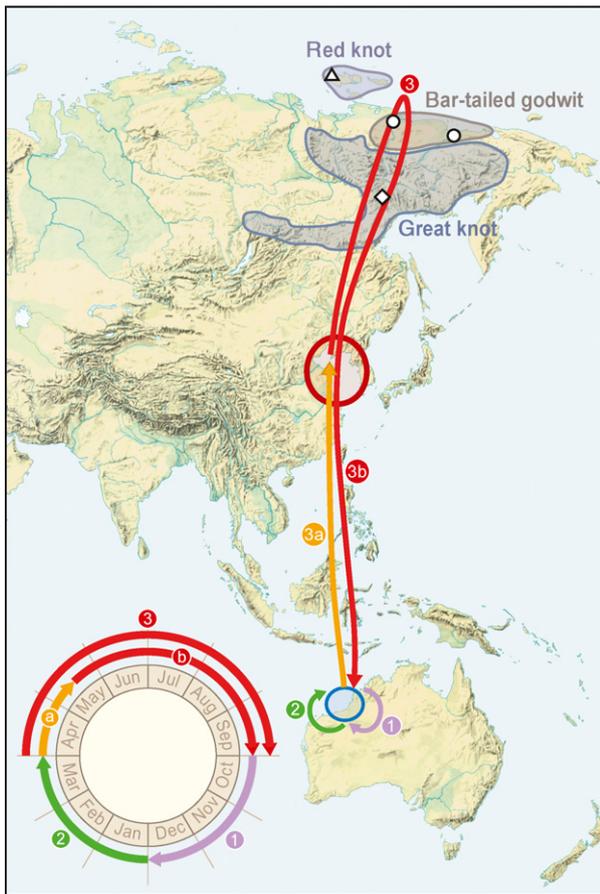


Fig. 1. Summary of the migrations of red knots, great knots and bar-tailed godwits between the non-breeding grounds in north-west Australia (blue circle), the staging areas somewhere along the Yellow Sea shores (red circle) and the various breeding areas in the Russian Arctic (blue-grey bordered bordered). The divisions of the seasons are indicated by the arrows numbered 1–3, with a further separation for red knots in 3a and 3b. The arrows represent the break-up of the annual cycle of all three species with respect to the part of the non-breeding season (first half = season 1 of three months, and second half = season 2 of three months) and migration and breeding (flight from north-west Australia to Yellow Sea = season 3a of one and a half months, everything between departure from the Yellow Sea to arriving back in north-west Australia = season 3b of four and a half months). Open symbols indicate weather stations (see Fig. 4).

grounds, including the use of the Yellow Sea by all three species, will be discussed with respect to explanations other than intertidal land-loss in the Yellow Sea (for which we provide a confirmatory independent data analysis), especially the possibility that unusual harsh weather occurred on the breeding grounds.

Materials and methods

DEMOGRAPHIC OBSERVATIONS AND ANALYSES

Estimates of seasonal survival are based on marking efforts of individual red knots, great knots and bar-tailed godwits at Roebuck Bay in north-west Australia (18°S 122°E). This coastal

wetland represents a major destination used during the non-breeding season (August through May) by each of the three species studied here (Rogers *et al.* 2003; Conklin, Verkuil & Smith 2014). Between December 2005 and June 2013, individuals of the three species were uniquely marked. The birds were captured with cannon-nets and within a few hours after capture released with unique combinations of colour-bands and a flag. For this analysis, first-year (juvenile) and older (adult) birds were distinguished based on plumage characteristics. In total, 821 bar-tailed godwits, 1064 great knots and 709 red knots were colour-banded (for numbers per non-breeding season, species and age class, see Table S1-1 in Supporting Information). Intensive efforts to visually ‘recapture’ (i.e. resight) marked individuals of all three species using zoom telescopes were carried out throughout the year in Roebuck Bay (2006–2013) and, in April–May, on red knots during their concentrated staging during northward migration in the Luannan coast of northern Bohai Bay, China (39°N 118°E, in 2009–2013).

The mark–recapture models outlined below were constructed using package RMark (Laake 2012) in program R (R Core Team 2015), and run with program MARK (White & Burnham 1999). Model selection was based on the Akaike’s information criterion, corrected for small sample size and overdispersion (QAIC_c) and Akaike model weights are reported to indicate relative model support (Burnham & Anderson 2002). Models with $\Delta\text{QAIC}_c < 2$ without uninformative parameters (Arnold 2010) were considered as supported by the data. We present the results of the most parsimonious model, i.e. the supported model with the fewest parameters. Reported standard errors and confidence intervals were adjusted for overdispersion.

Survival during three seasons

To enable survival to be estimated during three seasons, the non-breeding season was divided up into three four-month periods of marking and resighting: Jul–Oct, Nov–Feb and Mar–Jun. Because adult birds are mostly absent from Roebuck Bay between May and August (when they are on migration to and from, and breeding in, the High Arctic), adult birds were primarily observed between September and April. However, first-year (and some second-year) birds stay year-round in Roebuck Bay and were also observed in May–Aug. To define the intervals over which survival was estimated, we calculated the mean resighting date for the three four-month resighting periods (pooling the three species) which, as a consequence of the partial absence of adults in resighting periods Jul–Oct and Mar–Jun, differed between age classes (see Fig. S1-1). As we were primarily interested in seasonal differences in survival of actually migrating (i.e. adult) birds, we used the mean resighting dates (rounded to the closest 1st of the month) of adult birds and estimated survival for the following three ‘seasons’: Season 1 = the first half of the non-breeding season (1 Oct – 1 Jan, three months), season 2 = the second half of the non-breeding season (1 Jan – 1 Apr, three months) and season 3 includes the northward and southward migration periods and the breeding period (1 Apr – 1 Oct, six months). Note that in an additional analysis of red knots, we were able to distinguish four seasons (see below). Although the resighting periods are long relative to the intervals over which survival is being estimated, several simulation studies have shown that pooling resightings over a longer period did not bias and in fact increased the precision of the survival estimates (Hargrove &

Borland 1994; O'Brien, Robert & Tiandry 2005). This was confirmed by an explorative analysis of our data showing that estimates of adult survival remained similar but less precise when using resighting periods of one instead of four months (see Figs. S1-2 and S1-3).

Encounter histories started with the resighting period when the bird received its colour-rings. To account for any mortality as a result of catching, and for transient birds, survival in the season following capture (the marking season, Φ^1) was allowed to differ from subsequent survival (Φ^{2+}) in all models. Birds were considered adult from their second non-breeding season onward, which is the non-breeding season preceding their (presumed) first northward migration. To maintain statistical power in view of the amount of data available, we constrained juvenile survival after the marking season to be constant over time. With survival and resighting probabilities modelled as a function of species (spec), age, season (for survival), period (for resighting) and year, our full model was $\Phi_{\text{juv-spec-season-year}}^1 \Phi_{\text{ad-spec-season-year}}^1 \Phi_{\text{juv-spec}}^{2+} \Phi_{\text{ad-spec-season-year}}^{2+} P_{\text{age-spec-period-year}}$. This model is equivalent to modelling survival of each species in a separate model as: $\Phi_{\text{juv-season-year}}^1 \Phi_{\text{ad-season-year}}^1 \Phi_{\text{juv-constant}}^{2+} \Phi_{\text{ad-spec-season-year}}^{2+} P_{\text{age-spec-period-year}}$. Visual examination of parameter estimates indicated that juvenile survival after the marking season (Φ_{juv}^{2+}) was estimated as 1 for all three species. Running the model on a (100 times) cloned data set considerably reduced the 95% confidence intervals of these boundary estimates (a procedure called 'data cloning', implemented in program MARK (White & Burnham 1999)), indicating that these juvenile survival rates were not extrinsically inestimable (due to lack of data) but truly close to 1. As a result, the model without a species effect on Φ_{juv}^{2+} had the same model

deviance, but two parameters less than the model with this species effect, and was therefore a more parsimonious model. Data cloning further indicated that there were some years in which Φ or p could not be estimated for a specific season or period, yet we decided to maintain annual variation in Φ and p in the full model, as in most years, parameters for the different seasons and periods were estimable.

The goodness-of-fit of the full model with constant juvenile survival after the marking season (Φ_{juv}^{2+}) was assessed using the median- \hat{c} test in program MARK (White & Burnham 1999). On the basis of simulated data sets with levels of overdispersion of 1.10, 1.14, 1.18, 1.22, 1.26 and 1.30, each replicated 10 times, the median \hat{c} was estimated at 1.22 ± 0.01 .

We *a priori* selected biologically meaningful candidate models (parameterizations) for p , Φ^1 and Φ^{2+} (see Tables 1–4). Because of the many parameters involved, we performed a stepwise model selection procedure. In the first step, we assessed the support for alternative (reduced) parameterizations of resighting probability (p). In the second step, we used the most parsimonious parameterization of resighting probability to investigate alternative parameterizations of survival in the marking season (Φ^1). Finally, and of primary interest, we investigated alternative parameterizations of adult survival after the marking season (Φ_{ad}^{2+}) by constraining survival to be similar among years, seasons and species, using the most parsimonious parameterization from step 2. We first assessed reduced parameterizations for each season separately, and additionally considered models where survival was the same during the first and second half of the non-breeding season, or the same in all three seasons (step 3) and then combined the supported parameterizations per (pooled) season into a final

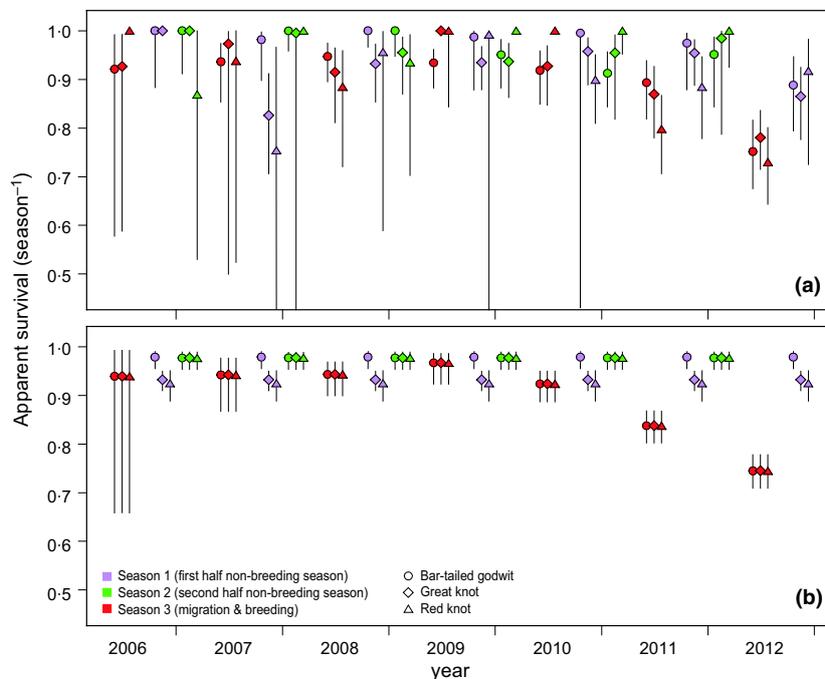


Fig. 2. Time trends in apparent seasonal survival of bar-tailed godwits, great knots and red knots using non-breeding areas in north-west Australia, 2006–2012, separating the year into three seasons (see Fig. 1). We present the estimates for adult survival after the marking season (Φ_{ad}^{2+}) using (a) the full parameterization of Φ_{ad}^{2+} with the best-supported parameterizations of resighting probability and survival during the marking season (model 1, Table 2) and (b) the most parsimonious parameterization of Φ_{ad}^{2+} (model 4, Table 4). Error bars denote 95% confidence intervals, using the profile likelihood function for the boundary estimates. Note that the seasons differ in length: seasons 1 and 2 cover three months, while season 3 covers six months.

Table 1. Model selection for the combined analysis of three shorebird species, results of step 1: reduced parameterizations of resighting probability (p). In all models, survival during and after the marking season were modelled as in the full model ($\Phi^1_{\text{spec-season-yr}}$ $\Phi^{2+}_{\text{juvconst}}$ $\Phi^{2+}_{\text{adspec-season-yr}}$)

Parameterization of p	K	ΔQ_{dev}	ΔQAIC_c	Model weight	Biological interpretation
(1) $p_{\text{period-yr-spec} + \text{period-a}}$	217	66.53	0.00*	0.89	Temporal variation may depend on species, whereas the age effect may be period-specific when juveniles are more likely to be seen at the start and end of the winter period than adults
(2) $p_{\text{a-spec-period-yr}}$	251	0.00†	4.23	0.11	Full parameterization
(3) $p_{\text{period-yr-a} + \text{period-spec}}$	195	185.04	72.93	0.00	Temporal variation may depend on age, as a result of age-specific movements (migration and temporary emigration)
(4) $p_{\text{period-yr} + \text{period-spec} + \text{period-a}}$	179	229.78	84.64	0.00	Temporal variation in resighting probability is likely due to differences in resighting effort. Resighting probabilities of species and age classes may vary depending on their behaviour: e.g. within a roost, great knots and bar-tailed godwits appear to be more easily observed than red knots (smaller and in the middle of the group); over the entire bay, species may use different roosts; moreover, the probability that species and age classes are temporarily absent from Roebuck Bay may differ
(5) $p_{\text{period-yr} + \text{period-spec-a}}$	185	224.29	91.53	0.00	Temporal variation, with different age-specific species effects per period
(6) $p_{\text{period-yr} + \text{period-spec}}$	176	348.30	196.97	0.00	Temporal variation (due to resighting efforts), with period-specific species effects
(7) $p_{\text{period-yr} + \text{spec} + \text{a}}$	170	415.25	251.57	0.00	Temporal variation, due to differences in resighting effort, with some species and age classes having higher resighting probabilities than others
(8) $p_{\text{period-yr} + \text{spec}}$	169	536.87	371.13	0.00	Temporal variation, with some species having higher resighting probability than others
(9) $p_{\text{period-yr} + \text{a}}$	168	713.07	545.28	0.00	Temporal variation, with juveniles generally having higher or lower resighting probabilities than adults
(10) $p_{\text{period-yr} + \text{period-a}}$	173	708.64	551.14	0.00	Temporal variation, with period-specific age effects (e.g. because adults are absent in part of the resighting periods at the start and end of the non-breeding season)
(11) $p_{\text{period-spec} + \text{period-a}}$	157	1104.25	913.84	0.00	No temporal variation (constant resighting effort), and period-specific effects of age and species

Φ^1 = survival in the marking season; Φ^{2+} = survival after the marking season; spec = species; yr = year; a = age class (juveniles (juv) versus adults (ad)); const = constant; “.” indicates an interaction between effects; K = number of parameters; ΔQ_{dev} = the QDeviance relative to that of the best fitting model (with the lowest QDeviance); ΔQAIC_c = QAIC_c relative to the best-supported model (with the lowest QAIC_c).

* QAIC_c = 25065.07.

†Qdeviance = 11790.23.

model set (step 4). If multiple parameterizations were supported (i.e. with $\Delta \text{QAIC}_c < 2$) in the different steps, we verified the consistency of the results of subsequent steps for the different supported parameterizations.

Red knot survival during four seasons

For this analysis, we only used the 348 red knots that were banded in Roebuck Bay and resighted at least once in Bohai Bay. Resighting periods were defined as Sep–Oct, Nov–Feb and Mar–Apr in Roebuck Bay, and Apr–Jun in Bohai Bay. Encounter histories started with the first sighting of the bird in Bohai Bay. All birds were adult (second year or older) when they were first seen in Bohai Bay, hence we did not include age effects for resighting and seasonal survival rates. With the above defined resighting periods, the seasons over which survival was estimated were: season 1 = the first half of the non-breeding season (1 Oct – 1 Jan in Roebuck Bay, three months), season 2 = the second

half of the non-breeding season (1 Jan – 1 Apr in Roebuck Bay, three months), season 3a = northward migration to Bohai Bay (1 Apr – 15 May, one and a half months) and season 3b = northward migration from Bohai Bay, breeding and southward migration (15 May – 1 Oct, four and a half months). The full model was $\Phi_{\text{season-year}} p_{\text{period-year}}$. On the basis of simulated data sets with levels of overdispersion of 1.30, 1.34, 1.38, 1.42, 1.46 and 1.50, each replicated 10 times, the median \hat{c} was estimated at $\hat{c} = 1.41 \pm 0.01$.

EXTENT OF COASTAL LAND CLAIMS IN CHINA

An assessment of the time patterns of loss of intertidal refuelling areas during 1990–2013 was based on Landsat images (Multi Spectral Scanner (MSS), Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+)) from the Yangtze estuary in the south, to the Yalu estuary in the north of China’s Yellow Sea coast. Details of the methods are summarized in Appendix S2.

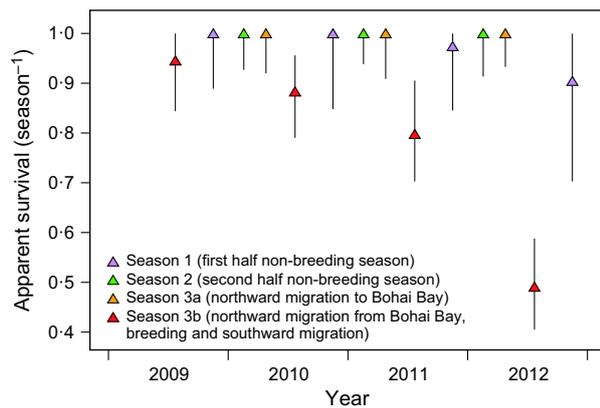


Fig. 3. Time trends in apparent seasonal survival of red knots spending the non-breeding season in Roebuck Bay (north-west Australia), 2009–2012, separating the year into four seasons (see Fig. 1). Estimates of four-season survival of red knots from the fully time-dependent (second best-supported) model (Table 3, model 2). The best-supported model only includes between-year variation in survival during the time between their presence in Bohai Bay and the return to Roebuck Bay (season 3b in Fig. 1); this shows that most variation in annual survival is due to variation in survival during the Bohai-Roebuck season. Error bars reflect 95% profile likelihood confidence intervals. Note that the seasons differ in length: seasons 1 and 2 cover three months, season 3a covers one and a half months and season 3b covers four and a half months.

Results

SIMULTANEOUSLY ESTIMATING SEASONAL SURVIVAL IN THREE SPECIES

We used data cloning to verify that all parameters of the most parsimonious model were estimable. Resighting probability was most parsimoniously modelled with species-specific temporal variation and age effects that varied between the three resighting periods (Table 1, see Fig. S1-4 for the estimates). Survival in the season of marking was most parsimoniously modelled as temporally variable with an additive effect of species (Table 2, see Fig. S1-5 for the estimates). After the marking season, survival of adult birds during the non-breeding season was best described as constant over the years, whereas there was considerable year-to-year variation in survival away from the non-breeding grounds (season 3) (Tables 3 and 4). During the first half of the non-breeding season, survival of bar-tailed godwits was consistently higher than of the two knot species.

The estimates of adult survival per species are shown both as 'rough' estimates ('full model', Fig. 2a), and as model estimates based on the most parsimonious model (Fig. 2b). Clearly, in all three species survival during the migration and breeding seasons began to decline in 2011, having lost 20 percentage points by 2012. Calculated over an entire year, by 2012 annual apparent survival had become as low as 0.71 in bar-tailed godwits, 0.68 in great knot and 0.67 in red knot (Table 5).

RED KNOT SURVIVAL OVER FOUR SEASONS

Most mortality of red knots occurred between their northward departure from Bohai Bay and their post-breeding arrival in Roebuck Bay (season 3b; Fig. 3). This was also the period in which survival most strongly varied between years, with a strongly decreasing tendency, as shown by the fact that the model which assumed constant survival during the first half of the non-breeding season (season 1), the second half of the non-breeding season (season 2) and northward migration to Bohai Bay (season 3a) was much better supported than the model with annual variation in survival in those seasons (Table 6). Resighting rates of the full model (model 2, Table 6) are shown in Fig. S1-6.

LOSSES OF COASTAL SHALLOW SEAS

Confirming the independent assessments of Murray *et al.* (2014) and Wang *et al.* (2014), between 1990 and 2013 the loss of shallow sea areas occurred all along the Yellow Sea coast of China (Appendix S2). In these 24 years, the total loss of shallow sea area (including the intertidal land that the shorebirds rely on for foraging) in China was estimated at 611 700 ha, with an average loss rate of 26 600 ha year⁻¹ (4% year⁻¹). The loss rate showed an upward trend and doubled between the period 1990–2005 and 2005–2013 from 19 000 to 40 900 ha year⁻¹ (Fig. S2-1e). Note that in the absence of annual estimates (Appendix S2, Murray *et al.* 2014), we were unable to use habitat loss rates in the Yellow Sea as a covariate to explain annual variation in survival.

Discussion

METHODOLOGICAL CONSIDERATIONS

Combining mark–recapture data of three different species during different periods of the year into a single analysis is as novel as it is informative by enabling a direct statistical assessment as to whether (seasonal) survival rates and year-to-year variation therein are similar between species. Since most resightings in the non-breeding grounds in Roebuck Bay were collected on high tide roosts where flocks consisted of a mix of the three species (see photos in Rogers *et al.* 2003), resighting probabilities were expected to be similar for the three species. However, we found strong support for species-specific differences in resighting rates that varied over time and were generally lower for red knots than for great knots and bar-tailed godwits (Fig. S1-4). In addition, the temporal variation in resighting rates appeared similar for great knots and bar-tailed godwits, but different for red knots. This can be explained by the fact that red knots have greater local space use than great knots and bar-tailed godwits (C.J. Hassell, Y.-C. Chan & T. Piersma unpublished data). The temporal variation in resighting rates of great knots and bar-tailed godwits may therefore

Table 2. Model selection for the combined analysis of three shorebird species, results of step 2: reduced parameterizations of survival during the marking season (Φ^1). In all models, resighting probability was modelled as in the best-supported model of step 1 ($p_{\text{period-yr-spec} + \text{period-a}}$) and survival after the marking season as in the full model ($\Phi_{\text{juvconst}}^{2+} \Phi_{\text{adspec-season-yr}}^{2+}$)

Parameterization of Φ^1	K	ΔQ_{dev}	ΔQAIC_c	Model weight	Biological interpretation
(1) $\Phi^1_{\text{season-yr} + \text{spec}}$	157	41.56	0.00*	0.66	Similar to model 2, but without the age effect
(2) $\Phi^1_{\text{season-yr} + \text{a} + \text{spec}}$	158	40.82	1.31	0.34	Similar to model 3, but now the effect of species and age are not season-specific
(3) $\Phi^1_{\text{season-yr} + \text{season-spec} + \text{season-a}}$	167	35.80	14.80	0.00	Temporal variation in Φ^1 may occur as a result of differences in catching effects per catching event, depending on for example weather conditions, time of the day, and the duration of captivity (depending on how many birds were caught). The number of transients in the catch may depend on species and age, and may vary between seasons (differently for species and age classes)
(4) $\Phi^1_{\text{season-a-spec}}$	154	72.50	24.78	0.00	There may be more transients/catching effects in some seasons compared to another which is comparable in all years
(5) $\Phi^1_{\text{season-yr}}$	155	72.40	26.73	0.00	The catching effects and presence of transients may be similar for age classes and species, but be variable between seasons and years
(6) $\Phi^1_{\text{season-yr} + \text{a}}$	156	72.33	28.72	0.00	Similar to model 2, but without species effects
(7) $\Phi^1_{\text{season-yr-a} + \text{spec}}$	175	34.33	29.80	0.00	One species may be more vulnerable or have more transients than another, with this difference being similar for the different age classes and periods
(8) $\Phi^1_{\text{season-yr-spec}}$	187	12.17	32.40	0.00	Transients may not be more common among juveniles than adults
(9) $\Phi^1_{\text{season-yr-spec} + \text{a}}$	189	11.58	35.93	0.00	Although more transients may occur among the juveniles, this age effect may be the same for the different species
(10) $\Phi^1_{\text{season-yr-spec} + \text{season-a}}$	193	8.05	40.66	0.00	There may be more transients among the juveniles, and this effect is the same for the different species (as in model 9), yet different between periods as more transients are likely to be caught during the migratory season (start and end of the non-breeding season)
(11) $\Phi^1_{\text{season-yr-a} + \text{season-spec}}$	181	33.29	41.13	0.00	One species may be more vulnerable or have more transients than another, with the amount of transients likely to differ between seasons (more transients at the start and end of the non-breeding season during migration)
(12) $\Phi^1_{\text{season-yr-a}}$	172	64.54	53.83	0.00	Species may show similar fidelity and may suffer similarly from catching
(13) $\Phi^1_{\text{season-yr-a} + \text{season-yr-spec}}$	208	6.53	70.18	0.00	The temporal variation in age effects may differ from the temporal variation in species effects, when age effects are mainly driven by more transients among juveniles, whereas species effects are probably driven by both. Although varying over time, the age effects are assumed to be similar for all the species
(14) $\Phi^1_{\text{season-yr-a-spec}}$	217	0.00 [†]	82.32	0.00	Full parameterization

For explanation of abbreviations, see Table 1.

* $\text{QAIC}_c = 25011.46$.

[†] $Q_{\text{deviance}} = 11856.77$.

primarily reflect variation in resighting effort, but for red knots may additionally be affected by temporal emigration.

Another issue is that the models estimate *apparent* survival, which is lower than true survival if there is significant permanent emigration. The lower *apparent* survival in the period away from Roebuck Bay could therefore also be caused by increased permanent emigration of birds that depart from Roebuck Bay for northward migration, and do not return to Roebuck Bay in subsequent non-breeding seasons. This scenario is unlikely however, as coastal shorebirds in the tropics generally

show high fidelity to their non-breeding grounds (e.g. Leyrer *et al.* 2012). Moreover, in the four-season analysis of red knots, additional resightings in Bohai Bay were included, which makes the importance of permanent emigration (from both the non-breeding and stopover area) even less likely.

DECLINING SURVIVAL RATES: EVALUATING ALTERNATIVE EXPLANATIONS

The very few season-specific survival rate estimates available for shorebirds refer to two subspecies of red knot in

Table 3. Model selection for the combined analysis of three shorebird species, results of step 3: reduced parameterizations of adult survival after the marking season (Φ_{ad}^{2+}), assessed for each (pooled) season separately while keeping the full parameterization (yr-spec) for the other season(s). In all models, resighting probability, survival during the marking season, and juvenile survival after the marking season were modelled as in the best-supported model of step 2 ($p_{period-yr-spec+period-a}$ and $\Phi_{season-yr+spec}^1$). Supported parameterizations per (pooled) season are highlighted in bold

Parameterization of Φ_{ad}^{2+}	K	ΔQ_{dev}	$\Delta QAIC_c$
(1) $\Phi_{yr-spec}^{s1} \Phi_{yr-spec}^{s2} \Phi_{yr-spec}^{s3}$	157	0.00 [†]	28.29
Reduced parameterizations of:			
Survival in season 1 (Φ^{s1})			
(2) $\Phi_{yr+spec}^{s1}$	145	13.63	17.30
(3) Φ_{yr}^{s1}	143	29.53	29.10
(4) Φ_{spec}^{s1}	139	26.02	17.40
(5) Φ_{const}^{s1}	137	43.09	30.37
Survival in season 2 (Φ^{s2})			
(6) $\Phi_{yr+spec}^{s2}$	145	2.27	5.94
(7) Φ_{yr}^{s2}	143	10.03	9.60
(8) Φ_{spec}^{s2}	139	13.22	4.59
(9) Φ_{const}^{s2}	137	16.61	3.89
Survival in season 3 (Φ^{s3})			
(10) $\Phi_{yr+spec}^{s3}$	145	11.71	15.38
(11) Φ_{yr}^{s3}	143	12.95	12.52
(12) Φ_{spec}^{s3}	139	81.92	73.29
(13) Φ_{const}^{s3}	137	84.45	71.73
Same survival in season 1 and 2			
(14) $(\Phi^{s1} = \Phi^{s2})_{yr-spec}$	136	27.08	12.32
(15) $(\Phi^{s1} = \Phi^{s2})_{yr+spec}$	124	39.30	0.00*
(16) $(\Phi^{s1} = \Phi^{s2})_{yr}$	122	46.91	3.52
(17) $(\Phi^{s1} = \Phi^{s2})_{spec}$	118	53.45	1.90
(18) $(\Phi^{s1} = \Phi^{s2})_{const}$	116	62.80	7.17
Same survival in all three seasons			
(19) $(\Phi^{s1} = \Phi^{s2} = \Phi^{s3})_{yr-spec}$	118	68.81	17.26
(20) $(\Phi^{s1} = \Phi^{s2} = \Phi^{s3})_{yr+spec}$	104	103.58	23.50
(21) $(\Phi^{s1} = \Phi^{s2} = \Phi^{s3})_{yr}$	102	109.12	24.96
(22) $(\Phi^{s1} = \Phi^{s2} = \Phi^{s3})_{spec}$	97	235.14	140.82
(23) $(\Phi^{s1} = \Phi^{s2} = \Phi^{s3})_{const}$	95	247.83	149.44

For explanation of abbreviations, see Table 1.

*QAIC_c = 24954.45.

[†]Qdeviance = 11898.32.

the East Atlantic Flyway (Leyrer *et al.* 2013; Rakhimberdiev *et al.* 2015) and show that during the years of these studies hardly any losses occurred during the migration and breeding periods; adult mortality occurred on the non-breeding grounds, or was quite evenly spread across the year. The latter also seems to be the case here for the years 2006–2010, after which strong and similar declines in apparent survival in all three shorebird species occurred during the season that included their use of the Yellow Sea (Fig. 2); in red knots we could narrow this down to the period after observation at the Chinese staging area (Fig. 3). Although this is precisely what we would predict if coastal wetland loss in the Yellow Sea is causing the declines of shorebirds in the East Asian–Australasian Flyway, two alternative explanations still require attention. Perhaps the low summer survival of the three species in 2011 and 2012 (Figs. 2 and 3) can alternatively

Table 4. Model selection in a combined analysis for three shorebird species (red knot, great knot and bar-tailed godwit), results of step 4: combining the supported season-specific parameterizations of adult survival after the marking season (Φ_{ad}^{2+}) from step 3. In all models, resighting probability, survival during the marking season, and juvenile survival after the marking season were modelled as in the best-supported model of step 2 ($p_{period-yr-spec+period-a}$ and $\Phi_{season-yr+spec}^1$). The most parsimonious model is highlighted in bold

Parameterization of Φ_{ad}^{2+}	K	ΔQ_{dev}	$\Delta QAIC_c$	Model weight
(1) $\Phi_{yr+spec}^{s1} \Phi_{const}^{s2} \Phi_{yr}^{s3}$	111	4.02	0.00*	0.25
(2) $\Phi_{yr+spec}^{s1} \Phi_{spec}^{s2} \Phi_{yr}^{s3}$	113	0.00 [†]	0.06	0.25
(3) $\Phi_{spec}^{s1} \Phi_{const}^{s2} \Phi_{yr}^{s3}$	107	12.25	0.08	0.25
(4) $\Phi_{spec}^{s1} \Phi_{const}^{s2} \Phi_{yr}^{s3}$	105	16.32	0.08	0.24
(5) $(\Phi^{s1} = \Phi^{s2})_{yr+spec} \Phi_{yr}^{s3}$	110	13.71	7.65	0.01
(6) $(\Phi^{s1} = \Phi^{s2})_{spec} \Phi_{yr}^{s3}$	104	27.95	9.67	0.00
(7) $(\Phi^{s1} = \Phi^{s2} = \Phi^{s3})_{yr-spec}$	118	15.38	25.63	0.00

For explanation of abbreviations, see Table 1 and 3.

*QAIC_c = 24946.08.

[†]Qdeviance = 11951.76.

Table 5. Estimates and 95% confidence intervals of annual apparent survival of the three shorebird species, based on the most parsimonious three-season survival model (model 4, Table 4)

Year	Bar-Tailed Godwit	Great Knot	Red Knot
2007	0.90 (0.84–0.94)	0.86 (0.81–0.90)	0.85 (0.79–0.89)
2008	0.90 (0.87–0.93)	0.86 (0.83–0.89)	0.85 (0.81–0.88)
2009	0.93 (0.90–0.95)	0.88 (0.85–0.90)	0.88 (0.85–0.91)
2010	0.89 (0.86–0.91)	0.84 (0.81–0.86)	0.84 (0.81–0.87)
2011	0.80 (0.77–0.83)	0.76 (0.73–0.79)	0.76 (0.73–0.79)
2012	0.71 (0.68–0.74)	0.68 (0.65–0.71)	0.67 (0.64–0.70)

be explained by mortality either: (i) during northward and southward migration periods as a consequence of running into adverse weather, e.g. cyclones, or (ii) on the breeding grounds?

The occurrence of severe low pressure systems such as cyclones, can have positive and negative effects depending on the ability of the birds to ‘ride’ the strong winds appropriately (i.e. on the correct side of the cyclones; see e.g. Gill *et al.* 2009, 2014). That there were no losses of red knots during the migration episode from north-west Australia to the Yellow Sea (Fig. 3), despite the occurrence of a cyclone over the Philippines in 2011, in combination with the congruence in seasonal survival patterns by three species with different timing and details of flight routes (Fig. 2), argues against a role for *en route* weather problems as an explanation for the declining summer survival rates.

Higher than average spring and summer temperatures in the High Arctic, correlated with earlier snow melt and availability of tundra invertebrates, are unlikely to affect adult survival, although it may affect recruitment (Boyd, Minton & Rogers 2005; Meltofte *et al.* 2007). The only documented cases of high summer mortality (in red knots)

Table 6. Model selection results for four-season apparent survival of red knots

Model		<i>K</i>	ΔQ_{dev}	$\Delta QAIC_c$	Model weight
(1)	$\Phi_{const}^{s1} \Phi_{const}^{s2} \Phi_{const}^{s3a} \Phi_{yr}^{s3b} P_{period-yr}$	26	0.93	0.00*	1.00
(2)	$\Phi_{season-yr} P_{period-yr}$	36	0.00†	20.32	0.00
(3)	$\Phi_{season-yr} P_{period-yr}$	23	48.16	40.93	0.00
(4)	$\Phi_{season-yr} P_{yr}$	22	65.36	56.05	0.00
(5)	$\Phi_{season-yr} P_{period}$	22	81.33	72.01	0.00
(6)	$\Phi_{season-yr} P_{period}$	8	123.48	85.32	0.00
(7)	$\Phi_{season-yr} P_{yr}$	9	126.12	89.99	0.00

's3a' and 's3b' refer to seasons 3a and 3b (see Fig. 1). For explanation of other abbreviations, see Tables 1 and 3.

*QAIC_c = 2085.47.

†Qdeviance = 762.49.

refer to the cold summers of 1972 and 1974 when snow melt in High Arctic Greenland and Canada was exceptionally late so that arriving birds had nothing to eat, ran out of stores and died of starvation (Boyd 1992; Boyd & Piersma 2001; Morrison, Davidson & Wilson 2005). In fact, after those summers individual red knots with relatively high fuel stores in Iceland were the most likely to have survived (Morrison, Davidson & Wilson 2005). A survey of the dates of snow melt in the breeding areas of bar-tailed godwits, great knots and red knots spending the non-breeding season in north-west Australia (Fig. 4), suggests that in 2012 snow melt was early at all four weather stations, while in 2011 snow melt was early on the New Siberian Islands where red knots breed. Therefore, adverse weather conditions at the breeding grounds appear an unlikely explanation for the declines in summer survival in 2011 and 2012. In any case, a loss of lemming cycles on the Arctic tundra has not led to any declines in breeding productivity so far (Aharon-Rotman *et al.* 2015).

We thus argue that the similarity in the recent declines in summer survival of red and great knots and bar-tailed

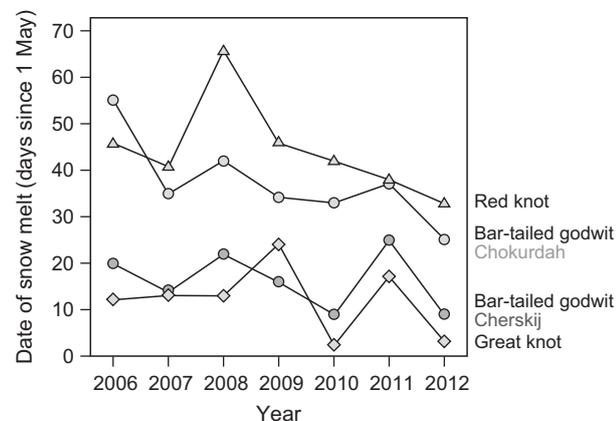


Fig. 4. Time-trends for the dates on which the tundra around weather stations in the breeding range of bar-tailed godwits, great knots and red knots started to become snow-free, 2006–2012. This was based on data from <http://www.ncdc.noaa.gov> for weather stations indicated in Fig. 1.

godwits is most likely driven by their shared presence along the Yellow Sea shores. Mortality does not have to be immediate, but could take effect as delayed, downstream carry-overs from poor refuelling in the Yellow Sea (see review by Senner, Conklin & Piersma 2015). Indeed, that three shorebird species using different parts of the Yellow Sea coastline during northward and southward migration are so similarly affected, is consistent with the finding that coastal wetlands are lost rapidly all along the coasts of China and the Korea (Appendix S2, and see Ma *et al.* 2014; Murray *et al.* 2014; Wang *et al.* 2014). The average rate of loss of shallow sea habitat between 1900 and 2013 of 4% year⁻¹ established in our study of satellite images (Appendix S2) is twice the estimated loss rate of 2% year⁻¹ of tidal flats specifically reported by Murray *et al.* (2014). As is illustrated by the sometimes extensive 'reclamations' right into the sea (e.g. in Bohai Bay, Fig. S2-1b), in the last two decades large areas of shallow sea were embanked in addition to the embanking of the 'shore-hugging' intertidal flats. As all three shorebird species have a tendency to focus foraging on the low lying parts of tidal flats (Rogers *et al.* 2006a), especially such downshore habitat losses are likely to include the very best feeding areas for knots and godwits.

This study then provides a second example of how resource losses on staging grounds cause increased mortality in a migrating bird (the first referring to overharvesting of horseshoe crabs *Limulus polyphemus* in Delaware Bay, USA affecting staging red knots *C. c. rufa*; Baker *et al.* 2004), due to density-dependent competition coming into play. Nevertheless, the finding that summer survival rates only started to decline after 2010 when the total reclaimed area exceeded 500 000 ha (Appendix S2), whereas the loss of intertidal lands had been an ongoing process (Murray *et al.* 2014), raises the question why the decline in summer survival showed a stepwise rather than a gradual pattern. Such an immediate response in both numbers and apparent survival to local resource losses was shown for red knots in the Dutch Wadden Sea (Kraan *et al.* 2009; Rakhimberdiev *et al.* 2015). We suggest that, perhaps because of earlier stresses on the popu-

lations due to previous episodes of habitat loss (An *et al.* 2007; Murray *et al.* 2014) leading to relatively low numbers along the East Asian–Australasian Flyway, at least from 2006 to 2010 the birds had ways to initially behaviourally ‘buffer’ overall habitat loss. They could have done so by concentrating at the best remaining coastal wetlands. Such concentration, in what we know were good feeding habitats in northern Bohai Bay (Yang *et al.* 2013), has indeed been shown for staging red knots who locally increased in number up to 2010 (Yang *et al.* 2011), but not since (H.-Y. Yang unpublished data). We argue that density-dependent effects of reduced feeding performance at high forager densities on the remaining mudflats (well described for red knots in captive and field settings; Bijleveld, Folmer & Piersma 2012; van Gils *et al.* 2015) have since become important.

PREDICTING PAST AND FUTURE POPULATION TRAJECTORIES

Iwamura and co-workers (Iwamura *et al.* 2013; Iwamura, Fuller & Possingham 2014) developed a sophisticated analytic framework to predict how losses of coastal intertidal habitat due to sea level rise can best be countered by strategic conservation investments in different parts of the flyway. In view of: (i) the rapid habitat loss that the migrating shorebird populations are confronted with now, (ii) the apparent negative consequences for survival shown here, and (iii) the desperate state of the remaining coastal wetlands of the Yellow Sea region (Murray, Ma & Fuller 2015), the question becomes whether the flyway populations of concern will even survive to the time they would have to cope with effects of sea level rise. In 2007–2010, survival rates were sufficiently high to achieve a slightly growing population, whereas after 2010 the populations of the three species started to decline (Appendix S3). If survival rates would remain similar to the rate in 2012, the three focal species are predicted to show annual losses of 18–20% year⁻¹, implying that the populations will be halved again (relative to the already reduced population sizes in 2012) in three to four years.

If the losses of high quality shoreline habitats in the Yellow Sea would continue at the present pace, a scenario of sustained low survival rates will not be unrealistic. These loss rates are such that the populations, now still numbering in the tens to 200 000s today, within a decade could be numbered in the mere thousands, i.e. reach the levels of the now critically endangered spoon-billed sandpipers *Calidris (Eurynorhynchus) pygmaeus* (Syroechkovski *et al.* 2010). The magnificent East Asian–Australasian Flyway (van de Kam *et al.* 2010) is most definitely at risk.

Dedication

We dedicate this paper to the memory of our friend and mentor Mark Barter. As an ‘amateur’ shorebird scientist, not only did he put on the map the immense values of

Yellow Sea coastal mudflats as key staging areas for shorebirds, he also forewarned the world about their disappearance.

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Data accessibility

The data underlying this study are available in the Dryad Digital Repository doi: 10.5061/dryad.kd00f (Piersma *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Additional information concerning the analyses of seasonal and species-specific survival rates.

Appendix S2. Estimates of extent of coastal land claims in China.

Appendix S3. Predicting population growth rates and trajectories.



Plate. 1. Bar-tailed godwits under assault. The plight of migrating shorebirds as a consequence of rapid shoreline habitat loss in the Yellow Sea is well illustrated by these staging Bar-tailed Godwits roosting on an active dredge-dumping site on 20 April 2012. The material was being excavated from a channel to improve access to the Donggang Fishing Port, Liaoning Province. The infilled area is planned to be part of an industrial park to be built on an area of intertidal mudflat that was excised from the Yalujiang National Nature Reserve by a boundary adjustment in 2012. Photo by David S. Melville.